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Cognitive representations of hand posture in ideomotor apraxia

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Abstract

Ideomotor apraxia (IM) is a disorder of skilled action characterized by spatiotemporal errors in pantomiming object use and in using objects. Recent evidence suggests that at least some patients with IM may exhibit particular deficits in forming hand configurations appropriate for object use. Sirigu et al. [Cortex 31 (1995) 41] reported an apraxic who positioned her hand inappropriately when attempting to use objects in accordance with stored knowledge of object-specific manipulation, but in reaching tasks could grasp the same objects appropriately in response to their structure. To this point, however, apraxics' ability to respond to functional and structural attributes of objects has not been empirically assessed. We investigated the hypothesis that patients with IM ($n = 9$) due to left inferior parietal damage would be impaired in producing and recognizing hand postures associated with familiar objects, indicating deficient memorial representations for object-specific hand postures. In contrast, we predicted relatively unimpaired ability to produce and recognize appropriate hand postures with novel objects, indicating integrity of "on line" spatiomotor procedures coding hand position in response to object structure. Apraxics' performance was contrasted with 10 healthy controls and 8 brain-lesioned non-apraxics. Consistent with our predictions, the apraxics responded abnormally with familiar objects but normally in recognizing hand postures appropriate for novel objects. In addition, performance with objects calling for a prehensile response (pinch or clench) was superior to that with objects evoking a non-prehensile response (palm or poke). These data suggest degradation of inferior parietally-mediated representations of the precise hand postures associated with familiar objects. Furthermore, they are consistent with possible over-reliance upon dorsal system procedures for calculating precision and power grip in response to object structure.

Keywords: Apraxia; Praxis; Ideomotor; Hand posture; Gesture; Affordance; Grasping; Action; Object use; Tool use; Object structure; Object function

1. Introduction

Patients with ideomotor apraxia (IM) make spatiotemporal errors in pantomiming skilled movements associated with object use, and, often, in actual use of objects [2]. For example, an apraxic might pantomime a toothbrushing gesture with oscillations of greatly exaggerated amplitude, use the forefinger as though it were the toothbrush rather than pantomiming how the handle of the brush should be held, and/or orient the arm and hand inappropriately relative to the head. The disorder occurs most frequently after lesions to the dominant (usually left) inferior parietal lobule, but can also be seen with superior parietal [3,4] and more anterior [5] damage. In some cases, IM patients also have difficulty distinguishing correct from erroneous gestures, suggesting that gesture representations are damaged, and not merely inaccessible to motor output mechanisms [5]. Heilman et al. (e.g. [5]) have demonstrated that gesture recognition may be impaired in subjects with inferior parietal, but not more anterior damage, suggesting that gesture representations may be localized to the left inferior parietal lobe (and see [21]).

While much of the literature to date focuses on IM patients' spatiotemporal difficulties in the production of gestures with the arm (e.g. hammering, sawing, etc.), there are indications that some patients may exhibit particular deficits in forming hand configurations appropriate for object use. Sirigu et al. [1] reported the case of an apraxic subject, LL, who appeared deficient in knowledge of the hand postures associated with familiar objects. Although LL could grasp objects normally in the context of reaching tasks, and exhibited appropriate trajectories of the arm when demonstrating object use, she was unable to position her hand properly. For example, when asked to demonstrate

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"eating soup with a spoon", LL clenched the handle of the spoon with the entire hand, rather than demonstrating the precise learned finger position associated with spoons. Nevertheless, the trajectory of the arm from an imagined bowl to the mouth was entirely appropriate. These data appear consistent with integrity of hand positioning in response to object structure (grasping task) but degradation of hand posture guided by function (object use task). This suggests that apraxics may suffer impairments in a subset of gesture engrams coding learned postural configurations of the hand. To our knowledge, however, LL is the only apraxic for whom production and knowledge of hand postures has been put to empirical test.

In this study, we assessed whether hand posture deficits are (a) prevalent in IM, and (b) specific to the apraxia syndrome, rather than reflecting neurologic damage more generally. We also assessed whether hand posture deficits, when present, are attributable to a motor production deficit, or rather to a loss of the representations underlying skilled hand configurations. Finally, we assessed whether particular patterns of hand posture impairment might be observed. To the degree that patients with IM suffer deficits specific to stored knowledge of the hand postures appropriate to objects, response to structural features of objects is predicted to be intact. If, on the other hand, apraxics' difficulties with hand posture reflect some degree of deficit external to the stored gesture system (e.g. within spatiomotor systems mediating object grasping), then impairment might be expected to emerge in responses to structural features of objects as well.

2. Study 1: Normative study with healthy adult subjects

The design of the experiments was inspired by a series of studies by Klatzky et al. [6] indicating that there is a strong relationship between object knowledge and knowledge of hand configurations. In one study, undergraduate subjects were asked to rate the likelihood of using one of four canonical hand configurations with each of 73 objects. The configurations, which resulted from the crossing of the factors prehensility and size of the contacting surface, were poke (small, non-prehensile), pinch (small, prehensile), palm (large, non-prehensile), and clench (large, prehensile). The ratings indicated that objects were reliably associated with certain hand postures (e.g. hammer-clench). Subjects also listed a functional context in which a given object might be contacted with a particular hand shape. There emerged three classes of functional context: hold/pick up (palm, pinch, and clench); feel/touch (poke, palm); and use (varied) [6]. This study indicated that there is strong relationship between object knowledge and gesture knowledge. Hand posture representations are reliably evoked by objects, and moreover, can be cognitively discriminated.

A second study in the series was designed to provide normative data on the link between structure and hand posture categories, and to assess whether structure alone was sufficient to predict the responses in the first study. Undergraduate subjects viewed 90 abstract shapes including 3D parallelograms (i.e. parallelepipeds) and spheres and rated which hand configuration they would be most likely to use to contact the object. A discriminant analysis was then performed to see if the modal response to each object was predicted by its structure (surface area and depth). The discriminant analysis assigned 63 of the 90 objects appropriately, i.e. to the modal response class. Flat shapes with a large surface area, for example, tended to be assigned to "palm", whereas indented shapes with a small surface area were frequently assigned to "poke". Projectile shapes with large and small surface areas were assigned to "clench" and "pinch", respectively. Objects incorrectly assigned tended to be those for which subjects themselves had difficulty agreeing.

Finally, the investigators assessed whether the discriminant function derived from the novel objects accurately classified the real objects of Study 1. There was good agreement for most objects, but there was a subset of objects for which functional considerations over-rode structural factors. One such subset were objects assigned by the discriminant analysis to the "poke" category by virtue of their shallow depth, but which are actually pinched in a functional context (e.g. nail, paperclip, and zipper). Another subset was categorized by the discriminant function as pinch, but actually function with a clench (e.g. hammer, knife, and saltshaker). Thus, structure alone was not sufficient to predict subjects' knowledge of the hand postures associated with these objects.

In Study 1, we adopted some of the methods used by Klatzky et al. [6] to assess healthy adults' responses to real and novel objects. The primary aim of the study was to provide normative data on the experimental tasks with which to compare brain-lesioned subjects.

2.1. Method

2.1.1. Participants

Ten healthy older adults were recruited from the community surrounding MossRehab. There were six females and four males. All subjects were right-handed, had normal or corrected-to-normal vision and hearing, and had no history of learning difficulties or central nervous system dysfunction. Their mean age was 65.8 (range 47–83) and mean years of education was 12.6 (range 9–18).

2.1.2. Materials

Photographs of four hand postures (clench, pinch, palm, poke; see Fig. 1) remained in view 10 cm to the right of subjects' midline throughout the experiment. Stimuli were 35 manipulable real objects (e.g. tools, kitchen implements, office supplies, etc.; see Table 1) drawn from the object corpus of Klatzky et al. [6] and 20 novel objects, each consisting of a blue parallelepiped positioned upon a white base.

Parallelepipeds were constructed similarly to those used in the Klatzky et al. [6] study. They ranged in depth from

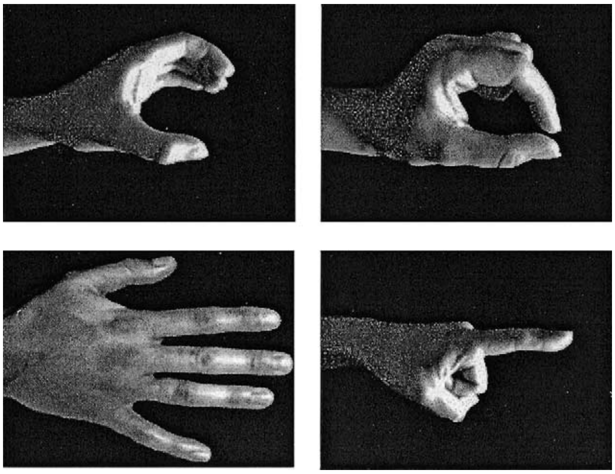


Fig. 1. Photographs of the clench, pinch, palm, and poke hand configurations used in the experiments. The photographs remained on the table-top, and subjects were permitted to refer to them throughout.

−1 cm below the surface of the base to 9.5 cm above the base surface. Horizontal (top) surfaces ranged from 0.64 cm^2 to 100 cm^2 (see Table 1 for dimensions).

2.1.3. Procedure

Subjects were seated at a table upon which the hand posture photographs and experimental stimuli were placed. Prior to initiation of the experiment, subjects examined the photographs of the four hand postures as the postures were named by the experimenter. To ensure subjects' appreciation of differences between postures, they were required to reproduce each posture with the left hand, and the examiner corrected configurations inconsistent with the photographs. Subjects were informed that on each trial, they would see a real or novel object, and that they would be required to select the hand posture most appropriate for each object. They were also informed that all four postures were relevant in the course of the experiment, and that they should be certain to try to produce all of them.

Subjects began each trial with the left hand positioned at midline palm-up on the tabletop. On each trial the examiner placed an object at the subject's midline, approximately 40 cm anterior to the body, and the subject was instructed to respond as soon as he or she was certain of the response. The left hand was used to enable comparison with the left-hemisphere lesioned apraxic subjects to be run in Study 2, who performed with the ipsilesional hand.

In the "Point" condition, subjects were asked to respond to each stimulus object by touching with the left hand the photograph showing the hand posture they would be "most likely to make to interact with or use the object". To discourage subjects from attempting to program a specific configuration of the hand in this condition, they were told that they should simply turn over their hand from the palm-up resting state, and touch the target photograph in whatever manner was easiest. In the "Pantomime" condition, instructions were the same, except that subjects were asked to actually form (pantomime) the target hand posture rather than touching a photograph. Subjects were instructed to form the hand posture precisely as it appeared in the photograph, using the left hand in the space directly anterior to the body wall, rather than reaching toward the object.

Blocks of real and novel object trials were presented in ABBA sequence. Five subjects performed the Point condition first, followed after a 15-min rest period by the Pantomime condition, and the other five subjects performed the experiment in the reverse sequence. Each block began with five practice trials, during which any "incorrect" responses were pointed out by the examiner and a correct response elicited from subjects. Each of the 35 real objects was presented once and each of the 20 novel objects presented twice in both Pantomime and Point conditions, for a total of 150 experimental trials. Performance was videotaped for subsequent analysis.

Subjects' responses in Point conditions were tallied and entered on prepared coding sheets during the test session. For Pantomime condition scores, two trained judges independently viewed each videotape and assigned each response to a hand posture category. Videotapes showed subjects' hands only, and judges were not aware of subjects' identities or the object to which the response was made.

Judges also indicated via a 3-point rating scale their confidence that the posture produced was assigned accurately to a hand posture category (1: very confident, 2: somewhat confident, 3: not at all confident). Judges were instructed that "hybrid" postures should be given ratings of 2 or 3, depending upon the judges' certainty. For example, a posture approximating a pinch (fingers opposed) but including three digits might be assigned a "2" or "3" rating. Confidence ratings of the two judges were tallied and averaged.

The following scoring guidelines were provided to the judges for the Pantomime condition (1) the four hand postures to be coded result from the "crossing" of the factors finger (few versus all) and hand shape (open versus closed). Poke and pinch responses use 1 and 2 fingers, respectively, whereas palm and clench incorporate all fingers. Poke and palm responses have an "open" hand shape, whereas pinch and clench have a "closed" hand shape, (2) postures that are ambiguous with respect to one or both of the above factors (finger and hand shape) are to be assigned to the posture category judged to be closest, and assigned a confidence rating less than 1, (3) if more than 1 response is produced on a given trial, the first response is to be coded, (4) for a response to be "scoreable", a given hand posture must be maintained for at least 1 s.

Subsequent to independent scoring by the two coders, discrepant scores were reviewed and one response category was agreed upon. This affected <2% of trials. For each object, the percentages of responses in each hand posture category were tallied.

The data from the Point condition with the novel objects were then entered into discriminant function analyses that

Table 1
Real and novel objects, dimensions, control responses, and classification

Real objects	Area (width × height^2)	Depth	Poke (% responses)	Pinch (% responses)	Palm (% responses)	Clench (% responses)	Category assigned by controls' modal response	Category assigned by discriminant function	Agreement of discriminant function and control response
Rolling pin	237.9	7.8	0	0	0	100	Clench	Palm	Conflict
Glass	117	7.8	0	0	0	100	Clench	Palm	Conflict
Wall switch	2	1	90	10	0	0	Poke	Pinch	Conflict
Typewriter	2.25	1	70	0	30	0	Poke	Pinch	Conflict
Keyboard	29	1.5	70	0	30	0	Poke	Clench	Conflict
Leaf	0.4	6	0	90	10	0	Pinch	Clench	Conflict
Envelope	19.2	10.5	0	80	20	0	Pinch	Clench	Conflict
Clothespin	9.8	1.2	0	100	0	0	Pinch	Clench	Conflict
Pencil	14.4	0.8	0	100	0	0	Pinch	Clench	Conflict
Shoelaces	30.2	0.5	10	80	10	0	Pinch	Clench	Conflict
Zipper	1.6	0.5	10	90	0	0	Pinch	Poke	Conflict
Nail	4	0.5	0	100	0	0	Pinch	Poke	Conflict
Hammer	68.4	3.8	0	0	10	90	Clench	Clench	No-conflict
Saltshaker	29.6	3.8	0	0	0	100	Clench	Clench	No-conflict
Hairbrush	12	2.5	0	0	0	100	Clench	Clench	No-conflict
Pliers	9	5	0	40	10	50	Clench	Clench	No-conflict
Apple	60	7.6	0	0	0	100	Clench	Clench	No-conflict
Doorknob	25	7	0	0	10	90	Clench	Clench	No-conflict
Lemon	56	7.5	0	0	0	100	Clench	Clench	No-conflict
Telephone receiver	32	5	0	0	0	100	Clench	Clench	No-conflict
Fur	930	12.8	0	14.3	71.4	14.3	Palm	Palm	No-conflict
Cushion	930	14	10	0	70	20	Palm	Palm	No-conflict
Sandpaper	307.5	0	0	30	70	0	Palm	Palm	No-conflict
Basketball	620.25	25	0	0	70	30	Palm	Palm	No-conflict
Bongo drums	400	0	0	0	100	0	Palm	Palm	No-conflict
Deadbolt	3.6	1.2	10	60	10	20	Pinch	Pinch	No-conflict
Chalk	9	1	10	90	0	0	Pinch	Pinch	No-conflict
Paperclip	3.3	0.85	10	80	10	0	Pinch	Pinch	No-conflict
Plug	2.4	3	0	80	10	10	Pinch	Pinch	No-conflict
Guitar pick	2	2.5	10	70	20	0	Pinch	Pinch	No-conflict
Key	4.4	2.2	0	100	0	0	Pinch	Pinch	No-conflict
Push button phone	2.2	−0.5	90	0	10	0	Poke	Poke	No-conflict
Thimble	2.2	−1	60	40	0	0	Poke	Poke	No-conflict
Doorbell	2.2	0.5	100	0	0	0	Poke	Poke	No-conflict
Calculator	0.64	0.5	80	0	20	0	Poke	Poke	No-conflict

Novel object code no.	Area (width $\times$ height^2)	Depth (cm)	Poke (% responses)	Pinch (% responses)	Palm (% responses)	Clench (% responses)	Category assigned by control's modal response	Modal percent
1	0.64	2	14	86	0	0	Pinch	86
5	0.64	3	14	86	0	0	Pinch	86
10	1.44	6	11	86	0	4	Pinch	86
9	25	3	0	7	11	82	Clench	82
2	4	−1	75	14	11	0	Poke	75
7	1.44	−1	75	14	11	0	Poke	75
6	64	6	0	0	29	71	Clench	71
24	16	2	0	18	14	68	Clench	68
3	1.44	0	64	7	29	0	Poke	64
4	6.25	−1	64	14	18	4	Poke	64
25	6.25	6	0	32	7	60	Clench	60
28	6.25	0.5	14	57	18	11	Pinch	57
23	25	0	21	14	54	11	Palm	54
30	25	1	0	18	29	54	Clench	54
8	64	−1	32	7	50	11	Palm	50
26	6.25	3	0	39	11	50	Clench	50
27	4	6	4	43	4	50	Clench	50
32	16	1	4	29	18	50	Clench	50
29	25	0.5	0	21	39	39	Palm	39
31	16	0.5	4	43	21	32	Pinch	32

predicted the modal response to each object from its area and depth. The analysis assigned 16 of the 20 objects (80%) appropriately, that is, to the modal response class, indicating that the form variables were strong predictors of response to the novel objects. Not surprisingly, the four objects misassigned by the analyses tended to be those for which subjects had difficulty agreeing; that is, those for which the modal response percentage was lowest.

The standardized coefficients from the discriminant function analysis were then used to assign each real object to a predicted response class. The following four equations were calculated, and real objects assigned to the class with the highest value for the equation. In each equation, a is the area and d the depth.

Clench:	
Value	$-3.144 + 0.0983a + 0.834d$
Palm:	
Value	$-6.681 + 0.196a - 0.04127d$
Pinch:	
Value	$-2.187 + 0.02668a + 0.612d$
Poke:	
Value	$-1.699 + 0.01313a - 0.182d$

For ease of exposition, we will hereafter refer to the response predicted by the discriminant function analysis as the structural response.

2.1.4. Results

Table 1 provides a list of the real objects, the distribution of responses to each object, and the structural response predicted by the discriminant function analysis.

There were 12 real objects for which the controls' modal response and the structural response disagreed. These were designated "real conflict" objects. There were 23 objects for which the modal response and structural response agreed ("real no-conflict" objects).

We also examined whether novel objects evoked a particular hand posture. There were 10 novel objects for which there was no strong modal response by control subjects ($\leq$60% of responses in any one category), and 10 novel objects for which there was a strong modal response (>60% of responses).

2.1.5. Discussion

Consistent with the data of Klatzky et al. [6], subjects were able to agree upon a hand posture configuration for real objects, and many novel objects as well. Had subjects been responding to the real objects on the basis of shape alone, all objects would have garnered high agreement between the structural response and subject response. In fact, there was a subset of real objects for which functional considerations over-rode structural factors (real conflict objects). These included objects whose structure predicted "pinch" but whose function required "poke" (piano key, typewriter key, wall switch), objects whose structure predicted "palm" but which are nevertheless "clenched" (rolling pin, glass), a third set whose structure predicted "poke" but which are instead "pinched" (e.g. zipper, nail), and a fourth set whose structure predicted "clench" but which are "pinched" (e.g. clothes pin, pencil).

Some general rules appeared to emerge for the novel objects, consistent with the findings of Klatzky et al. [6]. Objects with small surface areas were usually assigned to "pinch" if depth was positive (i.e. raised), and to "poke" if depth was neutral (flat) or negative (indented). Objects with large surface area were assigned to clench (if depth was positive; i.e. raised) or palm (if depth was neutral or negative). These data support the findings of Klatzky et al. [6]: canonical hand posture categories are reliably associated with objects, and can be cognitively discriminated.

3. Study 2: Study of brain-lesioned subjects

In this study, we compared the performance of nine apraxic and eight non-apraxic brain-lesioned subjects to the healthy controls run in Study 1. As in that study, we used pantomime and multiple-choice tasks to obviate the possibility of on line adjustment of hand posture in response to structural object properties. The experimental task enabled us to assess whether performance differed in tasks requiring pantomiming versus posture recognition. If both are impaired in the apraxic subjects, this would suggest that hand posture representations are degraded rather than merely inaccessible to motor output mechanisms. In addition, the experiment enabled us to assess responses to structural and functional factors. If gesture representations are impaired in apraxia, and structural factors are guiding the selection of hand posture, performance should be impaired with "real conflict" objects, but better with "no-conflict" objects. Subjects should also perform relatively well with novel objects, for which there is no stored functional information. In addition, errors should reflect the influence of structural factors. This is the pattern we predicted in the majority of patients with IM. If there are some apraxic patients for whom hand posture representations are relatively intact, then we expect responses to real objects to be better preserved than responses to novel objects. If both gesture representations and spatiomotor procedures enabling hand-shaping in response to object structure are impaired, then responses should be poor for both real and novel objects.

3.1. Method

3.1.1. Participants

Nine left hemisphere stroke patients were referred for the study by a neurologist or speech therapist based on clinical information consistent with probable IM. Four of these patients were referred from the outpatient population of Hôpital de la Salpetriere in Paris, and the remaining five patients were referred from the outpatient population of MossRehab in Philadelphia. Following Heilman and Gonzalez Rothi [7], presence of ideomotor apraxia was defined by spatiotemporal errors in pantomime. After an initial practice trial in which errors were corrected, subjects were shown one of IO common objects (scissors, watch, razor, fork, comb, toothbrush, bottle opener, eraser, and cigarette lighter) and asked to demonstrate how to use each object with the ipsilesional hand. Performance was scored "leniently" on the basis of gesture recognizability (1 point = recognizable as the target gesture; 0 points = unrecognizable as the target gesture). Performance was videotaped and scored from the tapes. There were no semantic gesture substitutions; all errors were spatiotemporal distortions. This suggested that all subjects understood the requirements of the task. Scores ranged from 10–70% correct (mean 31%, S.D. 21%).

Nine additional stroke patients were referred for the study based on probable absence of ideomotor apraxia. From this group, eight patients (five with left-hemisphere and three with right-hemisphere damage (hereafter referred to as LCVA and RCVA, respectively) were selected who, like the apraxics, had contralesional motor weakness (hemiparesis), but who made no errors on the gesture pantomime screening task described above (100% correct). These eight patients served as brain-lesioned controls.

Table 2 shows demographic and lesion information for the 17 brain-lesioned subjects. Lesion location for French patients was coded by a neurologist (Pascale Pradat-Diehl), and for American patients by a neurologist (H. Branch Coslett) and the first author, all of whom were blinded to subjects' group membership, from clinical MRI and/or CT scans using the templates of Damasio and Damasio [8]. Lesions for French subjects were coded from chronic scans performed near the time of testing. Lesions of American subjects were coded from acute scans performed during initial stroke-related hospitalizations, which were the only scans available for these subjects. Percent agreement of the two coders of the American scans was 93%. Disagreements were reconciled through additional review of the data.

3.1.2. Background testing

In addition to the main experimental tasks, to be described below, brain-lesioned subjects performed a battery of background tests to assess praxis, language function, gesture recognition, object knowledge, motor function, and tactile sensation. Detailed scoring of praxis tasks enabled assessment of the relationship of hand posture in gesture tasks and hand posture production and recognition on the experimental task. There were several additional aims of the background testing, which were exploratory in nature. One purpose of the battery was to provide data on the relationships between hand posture in grasping tasks and hand posture on the experimental task. Another question was the relationship of gesture recognition—a classic test of the integrity of gesture engrams—to hand posture recognition. A third question concerned the relationship of semantic manipulation knowledge for objects and hand posture knowledge. As exploration of these relationships were secondary to the major aims of the study, we did not include sufficient numbers of subjects for statistical (e.g. correlational) analyses. Results of backround testing are nevertheless included insofar as they may inform future work in this area. Results are displayed in Tables 3 and 4.

As can be seen in Table 3, all apraxic subjects had difficulties with all spatiotemporal components of gesture. Hand posture was rated particularly poorly on pantomime tasks for most subjects, but improved when actual objects were held. An example of the types of erroneous hand postures observed comes from a subject who produced a loose clench/palm hybrid with thumb out in pantomiming use of a bottle opener. Hand posture was significantly more impaired for transitive (object-related) gestures than intransitive (symbolic) gestures ($t = 4.1$, $P = 0.003$). Two of the brain-lesioned controls tended to exhibit the same pattern, leaving open the possibility that the transitive hand postures were more demanding (but see below for data suggesting an alternative possibility).

Ipsilesional grip strength, tactile sensation, and proprioception were grossly intact in all subjects. Table 4 shows that several subjects had mildly reduced ipsilesional dexterity. Grasping objects was normal for all subjects except A5.

Gesture recognition scores (which were available only for subjects A5–A9) were >2 SDs below the control mean (i.e. < raw score 27.7, or 92.3%, see Appendix A) for all apraxic subjects except A9, who was within the normal range. Only A7 showed more than mild impairment. One of the brain-lesioned controls (L3) was below the normal range as well.[1] Static posture imitation, on the other hand, was >3 SDs below the control mean (i.e. raw score 17.9, or 92.5%; see Appendix A) for the majority of the apraxics tested (subjects A5–A8) and <2 SDs for the remaining subject, A9. Again, one of the brain-lesioned controls (L1) was below the normal range as well.

All of the American apraxics exhibited aphasia on the Western Aphasia Battery (WAB) [9]. Performance was generally less impaired on the Philadelphia Comprehension Battery, a test of word–picture matching in which an auditory word must be matched to one of three within-category or across-category pictures [10]. Brain-lesioned control subjects L3, L4, and L5 also exhibited comprehension deficits on the WAB. On the Moss Object Probes Test, apraxic subjects performed at least somewhat better on items testing function knowledge as compared to manipulation knowledge (except A8, whose performance was equal on both). This pattern is consistent with previous findings by our group [11,12].

[1] The medical records from the acute hospitalization of this subject indicated that he was apraxic at that time.

Table 2
Subject demographics and lesion information

Group	Subject	Gender	Age	Handed ness	Locus of Lesion	Brodmann's areas	Time since lesion	Aphasia: original clinical diagnosis
Apraxic	A1	M	75	R	Small left temporo-parietal	22, **40**	2 months	Conduction
	A2	M	74	R	Large left parietal	1, 5, **39**, **40**	2 years	Broca
	A3	M	62	R	Small left temporo-parietal	22, **39**, **40**	6 months	Conduction
	A4	F	75		Small left parietal	**39**, **40**	4 years	Conduction
	A5	F	52	R	Large left frontotemporoparietal	4, 6, 7, s, 18, 19, 22, 28, 36, 37, **39**, **40**, 44, 45, 46	12 years	Broca
	A6	M	55	R	Left frontotemporoparietal	4, s, 6, 21, 22, **39**, **40**, 41–42	2 years	Broca
	A7	M	56	R	Large left frontotemporoparietal	4, 6, s, 21, 22, 25, 37, **39**, **40**, 41–42, 44, 45, 47	16 years	Broca
	A8	M	59	R	Large left frontotemporoparietal	4, 5, 6, 7, 8, 9, 10, s, 22, 23, 24, 31, 32, **39**, **40**, 41–42, 46	5 years	Broca
	A9	M	64	R	Large left frontotemporoparietal, subcortical	6, s, 21, 22, **39**, **40**, 41–42, 44, 45	3 years	Broca
Right CVA	R1	M	61	R	Right frontal, subcortical	47, putamen, globus pallidus	7 months	–
	R2	M	54	L	Right dorsolateral frontal, subcortical	4, 6, 8, s	6 months	–
	R3	M	54	R	Large right basal ganglia/external capsule	22, 37, putamen, basal ganglia, external capsule	7 months	–
Left CVA	L1	M	55	R	Left pontine, cerebellar peduncle	–	2 years	– (Dysarthria)
	L2	F	79	R	Left pontine	–	2 years	– (Dysarthria)
	L3	M	67	R	Large left dorsolateral frontotemporoparietal	40, 41, 42, 44, 45, 21, 22	8 years	Broca
	L4	M	50	R	Large left frontotemporal	1, 2, 3, 6, 22, 44, insula	1 year	Broca
	L5	F	54	R	Large left mesial frontal, dorsolateral prefrontal and frontal	23, 24, 32, 4, 6	8 months	Transcortical motor

Table 3
Scores on apraxia tests (percent correct)

Group	Subject	Content	Hand	Arm	Amplit.	Timing	Total spatiotemporal
Transitive gesture to sight							
Apraxic	A1	100	40	90	70	90	**73**
	A2	100	20	10	10	0	**10**
	A3	100	20	90	50	90	**63**
	A4	100	30	90	40	70	**58**
	A5	90	22	78	50	90	**64**
	A6	100	10	60	60	90	**55**
	A7	100	60	70	70	100	**75**
	A8	89	50	63	56	44	**56**
	A9	100	60	100	70	70	**75**
	Mean	**98**	**35**	**72**	**53**	**72**	**59**
Right CVA	R1	100	100	90	100	90	**95**
	R2	100	100	90	90	100	**95**
	R3	100	100	100	100	100	**100**
Left CVA	L1	100	90	100	70	90	**88**
	L2	100	100	100	100	100	**100**
	L3	100	90	100	80	100	**93**
	L4	100	90	100	90	100	**95**
	L5	100	90	90	90	100	**93**
Transitive gesture to imitation							
Apraxic	A5	100	20	80	70	80	**63**
	A6	100	50	60	100	90	**73**
	A7	100	30	80	90	100	**75**
	A8	100	30	70	70	70	**60**
	A9	100	70	60	80	100	**78**
	Mean	**100**	**40**	**70**	**82**	**86**	**70**
Right CVA	R1	100	100	100	100	100	**100**
	R2	100	100	100	100	100	**100**
	R3	100	100	100	100	100	**100**
Left CVA	L1	100	100	100	90	90	**95**
	L2	100	90	100	100	100	**98**
	L3	100	100	100	80	100	**95**
	L4	100	100	90	100	100	**98**
	L5	100	100	90	100	100	**98**
Object use							
Apraxic	A5	100	100	70	30	90	**73**
	A6	100	90	90	80	90	**88**
	A7	100	90	70	100	90	88
	A8	100	70	60	80	80	**73**
	A9	100	50	80	70	100	**75**
	Mean	**100**	**80**	**74**	**72**	**90**	**79**
Right CVA	R1	100	100	90	100	100	**98**
	R2	100	100	90	100	100	**98**
	R3	100	100	100	100	100	**100**
Left CVA	L1	100	90	100	90	100	**95**
	L2	100	100	100	100	90	**98**
	L3	100	10	10	9	10	**98**
	L4	100	100	90	90	100	**95**
	L5	100	90	90	100	100	**95**
Intransitive gesture to command							
Apraxic	A1	100	80	100	100	100	**95**
	A2	80	25	75	50	75	**56**
	A3	80	75	100	75	100	**88**
	A4	60	67	100	100	100	**92**
	A5	60	67	33	100	100	**75**
	A6	100	60	60	100	100	**80**
	A7	100	60	60	100	100	**80**
	A8	100	100	80	100	100	**95**

Table 3 (*Continued*)

Group	Subject	Content	Hand	Arm	Amplit.	Timing	Total spatiotemporal
	A9	100	60	80	80	100	**80**
	Mean	**87**	**66**	**76**	**89**	**97**	**82**
Right CVA	R1	100	100	100	100	100	**100**
	R2	100	100	100	100	100	**100**
	R3	100	100	100	100	100	**100**
Left CVA	L1	100	100	100	80	100	**95**
	L2	100	100	100	100	100	**100**
	L3	40	100	100	100	100	**100**
	L4	100	100	100	100	100	**100**
	L5	100	100	100	100	100	**100**
Intransitive gesture to imitation							
Apraxic	A5	100	50	75	100	100	**81**
	A6	100	60	60	100	100	**80**
	A7	100	100	50	100	100	**88**
	A8	100	80	60	100	100	**85**
	A9	100	100	100	100	100	**100**
	Mean	**100**	**78**	**69**	**100**	**100**	**87**
Right CVA	R1	100	100	100	100	100	**100**
	R2	100	100	100	100	100	**100**
	R3	100	100	100	100	100	**100**
Left apraxic	L1	100	100	100	100	100	**100**
	L2	100	100	100	100	100	**100**
	L3	100	100	100	100	100	**100**
	L4	100	100	100	100	100	**100**
	L5	100	100	100	100	100	**100**

3.1.3. Materials and procedure

Materials and procedure for the experimental tasks of Study 2 were the same as Study 1, except that the objects were limited to the 35 real objects and 10 novel objects for which there had been a modal response in Study 1. Each of the 35 real objects was presented once, and each of the 10 novel objects was presented twice, in both Pantomime and Point conditions, for a total of 110 experimental trials. Care was taken to ensure that subjects comprehended all task instructions, and practice trials were repeated until they were performed without error. Nine of the 17 brain-lesioned subjects performed the Pantomime condition first, and the other eight subjects performed the Point condition first. Subjects performed all experimental tasks with the ipsilesional hand. As in Study 1, performance in the Pantomime condition was scored from the videotapes by two independent coders. Disagreements arose on few trials(<3%), indicating that the scoring system was reliable. Trials with disagreements were reconciled by discussion.

3.1.3.1. Data analysis part 1: comparison of patient and control data; assessment of structural and functional response determinants. Control data from Study 1 were used as the basis for comparison of the patient data in Study 2. Given that there was some inherent ambiguity in coding of responses in the Pantomime condition, but no such ambiguity in the Point condition, control responses in the Point condition of Study 1 were taken as the "normative" response in most comparisons. To maximize the opportunity to observe differences between patients, many comparisons were performed using a "case-study" model in which each patient's individual data were compared to a control mean.

3.1.3.1.1. Response ambiguity analysis. The first analysis assessed whether brain-lesioned subjects' gestures were more ambiguous than control gestures. Mean confidence ratings of subjects were tallied for each response condition. Since the response ambiguity (confidence rating) data were not normally distributed due to restricted range (minimum = 1, maximum = 3), also tabulated were the number of trials on which subjects received confidence ratings of 2 or 3 (somewhat confident or not at all confident). The frequency counts of such trials in control, apraxic, RCVA, and LCVA groups was compared by Mann–Whitney *U*-tests.

3.1.3.1.2. Modal/non-modal analysis. The second analysis assessed whether brain-lesioned subjects produced unusual responses to real and/or novel objects. Based on controls' responses in the Point condition of Study 1, we first classified the modal, less frequent, and "never made" responses for each object. For example, if for "hammer" there were eight clenches and two pinches, then "clench" was modal, "pinch" was less frequent, and "palm" and "poke" were never made. We then tallied patients' responses according to these categories. For example, if a patient produced a "pinch" for "hammer", the response was tallied as

Table 4
Subjects' performance on background tests

Group	Subject	Dexterity[a]		Grasping[b]		Gest Recog (%)	Static posture imitation (%)	Philadelphia Comprehension Battery[c]		Western Aphasia Battery[c]			Moss Object Probes Test			
		L	R	L	R			Within catagory (%)	Across category (%)	Spontaneous speech (%)	compr (%)	Repet (%)	Name (%)	Funct (%)	Manip (%)	Phys (%)
Apraxic	A1	12.3	9.7	20	20											
	A2	4.3	0.7	20	NA											
	A3	9.3	3.3	20	20											
	A4	5.0	4.7	20	17											
	A5	6.7	0.0	17	NA	90	80	100	97	60	66	74	49	86	74	97
	A6	6.7	0.0	20	NA	90	10	88	100	50	89	40	86	97	91	94
	A7	9.7	0.0	20	NA	80	70	88	100	NA	NA	NA	34	94	83	83
	A8	10.3	0.7	19	20	90	50	94	96	75	73	75	91	97	97	91
	A9	8.7	0.0	19	NA	93	90	81	86	35	85	69	43	100	80	94
Right CVA	R1	0.0	10.0	NA	20	100	100	NA	NA	NA	NA	NA	100	100	100	97
	R2	7.3	8.7	20	20	100	100	NA	NA	NA	NA	NA	100	100	100	97
	R3	5.0	11.3	20	20	100	100	NA	NA	NA	NA	NA	77	100	100	94
Left CVA	L1	7.7	6.0	20	20	100	90	NA	NA	100	99	98	97	100	100	100
	L2	8.3	8.3	20	20	100	100	NA	NA	100	100	100	66	97	97	94
	L3	15.0	16.6	20	20	90	95	NA	NA	65	88	57	89	91	94	100
	L4	6.7	4.0	20	20	100	90	NA	NA	95	79	96	100	100	97	97
	L5	6.3	5.7	20	20	100	100	NA	NA	95	85	100	100	100	100	100

[a] Mean oscillations per 10 s.
[b] $n = 10$, maximum score = 20.
[c] WAB data not available for subject A7 or RCVAs.

"less frequent". As frequency counts in the "never made" cells were frequently extremely low, particularly for the brain-lesioned controls (e.g. 0 or 1), for purposes of statistical analysis we collapsed across the "less frequent" and "never made" categories to derive the total number of non-modal responses. The average (mean) control distribution of modal and non-modal responses was then compared to the distribution of each brain-lesioned subject by χ^2 analysis.

3.1.3.1.3. Response distribution analysis. The third analysis assessed whether brain-lesioned and control subjects produced different patterns of responses across the four hand posture categories. The distribution of responses to each object (number of pokes, pinches, palms, and clenches) was tallied for each brain-lesioned subject. Each patient's distribute was compared to the average (mean) control distribution of responses in the relevant Point condition by χ^2 analysis.

3.1.3.1.4. Pantomime versus point analysis. The fourth analysis assessed whether brain-lesioned subjects' performance differed in Pantomime versus Point conditions.

Responses matching the modal control response (i.e. "correct" responses) were tallied in the Pantomime and Point conditions, and the two conditions compared by χ^2 analysis.

3.1.3.1.5. Error rate analyses: structural responses. This analysis assessed whether subjects' errors with real conflict objects were more likely to be based on structural factors than would be predicted by chance. The expected rate of structural response errors (number of possible structural response errors over number of all possible errors) was calculated for real conflict objects in both Pantomime and Point conditions. The observed rate of structural response errors was calculated for the same conditions, and differences in the expected and observed rates assessed by Binomial Test. This procedure was performed separately on the data from the apraxic and control groups (the observed rate of errors in the brain-lesioned controls, 8 and 5 in Pantomime and Point conditions respectively, was too low to be analyzed).

3.1.3.1.6. Item analyses. In this analysis, brain-lesioned subjects' "correct" responses to each real object in Pantomime and Point conditions were tallied to ascertain whether there were some items that were inherently difficult for apraxic subjects. An "Item" was defined as a given object in a specific condition, e.g. "apple" in the Pantomime condition.

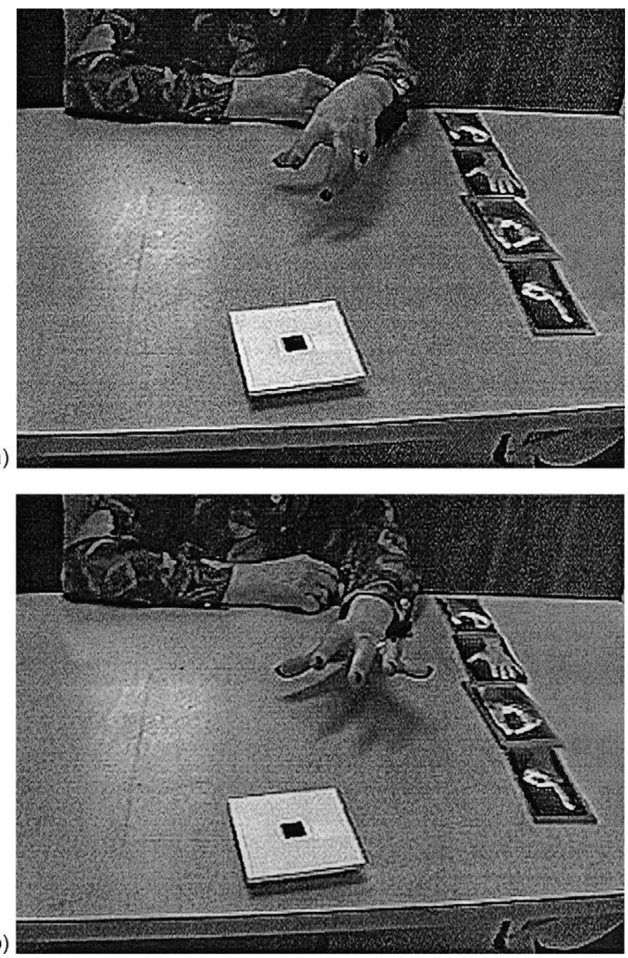
3.1.3.1.7. Regression analyses of gesture task and experimental tasks. Finally, to ascertain whether subjects' performance on the experimental tasks could be predicted from their praxis performance, we performed multiple regressions with the hand posture, arm posture, amplitude, and timing component of the gesture to sight of objects task of the background battery as independent variables, and modal responses in the Pantomime and Point conditions as dependent variables. We expected the hand posture component of transitive gestures to emerge as a strong predictor of experimental performance.

3.2. Results

3.2.1. Response ambiguity analysis

Apraxics' hand postures were qualitatively poor, resulting in coders' perception that it was difficult to assign them to a hand posture category. It should be emphasized that despite this subjective sense of difficulty, inter-rater reliability was strong. Disagreement between the two coders arose on few (<2%) trials. Fig. 2 shows examples of postures assigned a "2" or "3" ("somewhat confident" or "not at all confident") rating from the videotapes of apraxic subjects.

(a)



(b)

Fig. 2. (a and b) Still photographs taken from the videotape of an apraxic subject showing the subject's response to a novel object with negative (indented) depth and small surface area, which evoked a "poke" modal response in control subjects. The apraxic subject responded by producing two ambiguous postures in sequence. In accordance with our scoring guidelines, the first response (Fig. 2a) was assigned to a posture category ("clench"), and the judges indicated that they were only "somewhat confident" that the posture was indeed a clench (confidence score of 2).

Table 5
Subjects' responses coded with respect to modal, less frequent, and never-made responses of controls in Point condition

Group	Subject	Responses (number of trials)			χ^2	Significance	*P*
		Modal	Less frequent	Never	(Modal/non-modal)		
Pantomime condition							
Control	Range	37–52	3–18	0–1			
	Mean	**45**	**9**	**1**			
Apraxic	A1	34	9	12	5.4	*	0.03
	A2	22	18	15	20.2	***	0.0001
	A3	36	11	8	3.8		0.08
	A4	26	15	14	14.3	***	0.0003
	A5	19	29	16	25.2	***	0.0001
	A6	26	11	18	14.3	***	0.0003
	A7	35	13	7	4.6	*	0.05
	A8	12	21	21	38.8	***	0.0001
	A9	21	23	11	22.6	***	0.0001
RCVA	R1	52	3	0	4.3		0.07
	R2	51	4	0	2.9		0.15
	R3	52	3	0	4.3		0.07
LCVA	L1	48	6	1	0.6		0.59
	L2	46	8	1	0.2		0.79
	L3	51	4	0	2.9		0.15
	L4	51	4	0	2.9		0.15
	L5	51	1	3	2.9		0.15
Point condition							
Control	Range	36–53	2–19	0			
	Mean	**45**	**10**	**0**			
Apraxic	A1	46	7	2	0.1		0.999
	A2	29	12	14	10.6	**	0.002
	A3	19	19	17	25.2	***	0.0001
	A4	33	16	6	6.3	*	0.02
	A5	25	14	16	15.7	***	0.0001
	A6	19	6	10	7.9	**	0.008
	A7	41	9	5	0.9		0.48
	A8	18	17	20	27.1	***	0.0001
	A9	35	11	9	4.6	*	0.03
RCVA	R1	52	3	0	4.3		0.07
	R2	53	2	0	5.9	More modal*	0.03
	R3	51	4	0	2.9		0.15
LCVA	L1	47	7	1	0.3		0.07
	L2	50	5	0	1.9		0.16
	L3	48	5	2	0.6		0.15
	L4	49	0	6	1.2		0.27
	L5	50	1	4	1.9		0.16

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Recall that scores of 1 reflect high confidence and 3 low confidence. The mean confidence rating for apraxics' pantomimes was 1.6 (S.D. 0.7). For LCVA, the mean rating was 1.0 (S.D. 0.2), for RCVA it was 1.1 (S.D. 0.2) and for controls it was 1.0 (S.D. 0.1). In the apraxic group, a mean of 8.6 responses (S.D. 4.5) was given a 2 or 3 confidence rating. For the other groups, results indicated that relatively few responses were given scores of 2 or 3: LCVA: mean 0.4 responses (sd. 0.2); RCVA: mean 1.7 responses (S.D. 1.0); controls: mean 0.3 responses (S.D. 0.6). Mann–Whitney *U*-tests performed on the number of trials with confidence ratings >1 confirmed that significantly more of the apraxics' gestures were rated with low confidence than controls' gestures for all conditions (novel, real conflict, and real no-conflict objects) (U Prime >83, $P < 0.001$ for all). Apraxics were also rated with lower confidence than RCVA and LCVA for novel objects (U Prime >26.5, $P < 0.01$ for both). RCVA, LCVA, and controls did not differ in any comparisons.

3.2.2. Modal/non-modal analyses

Table 5 shows the distributions of modal, less frequent, and "never made" responses for the brain-lesioned subjects in Pantomime and Point condition, collapsed across real

Table 6
Distribution of responses: summary of significant differences from control subjects

Group	Subject	Distribution of modal/non-modal responses					
		Pantomime			Point		
		Real conflict	Real no-conflict	Novel	Real conflict	Real no-conflict	Novel
Apraxic	A1		*				
	A2		***	**	*t*	*	
	A3				**	**	**
	A4	*	**				
	A5	***	**	*	***	**	
	A6	*	*	**		*	
	A7	**			*		
	A8	***	***	***	***		
	A9	**	**	**	**		
RCVA	R1						
	R2						
	R3						
LCVA	L1						
	L2						
	L3						
	L4						
	L5						

t = trend ($P < 0.1$).
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

conflict, real no-conflict, and novel objects. In statistical comparisons of modal versus non-modal responses, all of the apraxics, but none of the brain-lesioned controls, differed significantly from the normative data (healthy controls in the Point condition),[2] in part because they produced an abnormally high number of "never made" responses. Table 6 provides summaries of the significant and non-significant effects when the analyses comparing controls and patients were performed for real conflict, real no-conflict, and novel objects separately.[3] Without exception, patterns of response differing significantly from the healthy controls were found only in the apraxics, and not in the LCVA or RCVA groups.[4] As can be seen, the apraxics exhibited many differences from the controls, particularly with real objects (both conflict and no-conflict). With the exception of subject A3, subjects performed normally with novel objects in the Point condition. Several subjects performed normally with novel objects in both Pantomime and Point conditions (A1, A4, and A7).

3.2.3. *Response distribution analysis*

The response distributions differing from controls are shown in Table 7. Again, performance patterns differing from the healthy control distribution were found only in the apraxic group. Although numerous patterns were evident, the following generalities emerged: nearly all significant patterns entailed fewer Poke responses than expected based on the control distribution, and many entailed more Pinch and/or Clench responses than expected. In general, fewer differences from normal performance were found in this analysis than in the preceding modal/non-modal analysis, probably because the pattern of responses was distributed over four possible response categories rather than three.

3.2.4. *Pantomime versus point analysis*

In the apraxic group, subjects A1 and A9 produced significantly more "correct" responses in the Point as compared

[2] Note that because the Point condition was used as the normative distribution for determination of modal, less-frequent, and never-made response, it was possible for the controls themselves to differ from this in the Pantomime condition (hence the "1" tallied in the "never-made" column of the Pantomime condition).

[3] To address the concern that cultural factors may have differently affected French and American subjects' responses, we also ran five French age-matched control subjects at the Institute des Sciences Cognitives in Lyon using the methods of Study 2. The distributions of modal/non-modal/never made responses in each condition (Real Conflict, No-Conflict, and Novel, for both Pantomime and Point) were compared for the French and American controls by χ^2 analyses. The distributions of French and Americans' poke, pinch, palm, and clench responses in each condition were also compared by χ^2 analyses. Of the 12 comparisons performed, there was only 1 reaching significance: in the Pantomime condition, French controls made significantly more modal responses and fewer non-modal responses to novel objects than Americans ($\chi^2 = 7.1$, $P < 0.05$) (i.e. their responses were slightly more canonical). The comparability of American and French control performance suggests that examining the French and American apraxic patients together is not likely to obscure cultural differences between these groups.

[4] Given the number of statistical comparisons performed, we considered performing statistical (e.g. Bonferroni) corrections to determine acceptable *P*-values. One difficulty is that too-stringent correction risks obscuring potentially meaningful patterns in the data, such as the observed pattern of significant *P*-values *only* in the apraxic group.

Table 7
Distribution of responses in four hand posture categories

Group	Subject	Real conflict				Real no-conflict				Novel			
		Poke	Pinch	Palm	Clench	Poke	Pinch	Palm	Clench	Poke	Pinch	Palm	Clench
Pantomime conditions													
Control	Mean	2	7	1	2	4	7	4	8	6	7	2	5
Apraxic	A1	0	10	1	1	0	12	2	9	8	9	0	3
	A2	1	7	1	3	1	12	0	10	**1**	**6**	**10**	**3**
	A3	0	7	0	5	3	4	5	11	9	10	1	0
	A4	0	6	0	6	**0**	**8**	**0**	**14**	**2**	**5**	**0**	**13**
	A5	**0**	**1**	**6**	**5**	2	4	6	11	**1**	**14**	**5**	**0**
	A6	0	5	1	6	1	12	3	7	11	4	2	3
	A7	0	4	4	4	**0**	**3**	**5**	**15**	5	9	0	6
	A8	**0**	**0**	**6**	**6**	**0**	**0**	**11**	**11**	**3**	**2**	**3**	**12**
	A9	0	4	0	8	**0**	**9**	**0**	**14**	**0**	**6**	**3**	**11**
	Total	1	44	19	44	7	64	32	102	40	65	24	51
Point conditions													
Control	Mean	2	7	1	2	4	7	4	8	6	7	2	5
Apraxic	A1	0	9	1	2	5	7	3	8	7	6	1	6
	A2	0	8	0	4	**0**	**13**	**0**	**10**	**0**	**14**	**0**	**6**
	A3	3	4	4	1	5	4	8	6	3	7	3	7
	A4	0	7	2	3	4	5	4	10	**0**	**10**	**0**	**10**
	A5	3	2	5	2	4	4	6	9	**0**	**13**	**1**	**6**
	A6	3	4	1	4	4	6	8	5	**7**	**7**	**6**	**0**
	A7	0	6	5	1	0	9	6	8	9	5	0	6
	A8	3	5	1	3	1	8	3	11	9	5	4	2
	A9	2	4	1	5	4	6	5	8	8	4	0	8
	Total	14	49	20	25	27	62	43	75	43	71	15	51

Values in bold are significantly different than control distribution by χ^2 ($P < 0.05$).

to Pantomime condition ($\chi^2 > 7.0$, $P < 0.05$ in both cases). Conversely, apraxic subject A3 produced more correct responses in the Pantomime condition ($\chi^2 = 10.5$, $P < 0.01$). The other apraxics performed equally in both response conditions. None of the RCVA or LCVA subjects exhibited significant differences between conditions.

3.2.5. Error rate analyses: structural responses

For each object, there was a correct response (e.g. pinch) and three possible error responses (e.g. palm, clench, and poke). There was a one in three (33%) chance that an observed error would be consistent with the structural response. In the healthy controls, the rates of structural response errors were 5/15 (33%) and 2/13 (15%) in Pantomime and Point conditions. These rates were not significantly different than chance ($P > 0.1$ by Binomial Test). The rates of structural response errors observed in the apraxic subjects, in Pantomime and Point conditions, respectively, were 22/58 (38%) and 15/55 (27%) (neither significantly different than chance, $P > 0.2$ for both). Thus, neither apraxic nor control subjects were more likely to make structural response errors than would be expected by chance.

3.2.6. Item analyses

As Table 8 shows, 13 items (recall that "item" refers to an object in a specific condition, e.g. apple/Pantomime) evoked a relatively great number (>6) correct responses by apraxics in Pantomime and/or Point conditions. All 13 of these items had pinch or clench as the controls' modal response. Thirteen items evoked a relatively small number (<3) correct responses in Pantomime and/or Point conditions. Twelve of these 13 items had poke as the controls' modal response.

3.2.7. Regression analyses of gesture task and experimental tasks

We performed two regression analyses with the data from all 17 brain-lesioned subjects in which hand posture, arm posture, amplitude, and timing component scores from the gesture to sight of objects task were used to predict scores in Pantomime and Point conditions of the experimental tasks. Gesture scores strongly predicted performance of the experimental tasks. The multiple adjusted r^2 for the model in which gesture was used to predict the experimental Pantomime condition was 0.71 ($F = 11.0$, $P < 0.0005$). The strongest independent predictor of experimental performance was the hand posture gesture component (standard coefficient $= 0.93$, $P = 0.01$), followed by timing (standard coefficient $= 0.66$, $P = 0.05$). The other gesture components did not contribute to the model ($P > 0.2$). Similarly, the multiple adjusted r^2 for the model in which gesture scores were used to predict the experimental Point condition was 0.72 ($F = 11.1$, $P = 0.0005$). The *only* gesture component to independently predict experimental performance was the

Table 8
Item analysis: numbers of correct responses to real objects

	Control modal response	No. correct
Pantomime		
Conflict objects		
Glass	Clench	8
Rolling pin	Clench	7
Zipper	Pinch	7
Hammer	Clench	5
Leaf	Pinch	5
Pencil	Pinch	5
Nail	Pinch	4
Envelope	Pinch	3
Shoelaces	Pinch	3
Keyboard	Poke	1
Typewriter	Poke	0
Wall switch	Poke	0
No-conflict objects		
Apple	Clench	8
Paperclip	Pinch	7
Clothespin	Pinch	7
Saltshaker	Clench	7
Plug	Pinch	6
Guitar pick	Pinch	6
Lemon	Clench	6
Sandpaper	Palm	6
Hairbrush	Clench	6
Phone receiver	Clench	6
Doorknob	Clench	5
Fur	Palm	5
Key	Pinch	5
Pliers	Clench	5
Basketball	Palm	4
Cushion	Palm	4
Bongo drums	Palm	3
Thimble	Poke	3
Chalk	Pinch	2
Doorbell	Poke	2
Calculator	Poke	1
Deadbolt	Pinch	1
Push button phone	Poke	0
Point		
Conflict objects		
Pencil	Pinch	7
Chalk	Pinch	6
Leaf	Pinch	6
Shoelaces	Pinch	6
Hammer	Clench	5
Nail	Pinch	5
Glass	Clench	5
Rolling pin	Clench	5
Zipper	Pinch	4
Envelope	Pinch	3
Typewriter	Poke	2
Wall switch	Poke	2
Keyboard	Poke	0
No-conflict objects		
Paperclip	Pinch	8
Apple	Clench	8
Clothes spin	Pinch	8
Guitar pick	Pinch	7
Phone receiver	Clench	7
Bongo drums	Palm	6
Cushion	Palm	6
Basketball	Palm	5
Fur	Palm	5
Plug	Pinch	5
Key	Pinch	5
Sandpaper	Palm	5
Saltshaker	Clench	5
Hairbrush	Clench	4
Deadbolt	Pinch	4
Doorknob	Clench	4
Lemon	Clench	4
Pliers	Clench	4
Thimble	Poke	4
Doorbell	Poke	3
Push button phone	Poke	2
Calculator key	Poke	1

hand posture component (standard coefficient = 0.99, $P = 0.007$).

3.2.8. Discussion

On tests assessing production and recognition of hand postures in response to real and novel objects, patterns of performance differing from healthy controls were prevalent in the apraxic group, but not observed in LCVA or RCVA patients without apraxia. Apraxics' performance differed, in particular, from the performance of LCVA non-apraxics with moderately large cortical lesions and comprehension impairments. We also observed a highly specific predictive relationship between performance on the hand posture component of the gesture to sight of objects pantomime task and the experimental tasks. Recall that apraxics' errors in the gesture pantomime tasks were spatiotemporal, rather than content-related, in nature. The strong association of spatiotemporal hand posture errors on the praxis tasks and deficits on the experimental tasks suggests that the latter performance is unlikely to be an artifact of overall cognitive severity or comprehension difficulties. Instead, it suggests that apraxic subjects suffer a particular deficit in cognitive representations of hand posture.

Apraxics were impaired in numerous aspects of experimental task performance. Most were impaired in terms of their agreement with control subjects' modal responses, and produced many atypical responses. Several were impaired as well in terms of the distribution of responses in each of the four response categories. Examination of the pattern of responses suggested that subjects were making fewer pokes, and more clench and pinch responses than expected. Additionally, apraxics' hand postures were judged subjectively to be more difficult to assign to a posture category than the brain-lesioned control subjects.

The majority of apraxic subjects were impaired with real objects in both Pantomime and Point conditions. Even with the opportunity to select an appropriate hand posture from a choice of four photographs, most subjects performed quite poorly. This suggests that for most of the apraxics, knowledge of the hand postures associated with objects is degraded, and not merely inaccessible to motor output mechanisms.

Eight of the apraxic subjects who performed abnormally with real objects performed *normally* with novel objects in the Point condition. Consistent with our predictions, this indicates that for the majority of apraxic subjects, knowledge of the hand configuration appropriate to object structure is intact. The specificity of this pattern is additional evidence that neither overall severity nor deficient comprehension is likely to explain the present data. To our knowledge, this is the first empirical demonstration of this pattern in IM. In this context, only three of these eight apraxic subjects (and an additional subject) performed normally with novel objects in the Pantomime condition. For most subjects, the impairment in pantomiming thus occurs irrespective of object type, suggesting that deficits in spatiomotor production are a factor additional to the deficit in evoking stored gesture representations. In other words, the pattern of performance in the majority of apraxics appears to result from the interaction of two factors: a degradation of gesture representations affecting both production and recognition for responses to *real* objects, and additional production deficits affecting *pantomime* for all objects, whether familiar or novel. We will discuss this pattern further in the General Discussion.

While we had expected that most patients would exhibit relatively good performance with real objects for which structural and functional influences were in agreement, this was not the case. One possibility is that stored hand-posture representations may be activated automatically by objects, even when damaged. Reliance upon the damaged information may over-ride the relative integrity of procedures enabling responses to structural factors.

Although apraxics' unimpaired performance with novel objects indicates relative integrity of response to object structure, their errors in the real conflict condition did not follow the predicted pattern, i.e. they were not largely consistent with structural responses. The determinants of apraxics' errors with real objects for which structure and function conflict thus remain unclear. The observation that they made more clench and pinch responses than expected (see above) suggests the possibility that objects might be differentially "easy" or "difficult" for the apraxic subjects as a function of the response associated with them. That is, it is possible that subjects performed correctly on "pinch" and "clench" objects (i.e. objects whose modal response was prehensile) but erred on "palm" and "poke" objects (i.e. non-prehensile objects). We performed several post hoc analyses to pursue this possibility. As the study was not originally designed to assess the prehensile/non-prehensile distinction, the number of real and novel objects in each of these groups was not balanced, and the analyses to follow should be viewed as points of interest for future investigation.

3.2.8.1. Data analysis, part 2: prehensile and non-prehensile posture analyses.

3.2.8.1.1. Prehensile versus non-prehensile analyses. Each brain-lesioned subject's "correct" responses were tallied for objects for which the controls' modal response was prehensile (pinch, clench) versus those for which the modal response was non-prehensile (palm, poke), and the conditions compared by χ^2 analysis.

3.2.8.1.2. Error rate analyses: prehensile responses. As we had done with structural response errors, we determined whether errors that were prehensile responses (clench and pinch) occurred over chance rates by comparing the expected rate of prehensile errors (number of possible prehensile errors over number of all possible errors) to the observed rate of prehensile errors. We then subjected the data to binomial tests. This procedure was performed separately for the apraxic and healthy control groups using data from the real object condition. There were too few errors in the Brain-lesioned control groups (eight and five in Pantomime and Point conditions, respectively) to perform this analysis.

3.3. Results

3.3.1. Prehensile versus non-prehensile analyses

As Table 9 shows, in Pantomiming with real objects, five apraxics (A1, A2, A4, A6, A9) were more often correct with prehensile (modal response clench or pinch) than non-prehensile objects (modal response palm or poke), and three of the same, and an additional subject (A1, A2, A4, and A7) showed the same pattern in the Point condition. One of the eight brain-lesioned control subjects (L5) showed this pattern in the Point condition as well; however, both prehensile and non-prehensile scores (100 and 75% correct, respectively) were above the range of apraxics. With novel objects, two apraxics (A4 and A6) more often pantomimed correctly with prehensile than non-prehensile objects, and the same two subjects and two additional subjects (A2, A4, A5, and A6) showed the same pattern in the Point condition. None of the brain-lesioned control subjects showed significant differences between prehensile and non-prehensile objects.

Wilcoxon signed-rank tests performed on the group data from the apraxic subjects confirmed that overall, responses were significantly more often correct for prehensile as compared to non-prehensile objects (Pantomime: $z = -2.3$, $P = 0.02$; Point: $z = -2.5$, $P = 0.01$).

Given the finding that apraxics were relatively impaired with non-prehensile hand postures, we next explored whether they were equally impaired with poke and palm configurations. We tallied "correct" responses for poke versus palm trials (i.e. trials for which poke or palm were the modal control responses), collapsing across real conflict, real no-conflict, and novel objects, and across Pantomime and Point conditions, to gain additional statistical power.

Table 9
Comparison of responses to prehensile and non-prehensile objects

Group	Subject	Real prehensile ($n = 23$) no. correct (%)	Real non-prehensile ($n = 12$) no. correct (%)	Significance of comparison	Novel prehensile ($n = 12$) no. correct (%)	Novel non-prehensile ($n = 8$) no. correct (%)	Significance of comparison
Pantomime condition							
Apraxic	A1	16 (70)	3 (25)	*	8 (67)	7 (88)	
	A2	15 (65)	2 (17)	**	4 (33)	1 (13)	
	A3	19 (83)	8 (67)		4 (33)	5 (63)	
	A4	17 (74)	0 (0)	***	7 (58)	2 (25)	***
	A5	7 (30)	5 (42)		6 (50)	1 (13)	
	A6	15 (65)	3 (25)	*	8 (67)	1 (13)	*
	A7	15 (65)	4 (33)		10 (83)	5 (63)	
	A8	5 (22)	3 (25)		1 (8)	2 (25)	
	A9	15 (65)	1 (8)	**	5 (42)	0 (0)	
RCVA	R1	23 (100)	12 (100)		9 (75)	8 (100)	
	R2	23 (100)	10 (83)		12 (100)	7 (88)	
	R3	23 (100)	11 (91)		10 (83)	7 (88)	
LCVA	L1	23 (100)	11 (92)		10 (83)	4 (50)	
	L2	23 (100)	10 (83)		7 (58)	8 (100)	
	L3	23 (100)	11 (92)		12 (100)	7 (88)	
	L4	22 (96)	10 (83)		10 (83)	7 (88)	
	L5	23 (100)	10 (83)		12 (100)	6 (75)	
Point condition							
Apraxic	A1	22 (96)	7 (58)	**	11 (92)	6 (75)	
	A2	17 (74)	1 (8)	***	11 (92)	0 (0)	***
	A3	7 (30)	7 (58)		5 (42)	0 (0)	*
	A4	20 (87)	4 (33)	**	9 (75)	0 (0)	***
	A5	9 (39)	4 (33)		12 (100)	0 (0)	***
	A6	11 (48)	8 (66)		11 (92)	0 (0)	***
	A7	18 (78)	4 (33)	*	11 (92)	8 (100)	
	A8	6 (26)	2 (17)		5 (42)	5 (63)	
	A9	15 (65)	4 (33)	*	10 (83)	7 (88)	
RCVA	R1	23 (100)	12 (100)		9 (75)	8 (100)	
	R2	22 (96)	11 (92)		12 (100)	8 (100)	
	R3	23 (100)	12 (100)		10 (83)	7 (88)	
LCVA	L1	22 (96)	10 (83)		12 (100)	7 (88)	
	L2	23 (100)	10 (83)		9 (75)	8 (100)	
	L3	21 (91)	9 (75)		12 (100)	6 (75)	
	L4	22 (96)	11 (92)		10 (83)	8 (100)	
	L5	23 (100)	9 (75)	*	10 (83)	8 (100)	

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Subjects were clearly impaired in the production of both palm (mean 54.4% correct) and poke (mean 25.4% correct) postures, but were significantly more impaired with the latter ($Z = -2.25$, $P = 0.02$ by Wilcoxon Signed Ranks Test). Analyses of individual subject data showed that four apraxics (A3, A4, A5, and A6) were significantly more impaired on poke than palm trials ($\chi^2 > 5.9$, $P < 0.05$ for all comparisons). No subjects showed significant differences in the other direction.

To assess whether subjects had equal difficulty with palm and poke trials in Pantomime and Point conditions, we examined these separately. There were five trials each in Pantomime and Point conditions for which palm was the modal response, and 15 trials each in Pantomime and Point conditions for which poke was the modal response. Apraxics showed the same pattern (few pokes or palms) in both Pantomime (poke mean = 3.2, palm mean = 2.4) and Point (poke mean = 4.4, palm mean = 3.0) conditions ($t < 1.5$, $P > 0.14$ for all comparisons).

3.3.1.1. Error rate analyses. Of the 105 possible errors with the real objects, there were 47 opportunities (45%) for prehensile errors (i.e. errors that were pinches or clenches). The observed rate of prehensile errors in the Pantomime and Point conditions, respectively, were as follows: healthy controls: 26/54 (48%) (non significant by Binomial Test) and 20/51 (39%) (non significant); apraxics: 128/164 (78%) ($P < 0.0001$) and 82/151 (54%) ($P < 0.05$).

3.3.2. Discussion

Apraxics are more likely to produce responses like those of control subjects for objects that require a prehensile response than for those that do not. Six of nine apraxics performed better with real prehensile than non-prehensile objects in Pantomime, Point, or both conditions. Four apraxics were similarly better with novel prehensile than novel non-prehensile objects. Additionally, errors produced by apraxics were prehensile (clenches or pinches) significantly more often than would be expected by chance. Finally, analyses of non-prehensile trials showed that while apraxic subjects were impaired in producing both palm and poke postures, they were particularly deficient in the latter. One possibility is that the requirement to isolate a single digit from the others renders poke configurations particularly difficult to represent in a computational sense. Because the pattern of poor performance with non-prehensile hand postures was evident in the Point condition, in which subjects did not have to program a hand configuration response, this finding can not be attributed to difficulty with motor programming of pokes or palms. Apraxics' failure to recognize the correct hand posture in a forced-choice context suggests that they are deficient in representations of hand posture configurations for non-prehensile responses to objects.

However, another possibility that must be considered is that apraxic subjects, due to aphasia or general cognitive impairment, may have understood the task instructions to mean "show how you would take (grasp) the object". If so, they would have produced many inappropriate prehensile responses. There are several lines of evidence suggesting this is unlikely to have been the case. First, as noted, several of the non-apraxic LCVA patients had moderately large cortical lesions and comprehension impairments, yet performed normally on the experimental tasks. Second, as is evident in Table 7, all of the apraxics produced non-prehensile responses—albeit not as many as the control subjects—indicating that no patient exhibited an overall misunderstanding of the task. Third, the apraxics performed poorly even with non-prehensile objects for which there was unanimity or near unanimity (agreement 90% or better) among control subjects. For example, doorbell was associated with a poke response with 100% agreement among controls, but only two of the eight apraxics produced a poke (see Table 8). Push-button telephone had a 90% agreement rate among controls, but none of the apraxics produced a poke. Bongo drums had 100% agreement for a palm response, and only three apraxic subjects produced a palm. The numbers were similar for the Point condition. Thus, even when non-prehensile functional responses are very strongly associated with objects, the apraxics still frequently failed to produce or recognize them. Finally, as noted earlier, the hand posture component of the background transitive gesture testing was a strong independent predictor of experimental task performance, consistent with the possibility that the same representations mediate performance on both tasks.

4. General discussion

In this study, we explored whether deficits in the production and recognition of hand postures associated with objects are prevalent in ideomotor apraxia (IM), and if so, whether they are specific to the apraxia syndrome. The experimental task required responses to real objects for which function and structure agreed or conflicted, as well as novel objects for which structure was the sole informant of hand posture. On the assumption that IM most frequently results from deficient access to or integrity of stored gesture representations, we expected the majority of apraxics to exhibit a pattern of performance consistent with impairment of hand posture representations, but integrity of responses to structure.

Our predictions were largely confirmed. All of the apraxic subjects, but none of the non-apraxic brain-lesioned subjects, produced abnormal hand posture responses to objects. In the case of real objects, most apraxics were impaired in recognition as well as in production, indicating damage to the representations underlying knowledge of appropriate hand postures for functional object interactions. In contrast, nearly all of the apraxic subjects performed *normally* in recognizing the hand postures appropriate for interacting with novel objects, suggesting relative integrity of response to object structure.

Several investigators have proposed a distinction between object-oriented actions programmed and adjusted "on line" in response to object properties, and actions based upon memorial representations of objects. These different types of action have been proposed to be mediated by the dorsal and ventral visual processing systems, respectively. The dorsal stream projects from striate to posterior parietal cortex and premotor regions of the frontal lobe [13]. It was originally characterized as a spatial system coding object location ("where" information), in contrast to the "what" representations of the ventral system. More recent physiological evidence has indicated, however, that the dorsal system is largely dedicated to computation of movements of the effectors required to bring objects into proximity (e.g. foveation, head turning, reaching with the limbs), leading Milner and Goodale [14] to characterize it as the "how" system.

A large neuronal population in the dorsal stream is involved in the coding of hand grasping movements. Neurons in the premotor area F5 in the monkey are selective for different types of grip responsive to the structural properties of objects: precision grip, finger prehension, and whole-hand prehension [15]. Neurons coding different types of grip in response to object structure are also present in a part of the intraparietal sulcus (area AIP) which is connected closely with area F5 [16] According to Gallese et al. [17], both F5 and AIP may participate in the transformation of visual information about object structure into information about "graspability" of objects in terms of affordances.

The ventral system's representation of objects is proposed to differ from this in two ways. Consistent with the "how" versus "what" distinction, Jeannerod [18] has proposed that the dorsal system generates a "pragmatic" representation of object attributes relevant to action, as contrasted with a "semantic" mode important for object recognition and categorization, coded by the ventral system. According to Goodale et al. [19], the primary distinction concerns the type of representation processed by each system. Unlike the target-directed actions computed by the dorsal system, which operate in real time, ventral structures are specialized for computing and storing memorial information about objects over longer time intervals. For example, the requirement to pantomime a gesture near an object, rather than acting directly upon it, requires buffering and spatiomotor transformation of information that places relatively strong demands on representational motor memory. Thus, the dorsal system in isolation is not equipped to act in locations other than those containing target objects.

These characterizations of the dorsal/ventral division of labor (which, incidentally, are not mutually exclusive) suggest a potential explanation for our apraxic subjects' pattern of performance. Apraxics' relatively unimpaired structural responses to novel objects may be mediated by intact dorsal stream processes, whereas their impaired responses to familiar objects and deficient pantomimes are attributable to damage to structures in the inferior parietal lobe aligned relatively more closely to the ventral system. Although concerned with actions upon objects (like the dorsal system), the inferior parietal lobe appears to mediate stored representations, as opposed to "on line" computations (for review see [20]).

Lesion data suggest all 9 apraxics have lesions including Brodmann areas 39 or 40 (angular and supramarginal gyri of the inferior parietal lobule), and 8 of these subjects have involvement of both of these regions. Conversely, inferior parietal regions were involved in only one of the eight non-apraxic controls. This difference is significant ($\chi^2 = 3.9$, $P < 0.05$). The control subject with inferior parietal involvement on acute neuroimaging scans had been apraxic acutely, as evidenced by hospital records, suggesting the possibility that the inferior parietal damage may have resolved to some degree. The neuroanatomic data suggest that poor performance on the experimental task may be associated with inferior parietal damage. This is consistent with a recent lesion study with 41 left hemisphere stroke patients demonstrating that ideomotor apraxia may be associated with lesions of the left inferior parietal lobe and intraparietal sulcus [21].

Given that none of the apraxic subjects have inferior parietal sparing, it remains possible that apraxia resulting from lesions that spare the inferior parietal lobe would also be associated with deficits in hand posture representations. Additional support for the present account would be obtained if it could be shown that apraxic patients with inferior parietal sparing are unimpaired in recognizing learned hand postures. Data we are currently collecting on a gesture recognition task with large numbers of apraxic patients should be helpful in this regard.

The neuroanatomic basis for the relative preservation of subjects' performance with novel objects is at least potentially consistent with the possibility of dorsal system mediation. The superior parietal lobe (areas 5 and/or 7) is spared in five of the eight apraxics. None of the apraxics had lesions involving both areas five and seven. It is thus the case that all of the apraxics had sparing of at least some of the superior parietal architecture. Larger group studies are required to confirm these trends.

Given that several apraxics did have superior parietal involvement, what is the behavioral evidence that the dorsal stream is in fact functioning relatively normally in these subjects? The first line of evidence is that in contrast to their difficulties with evocation of stored representations and with performance of pantomime, the apraxics performed relatively normally in reaching and grasping tasks, in which relevant information is delivered "on line" by visual perception. This pattern of performance doubly dissociates from patients with lesions to dorsal structures (most frequently superior parietal lobule) who exhibit optic ataxia. Optic ataxics are impaired in visually-guided reaching and object-oriented grasping, but are frequently unimpaired in gesture production [22]. The fact that the apraxics did not exhibit disturbances of goal-directed reaching is consistent with integrity of the dorsal system (see [14,16,17,19,22]).

Although admittedly more speculative, an additional line of evidence potentially consistent with apraxics' reliance upon dorsal stream processes are the data from the analyses suggesting relative integrity of production and recognition of prehensile postures. Recent work by Sirigu et al. [1] (in preparation) using 3D kinematic analyses of hand posture supports the contention that non-prehensile hand postures are performed relatively poorly by patients with IM. One possibility, not inconsistent with the "pragmatic" versus "semantic" distinction proposed by Jeannerod [18], is that prehensile hand posture representations are mediated by the dorsal system, which is relatively intact in IM. In contrast, non-prehensile configurations such as poke and palm are exploratory hand postures that are important in object identification. Consequently, they may be relatively closely aligned with ventral systems coding object identity information, and thus localized to neuroanatomic structures inferior to the system representing prehensile postures. A possible locus for the computation of non-prehensile hand posture representations is the inferior parietal lobule.[5]

Non-prehensile, exploratory representations like poke and palm may not be the only postures mediated by the gesture representation system. This system may contain

[5] Milner and Goodale [14] have demonstrated that prehensile postures such as clench and pinch may be used for exploration as well, but that applied force and skin contact area differ when the postures are used for the purpose of grasping versus exploration. Unlike non-prehensile postures, prehensile postures may be redundantly represented in both the dorsal and gesture engram systems and activated differently in different contexts. If so, these two types of prehensile representations could theoretically be differentially damaged by brain lesions.

the features of even prehensile hand postures when these are object-specific, responsive to function, and critical in distinguishing a given posture from others. To return to the example from the apraxic patient of Sirigu et al. [1], cited in Section 1, although a spoon can be grasped with a whole-hand power grip, the precise learned hand posture appropriate to eating with a spoon entails holding the spoon's handle between the forefinger and thumb while it rests along the third knuckle of the middle finger. These attributes of a spoon-hold are likely to be represented in the gesture engram as a range of values across various parameters such as "thumb-forefinger aperture", "finger flexion/extension", etc. Such parameters for finger position and hand configuration are normally activated when the specific "spoon" posture is evoked by the intention to eat with a spoon, and precise values along each parameter are subsequently specified in response to the spatial features of the particular spoon to be used. Our data suggest that in apraxic patients, the damaged memorial parameters for specific finger and hand configurations may be over-ridden by more generic representations of precision and power grip computed in response to object structure.

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Appendix A. Background tests

A.1. Praxis testing

Subjects performed a battery of gestural praxis tasks which included transitive gesture to sight of objects, transitive gesture upon imitation of the examiner (no object present), and gesture with object in hand (Object Use condition). The same 10 gestures (pantomimed use of scissors, watch, razor, fork, comb, toothbrush, bottle opener, eraser, and cigarette lighter) were assessed in each condition. Subjects were asked to "pretend you are actually holding and using (the object)". Subjects also performed five intransitive gestures (wave goodbye, salute, hitchhike, come here, and stop) to command and imitation. Gestures were scored with the system reported in Buxbaum et al. [4] by an experienced coder naive to subjects' identity and background. First, each gesture received a score of 1 or 0 for content. Substitutions of an incorrect (e.g. semantically related) but recognizable gesture were scored 0. Gestures receiving a 1 on the Content scale were scored 0 or 1 on four Spatiotemporal scales: hand Posture, Arm Posture, Amplitude, and Timing. To ascertain that subjects understood the requirement to pantomime the hand posture associated with using the object, the first instance of body part as object (BPO) error (e.g. use of finger as a toothbrush) was corrected, and subjects were permitted a second attempt for that trial. Any subsequent BPO errors resulted in a "0" score for hand Posture. Detailed scoring guidelines are provided in Buxbaum et al. [4]. Due to scheduling constraints, French subjects performed only the gesture to sight of object and intransitive gesture to command tasks.

A.2. Sensory-motor battery: grip strength, dexterity, tactile sensation, proprioception

Manual strength of each hand was assessed by subjective grip test and characterized as either normal or paretic. Manual dexterity was measured with three digit movement tasks: alternating extension and flexion of the first and last digits, crossing and uncrossing of the second and first digits, and thumb-finger sequential touch. The number of repetitions in 10 s was tallied. Tactile sensation was tested with three trials in which a light pinprick was applied to the dorsum of each hand and three trials in which the pinprick was withheld (in randomized order); subjects indicated by yes/no response whether they had felt a touch. There were three measures of proprioception, performed with the subjects' eyes closed: two tasks requiring reproduction with one hand of a position formed by the experimenter with the subject's other hand, and a third task requiring judgments of finger movements in the vertical plane (up or down).

A.3. Grasping objects

Subjects' ability to form an appropriate hand aperture for object grasping was also assessed. Ten of the objects from Study 2 (doorknob, light switch, clothespin, drinking glass, pliers, saltshaker, calculator, apple, lemon, and crayon) were placed on a table top at midline 40 cm from subjects' body wall. Subjects were asked to reach out and grasp each object, once with each hand (when contralesional hand use was possible). Performance was videotaped and each grasp was coded on a 3 point scale by a single coder who was naive as to subjects' identities (2: normal hand aperture for object, 1: clumsy or mildly imprecise, 0: grossly abnormal; includes ineffective grasp, aperture much too narrow or wide). Maximum score was 20 points.

A.4. Gesture recognition

Subjects completed a subtest of the Florida Apraxia Battery [23] which assesses recognition of 30 videotaped transitive gestures. After viewing a gesture performed twice in succession, subjects were shown a choice of three words, one of which denotes the gesture (e.g. "hammering a nail"), one of which is a semantically-related gesture (e.g. "screwing in a screw") and one of which is unrelated. The words were read aloud by the examiner, and the subject was required to select the word corresponding to the seen gesture. Fifteen older control subjects (mean age 54.5, range 40–74) obtained a mean score of 29.3 (range 28–30; S.D. 0.8).

A.5. Static posture imitation

In a task modeled closely after one reported by Goldenberg [24], subjects viewed a videotape of the head and shoulders of an actor, posing on each trial with her left hand in 10 different positions relative to her head (e.g. hand under chin, palm forward; hand beside left ear, etc.). There were 2 trials with each posture, presented in randomized order. Each posture was displayed for 10 s, with a 7 s inter-stimulus interval. Subjects were required to imitate the posture as precisely as possible and were permitted to begin while watching the model.

Goldenberg [24] reported data from 60 healthy control subjects (mean age 54.9, S.D. 14.0) who performed a version of the task with the same static postures we used, presented once to each subject, but scored 2 points for correct performance on the first try and 1 point for correct performance on the second try. Mean Score was 19.7 (S.D. 0.6, range 18–20).

A.6. Moss Object Knowledge Probes Test

Black-and-white photographs of each of the 35 real objects of the experimental tasks of Study 2 were presented singly to brain-lesioned subjects. Subjects were asked to name each object; failing this, they received a single phonemic cue (e.g. hammer → ha, etc.). Objects that were not named correctly even with phonemic cueing were not further assessed. For named objects, three aspects of semantic object knowledge were assessed with a forced-choice format in which two printed words *or* phrases were displayed below each photograph. In the "Function" condition, the two choices referred to possible functions of the stimulus (e.g. tightening, pounding). In the "Manipulation" condition, the forced-choice concerned how the object is held and used (e.g. swung up and down, moved in a circle). In the "Physical" condition, the forced-choice concerned the object's visual or tactile characteristics (e.g. soft or hard); efforts were made to avoid characteristics that could be gleaned directly from the photographs. Conditions were blocked. The printed items were read aloud by the examiner (e.g. "is this object for tightening, or for pounding?") while the subjects examined them, and subjects indicated their choice by pointing response.

Ten healthy older adult control subjects (mean age 64.9 years, range 51–76; mean education 13.6 years, range 11–18) obtained the following scores: function mean 100% correct, S.D. 0%; manipulation mean 100% correct, S.D. 1%, range 97–100%; physical mean 97% correct, S.D. 2%, range 94–100%.

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