Deficits in Movement Planning and Intrinsic Coordinate Control in Ideomotor Apraxia

Steven A. Jax[1,2], Laurel J. Buxbaum[1,3], and Adrienne D. Moll[1]

Abstract

■ Two central issues in the field of motor control are the coordinate frame in which movements are controlled and the distinction between movement planning and online correction. In this study we used these issues to frame several hypotheses about the deficits underlying ideomotor apraxia (IMA). In particular, we examined whether ideomotor apraxics exhibited (1) deficits in movement control in intrinsic (body relative) coordinates with better control in extrinsic (workspace relative) coordinates, (2) deficits in movement planning that are compensated for by an overreliance on online correction, or (3) both deficits. Patients with IMA and two comparison groups performed movement tasks that relied preferentially on either intrinsic or extrinsic coordinate control when online correction was either possible or impossible. Participants performed posture imitation and grasp imitation movements to body- and object-relative end positions in the presence or absence of visual feedback. Consistent with the intrinsic coordinate control hypothesis, patients with IMA showed a significantly greater disparity than the other two groups between movements made to body-relative and object-relative targets as well as between imitation of meaningless postures and grasping. Consistent with the correction overreliance hypothesis, the IMA group was more disrupted than the other groups by the removal of vision. Thus, IMA patients exhibit behavioral patterns consistent with both deficient intrinsic coordinate control and overreliance upon visual feedback. Finally, lesion analysis suggests that damage to the left inferior parietal lobe (Brodmann's areas 39 and 40) may play a key role in both behavioral deficits. ■

INTRODUCTION

One of the central issues in the field of motor control is the coordinate frame in which movements are controlled (for a recent review, see Vindras, Desmurget, & Viviani, 2005). Many theories have proposed that movements are controlled in workspace-specified extrinsic coordinates, such as the spatial vector describing a desired movement's direction and amplitude (Vindras & Viviani, 1998; Gordon, Ghilardi, & Ghez, 1994). These accounts are contrasted with those that propose control in body-specified intrinsic coordinates, such as the shoulder and elbow angles during reaching (Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001). Extensive evidence for both types of control has led to a third group of accounts proposing that control is an interactive process that uses both extrinsic and intrinsic coordinate frames (Van Thiel, Meulenbroek, & Hulstijn, 1998; Kawato, 1996). Although dual coordinate frame accounts can accommodate evidence for control in either coordinate frame, they often lack a clear explanation for the utility of such a strategy. One possibility is that dual coordinate control may allow the motor system to flexibly utilize the most appropriate coordinate frame for a particular task. For example, Ghafouri, Archambault, Adamovich, and Feldman (2002) suggested that movements to stationary targets are controlled in extrinsic coordinates, whereas movement to targets that move along with the body are controlled in intrinsic coordinates.

Additional support for the use of task-specific coordinate frames comes from the pattern of movement deficits exhibited by patients with ideomotor apraxia (IMA). These patients are commonly impaired in pantomiming and imitating object-related actions, such as hammering or sawing, when the object is not present (Buxbaum, Giovannetti, & Libom, 2000; Poizner et al., 1998) but perform more accurately with the object in hand (Goldenberg, Hentze, & Hermsdörfer, 2004; Heilman & Gonzalez Rothi, 1993). Previous explanations of this difference have focused on the additional tactile feedback available when objects are held (Poizner et al., 1998; but see Goldenberg et al., 2004, for conflicting evidence). An alternative, although not mutually exclusive, explanation is that pantomime and imitation without an object are strongly weighted toward intrinsic control (e.g., specifying joint rotations at the shoulder and elbow to make a hammering motion), whereas object-related actions may be more strongly weighted toward extrinsic control (e.g., specifying the trajectory

[1]Moss Rehabilitation Research Institute, Philadelphia, [2]University of Pennsylvania Medical School, [3]Thomas Jefferson University, Philadelphia

of the hammer through space). On this assumption, the pattern of performance in patients with IMA is consistent with deficits in intrinsic coordinate control in the face of relatively intact control in extrinsic coordinates (Buxbaum, 2001; Buxbaum et al., 2000).

Two other findings in IMA are consistent with this intrinsic coordinate control hypothesis. First, patients with IMA commonly exhibit difficulties when imitating meaningless body-related movements, such as placing a horizontally oriented hand below the chin (Goldenberg & Hagmann, 1997; De Renzi, 1985). Like imitation and pantomime without an object in hand, performing meaningless movements requires the specification of a coordinated pattern of joint rotations, an intrinsic coordinate frame control process. Second, patients with IMA exhibit relatively intact grasping of objects (Buxbaum, Johnson-Frey, & Bartlett-Williams, 2005; Hermsdorfer, Ulrich, Marquardt, Goldenberg, & Mai, 1999). In the present account, this task is primarily performed by specifying a spatial vector (an extrinsic coordinate property) between the location of the hand and the location of the object to be grasped. Computational models using this method of control can simulate reaching well (Bullock, Grossberg, & Guenther, 1993; Bullock & Grossberg, 1988).

Although the distinction between intrinsic and extrinsic coordinate frames has been central in the study of movement control, the process of control itself is commonly subdivided into planning and online correction components (Glover, 2004; Elliot, Helson, & Chua, 2001; Woodworth, 1899). Planning is the preparation of a movement plan before movement initiation, and online correction is the adjustment of the movement plan during movement execution. We have recently proposed that IMA may be attributable in part to deficits in planning actions with relatively intact online correction (Buxbaum, Johnson-Frey, et al., 2005). To support this claim, we compared performance on a grasping imagery task, which entailed movement planning, but not correction, to actual grasping, which entailed both planning and correction. The results showed that patients with IMA exhibited abnormal imagined grasping with relatively intact actual grasping. Similar motor imagery deficits have been reported by Sirigu et al. (1996). Additional evidence that patients with IMA have deficits in movement planning but not online correction is that reaching performance deteriorates in IMA patients much more than in controls when online correction is not possible, such as when vision of the arm or object is not available (Laimgruber, Goldenberg, & Hermsdorfer, 2005; Haaland, Harrington, & Knight, 1999; although see Ietswaart, Carey, Della Sala, & Dijkhuizen, 2001, for conflicting results). Thus, not only do IMA patients have relatively intact online correction abilities, they also seem to be overly reliant on them.

The goal of the current study was to jointly test the intrinsic coordinate control and correction overreliance hypotheses by examining how patients with IMA performed on tasks that rely preferentially on either intrinsic or extrinsic coordinate control when online correction was either possible or impossible. Three groups of participants were assessed: patients who had suffered left cerebral vascular accidents (LCVAs) and exhibited IMA (hereafter, the IMA group), patients who had LCVAs without IMA (hereafter, the LCVA group), and neurologically intact age-matched controls (hereafter, the control group). All participants were tested on grasping and meaningless posture imitation tasks. Meaningless, and not meaningful, posture imitation was used because it allowed us to examine the movement production abilities of patients with IMA without the possible influence of damage to stored gesture representations (Goldenberg & Hagmann, 1997). For both tasks we manipulated how movement end positions were defined. Half of the movements were made to end positions defined by an object in the environment (e.g., grasping a bottle; producing a stop hand posture above a pair of scissors), and the other half were made to end positions defined by the participant's body (e.g., grasping the earlobe, producing a stop hand posture to the left of the left ear). All four movement types (object-relative posture, object-relative grasp, body-relative posture, body-relative grasp) were tested with and without visual feedback, thus manipulating the possibility of online correction.

Given that IMA patients exhibit particular deficits in the production of accurate hand postures relative to other movement components (Buxbaum, Kyle, Grossman, & Coslett, in press; Buxbaum, Sirigu, Schwartz, & Klatzky, 2003; Sirigu et al., 1996), movement production was measured by using four hand-related subcomponents. Two of the components (hand configuration and wrist angle) were putatively specified in an intrinsic coordinate frame, whereas the other two (orientation of the hand in space and location of the hand) were putatively specified in an extrinsic coordinate frame. Finally, to ensure that deficits on these tasks could be ascribed to movement control processes and not more elementary deficits in perception or working memory, we included a movement perceptual matching task that had no movement production component.

We derived several predictions from each hypothesis. The intrinsic coordinate control hypothesis predicts that the IMA group (as compared to the control and LCVA groups) would be (1) less accurate on posture imitation than grasp imitation due to the relative reliance on intrinsic control during posture imitation, (2) less accurate on body-directed than object-directed movements due to the relative reliance on extrinsic control for object-directed movements,[1] (3) more impaired in movement components specified in intrinsic than extrinsic coordinates, and (4) unaffected by the removal of vision during movement production.

The correction overreliance hypothesis, in contrast, predicts that the IMA group (as compared to the control

and LCVA groups) would be (1) equally good at grasp and posture imitation, (2) equally good at movements made to body-relative and object-relative end positions, (3) equally good at all movement components, and (4) more negatively affected by the removal of vision. Clearly, the two hypotheses described above are not mutually exclusive, and thus a final possibility is that both hypotheses are correct, which would predict effects of all the factors examined.

Previous studies indicate that IMA most often results from damage to the left inferior parietal lobule (IPL; Brodmann's areas [BAs] 39 and 40; Buxbaum, Johnson-Frey, et al., 2005; Buxbaum, 2001; Haaland, Harrington, & Knight, 2000; Heilman, Gonzalez Rothi, & Valenstein, 1982). However, it has also been reported to result from damage to the left middle frontal gyrus (BAs 6, 8, 9, and 46; Haaland et al., 2000) as well as the superior parietal lobes (BAs 5 and 7), which may be especially important for action production but not action recognition (Buxbaum et al., 2000; Rapcsak, Ochipa, Anderson, & Poizner, 1995; Heilman, Gonzales Rothi, Mack, Feinberg, & Watson, 1986). In addition to areas that are commonly damaged in IMA, neuroimaging studies have identified the importance of the inferior prefrontal cortex (BAs 44 and 45) in action production during imitation (Iacoboni, 2005; Johnson-Frey et al., 2003). Guided by this work, we examined which, if any, of these regions were significantly associated with movement production deficits on the tasks used in the present experiment.

METHODS

Participants

Eleven post-acute LCVA patients with IMA, four post-acute LCVA patients without IMA, and six neurologically intact participants completed the experiment. All participants were right-handed. IMA was diagnosed by averaging scores on 10 trials of pantomime to sight of object and 10 trials of meaningless posture imitation, all of which were performed using the left arm. Each trial was scored on four movement components (hand posture, arm posture, amplitude, and timing), each of which could be scored correct or incorrect (see Buxbaum et al., 2000, for details of the scoring criteria). On these tasks, all patients in the IMA group scored two standard deviations or more below the mean of a group of 10 age-matched controls (see Buxbaum, Kyle, & Menon, 2005, for details). Scores on these tests for both the IMA and LCVA groups of the present study, along with other participant information, are shown in Table 1. Using single-factor analyses of variance (ANOVAs), we found that the three groups did not differ in age ($p = .48$) or education ($p = .13$), and the IMA and LCVA groups did not differ in the time since stroke onset ($p = .94$) or lesion volume ($p = .20$). All participants consented to the study in accordance with the guidelines of Albert Einstein Medical Center Institutional Review Board and were paid for their participation.

Materials, Design, and Procedure

Movement Production Tasks

In the movement production tasks, participants imitated movements made to static end positions using their left arms. Ten different movements from each of the four possible production conditions (object-relative posture, object-relative grasp, body-relative posture, body-relative grasp) were used. The postures used were similar to those used by Goldenberg and Hagmann (1997), and the objects used to define the end positions were common objects (mug, pen, bottle, etc.). The movements to be imitated were presented by using video clips displayed on a computer screen located approximately 100 cm in front of the participant. Each video clip was approximately 3.5 sec long and was presented twice with a 1-sec delay between clips. Because the participants' ability to reproduce the final position was of primary interest in the study, each clip was created so that the final position was maintained for 2.5 sec in all videos.

For all four movement production conditions, there were three different movement initiation conditions. The first initiation condition permitted participants to initiate movements as they watched the video clips (immediate initiation). A second and third condition were used to directly compare movement production with and without possible online correction. In the second condition, where online correction was not possible, participants were blindfolded at the conclusion of the second video, and responded when they heard a tone that sounded 5 sec after the end of the second video (delayed blindfolded initiation). The third condition, which served as a control for the delay aspect of the second condition required to position the blindfold, was identical to the delayed blindfolded condition except that subjects were not blindfolded (delayed initiation). Each participant completed 10 trials in each of the 12 conditions: 3 (initiation levels) $\times$ 2 (movement tasks) $\times$ 2 (end positions). The initiation factor was blocked and counterbalanced across participants; movement task and end position factors were randomized within blocks.

If participants made any observable movements before the tone in either the delayed or delayed blindfolded conditions, the experimenter reminded the participant to wait for the tone. Trials in which this occurred (<7% of trials) were rerun at the end of the block. To ensure they understood the task, participants were given two practice trials the first time they were tested in each of the three initiation conditions, during which they were given feedback about their performance. All practice

Table 1. Participant Information

Group	*Subject*	*Sex*	*Age*	*Education (years)*	*Months Poststroke*	*Pantomime to Sight of Object (%)*	*Meaningless Imitation (%)*	*Lesion Volume (mm^3)*
IMA	I1	M	61	16	81	55.0	47.5	148,831
	I2	F	70	12	47	72.5	65.0	8,501
	I3	M	82	11	51	60.0	50.0	40,902
	I4	M	53	9	19	87.5	75.0	32,695
	I5	M	62	12	165	77.8	72.5	146,472
	I6	F	59	12	22	80.0	82.5	[a]
	I7	M	72	8	156	87.5	65.0	269,930
	I8	M	61	9	32	87.5	65.0	101,058
	I9	M	62	12	11	75.0	72.5	14,871
	I10	F	51	16	76	82.1	65.0	95,940
	I11	M	59	18	60	70.0	75.0	266,061
Mean			62.9	12.3	65.5	75.9	66.8	112,526
SD			8.8	3.2	52.1	11.0	10.6	96,082
LCVA	L1	M	67	11	120	95.0	90.0	137,337
	L2	M	54	10	51	95.0	95.0	7,927
	L3	M	57	14	9	92.5	95.0	12,760
	L4	F	47	13	91	97.5	95.0	11,790
Mean			56.3	12.0	67.7	95.0	93.8	42,453
SD			8.3	1.8	48.5	2.0	2.5	63,290
Control	C1	F	48	16				
	C2	F	74	16				
	C3	M	74	13				
	C4	F	55	13				
	C5	F	58	16				
	C6	F	62	16				
Mean			61.8	15.0		90.9[b]	94.3[b]	
SD			10.5	1.6		5.5[b]	4.7[b]	

[a]Subject was excluded from lesion analysis, see Footnote 3.

[b]Data reported for 10 previously tested age-matched controls used to identify apraxia in the current study (from Buxbaum et al., 2005).

trials used movements that were not used in the later experimental trials.

Movement Matching Task

In the movement matching task, participants watched a pair of short video clips, each showing an actor making a movement. The two clips were presented sequentially with 1 sec of blank screen between them. Immediately after the presentation of the second clip, the screen was again blanked and the experimenter asked the participant if the movements in the clips were the same or different. The participants' task was to verbally respond to this question. If patients had difficulties making verbal responses, the experimenter had them point to a sheet of paper with two boxes, one labeled ''yes'' (indicating the clips were the same) and one labeled ''no'' (indicating the clips were different). In the event that no response was given within 5 sec, the experimenter encouraged the participant to make a guess.

Forty pairs of matching task clips were used. One of the clips within the pair was taken from the 40 clips used in the movement production tasks described above. In half of the second clips, the same actor produced the same movement a second time (''same'' trials). In the other half of the clips, the actor produced a slightly different movement (''different'' trials). In the matching trials of the grasp task, the movement in the ''different'' clip required the same final hand configuration but grasped the target (the object in the object-relative end positions or the body part in the body-relative end positions) in a different location. For example, if the first clip required a grasp of the center of a telephone headset, the second clip required a grasp of the end of the headset. In the matching trials of the posture task, the movement in the ''different'' clip required the same final hand location but a different hand posture. For example, if the first clip required the production of a stop hand posture above a telephone headset, the second clip required a hand posture ending above the phone but with the fingers together and pointing to the right with the palm facing the participant's body (using the left hand).

Scoring Criteria for Movement Production Trials

A videotape of each participant's performance was analyzed, and the final hand posture on each movement production trial was scored on four components: hand configuration, wrist angle, hand orientation, and hand location. Each of the four components could be scored as correct (1) or incorrect (0). The hand configuration component was scored as correct if the hand was correctly configured or not flagrantly misconfigured (e.g., fingers were slightly spread when the target hand configuration required all fingers be pressed tightly together). The wrist angle component was scored as correct if the hand would have to be rotated less than a total of 30° along any of the wrist's axes to be correct. The hand orientation component was scored as correct

Figure 1. Examples of performance by patients in the IMA group. (A) and (D) illustrate the target actions for the body-relative posture task and object-relative grasp task, respectively. (B) Exemplifies the deficits of IMA patients on the body-relative posture task (the task which putatively relied most strongly on intrinsic coordinate control), even when online correction was possible (black covering over face added during figure preparation to mask the patient's identity). (E) Exemplifies accurate performance on the object-relative grasp task when online correction was possible (the task that putatively relied most strongly on extrinsic control). Accuracy was reduced without online correction as compared to when online correction was possible for both the body-relative posture (C) and object-relative grasp tasks (F).

if the orientation of the hand posture could be made correct with a rotation of less than 30°. The hand location component was scored as correct if the center of the hand would be in the correct end location with a movement that was less than 30% of the length of the target body part or object. Two different coders independently scored the movements from three participants, and the percent agreement between coders for each of the four criteria was high (94% agreement or higher for all four criteria).

Lesion Analysis

Lesions were segmented by an experienced research team member under the supervision of a neurologist (who was blind to the behavioral data) using the MRIcro image analysis program (www.psychology.nottingham.ac.uk/staff/cr1/mricro.html). Reliability in lesion segmentation across team members was established by using a method devised by Fiez, Damasio, and Grabowski (2000). All team members achieved reliability comparable to or better than that of Fiez et al. (2000) on three measures: percent volume difference (7.99%), percent discrepant voxels (4.18%), and percent nonoverlapping voxels (31.5%). After the lesions were segmented, proportion of damage to Brodmann's areas was calculated by using Brodmann maps included in the MRIcro program, which were based on the templates developed by Damasio and Damasio (1989). The proportion of damage to larger regions of interest were computed as the average damage to the region's component Brodmann's areas (e.g., BAs 39 and 40 for the IPL), weighted by the number of voxels in each area.

RESULTS

All effects of interest were assessed with mixed-factor ANOVAs, where all factors were manipulated within participants except the group factor (control, LCVA, or IMA). When required, post hoc comparisons were performed using Bonferroni-corrected *t* tests.

Movement Production with Online Correction

We first assessed the predictions relevant to movement production with full vision (immediate initiation condition), in which online correction was possible. Analyses focused on the effects of Movement Task (grasp or posture) and End Position (object relative or body relative). Examples of performance by patients in the IMA group in this condition are shown in the middle column of Figure 1.

Mean Score

We first examined the mean scores (average of the four component scores) for all movement production tasks (Figure 2). There was a main effect of Group, $F(2,18) = 14.00$, $p < .001$, with mean scores being lower for the IMA group than the control ($p < .001$) and LCVA ($p = .005$) groups, which did not differ from one another ($p = .69$). In addition to the main effect of Group, there was a main effect of End Position, $F(1,18) = 38.42$, $p < .001$, and an interaction between Group and End Position, $F(2,18) = 5.26$, $p = .016$. Although all three groups had lower scores on body-relative end positions than object-relative end positions ($p \leq .042$), the differ-

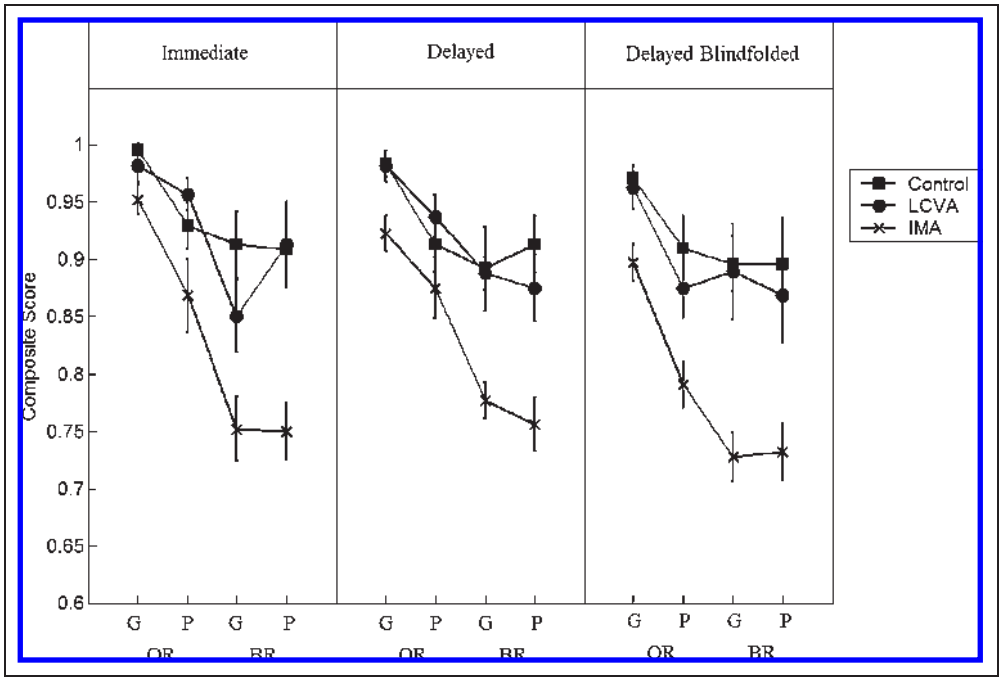

Figure 2. Mean scores (±1 *SE*) for all movement production tasks. Separate panels are used for the immediate, delayed, and delayed blindfolded conditions. Within each panel, data are plotted separately for the grasp (G) and posture (P) imitation movements made to object-relative (OR) and body-relative (BR) end positions.

ence between the end positions was larger in the IMA group (.75 vs. .91) than the LCVA (.88 vs. .97, $p = .048$) and control (.91 vs. .96, $p = .018$) groups, which did not differ ($p = .43$). Finally, there was an interaction between Movement Task and End Position, $F(1,18) = 11.35$, $p = .003$, in which there was an effect of Movement Task (posture < grasp) for object-relative end positions ($p = .002$), but not for body-relative end positions ($p = .40$). All other remaining effects were not reliable ($p \geq .20$).

Component Scores

Next, we examined how the individual components (hand configuration, wrist angle, hand orientation, hand location) contributed to the effects reported for the mean scores. To do so, we repeated the mean score analysis separately for each of the four component scores. For conciseness, we will focus on the significant effects of Group and the interactions between Group and other factors in these ANOVAs, which are plotted in Figure 3.

Main effects of Group (Figure 3A) were observed for all components ($p \leq .02$) except the hand configuration component, which did not reach significance ($p = .13$). For the three components with main effects of Group, the IMA group had lower scores than the LCVA ($p \leq .037$) and control groups ($p \leq .011$), which did not differ ($p = .21$).

Finally, although no interaction between Group and Movement Task had been observed for the mean score analysis reported earlier, this interaction was significant for the wrist angle component, $p = .017$ (Figure 3B). An effect of Movement Task was observed for the IMA, $p < .001$, and control, $p = .01$, groups, with the magnitude of the difference between posture and grasp tasks being greater for the IMA group (.85 vs. .96) than the control (.95 vs. .99) group ($p = .045$).

Movement Production without Online Correction

Next, we assessed the predictions relevant to movement production without visual feedback (delayed blindfolded

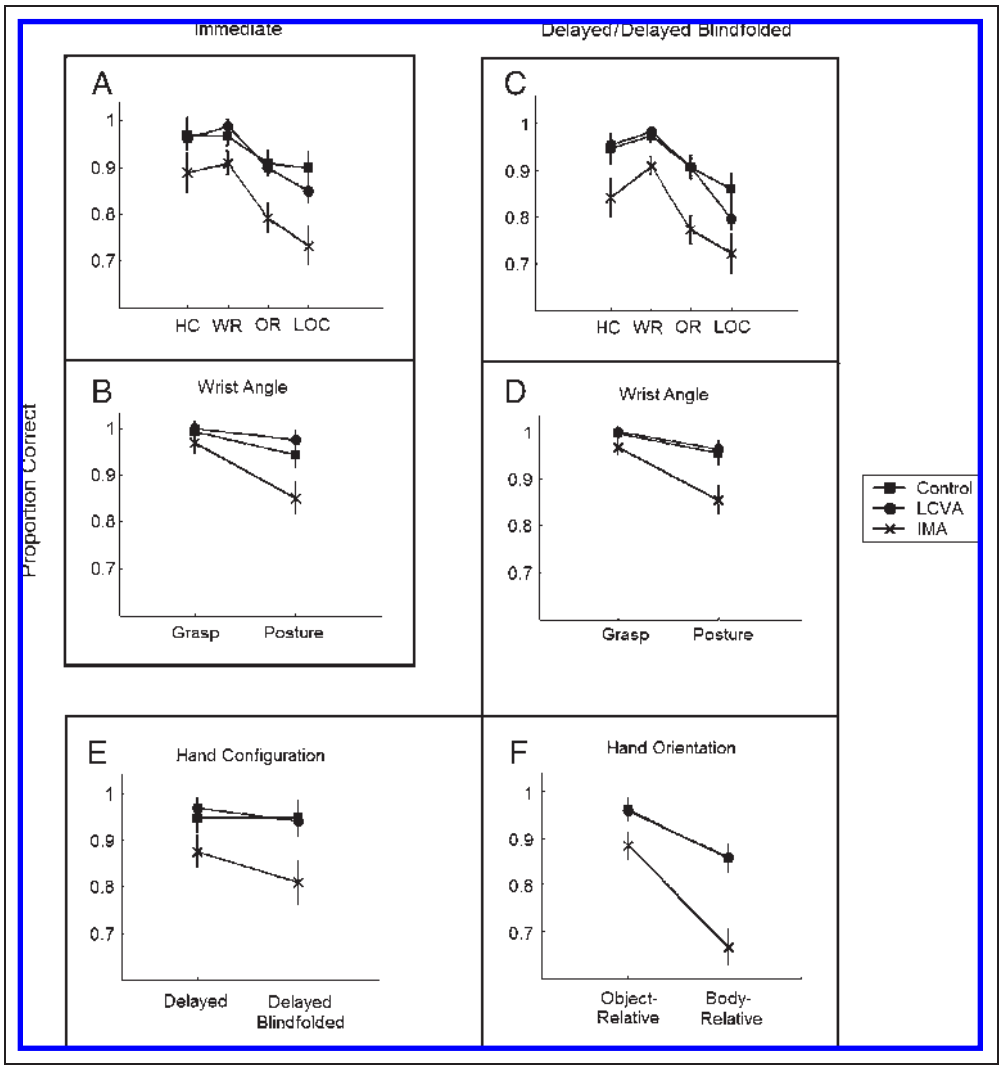

Figure 3. Mean scores (±1 *SE*) for the significant effects of the component score analyses of the immediate (A–B) and delayed/delayed blindfolded (C–F) conditions. (A, C) Main effects of group for the hand configuration (HC), wrist angle (WR), hand orientation (OR), and hand location (LOC). (B, D) Interaction between group and movement task for the wrist angle component. (E) Interaction between group and initiation for the hand configuration component. (F) Interaction between group and end position for the hand orientation component.

initiation condition), in which online correction was impossible. Example movements made by IMA patients in this condition are shown in the right column of Figure 1. The delayed blindfolded initiation condition was compared to a second condition (delayed initiation condition) in which online correction was possible and, unlike the immediate imitation condition, controlled for the delay aspect required to position the blindfold.[2] Analyses focused on the effects of Initiation (delayed or delayed blindfolded), Movement Task (grasp or posture), and End Position (object relative or body relative).

Mean Score

As was observed in the immediate initiation condition, there was a main effect of Group on mean scores, $F(2,18) = 22.86$, $p < .001$, with the IMA group having lower scores than the control ($p < .001$) and LCVA ($p = .001$) groups, which did not differ from one another ($p = .56$; see Figure 2).

In addition to the main effect of Group, there was a main effect of Initiation, $F(1,18) = 13.24$, $p = .002$, and an interaction between Group and Initiation, $F(2,18) = 4.13$, $p = .03$. Effects of Initiation were only observed for the IMA group, with scores being lower in the delayed blindfolded than the delayed initiation condition (.78 vs. .83, $p < .001$).

Replicating the results in the immediate initiation condition, there was a main effect of End Position, $F(1, 18) = 55.77$, $p < .001$, and an interaction between Group and End Position, $F(2, 18) = 8.36$, $p = .003$. Although all three groups had lower mean scores for body-relative than object-relative end positions, this difference was larger in the IMA group (.74 vs. .87) than the LCVA (.88 vs. .94, $p = .04$) and control groups (.90 vs. .94, $p = .009$), which did not differ ($p = .52$).

Finally, there was a main effect of Movement Task, $F(1, 18) = 14.01$, $p = .001$, and an interaction between Movement Task and End Position, $F(1, 18) = 16.86$, $p < .001$, with effects of Movement Task being observed for object-relative end positions, $p < .001$, but not for body-relative end positions, $p = .40$. All other remaining effects were not reliable, $p \geq .225$.

Component Scores

As was done for the immediate initiation condition, we repeated the mean score analysis separately for each of the four component scores. Again, we will focus on the significant effects of Group and the interactions between Group and other factors in these ANOVAs, which are shown in Figure 3.

Main effects of group were observed for all components ($p \leq .016$; Figure 3D). For each of the components, the IMA group had lower scores than the LCVA ($p \leq .045$) and control ($p \leq .041$) groups, which did not differ ($p = .65$).

As in the analyses for the immediate condition, although no interaction between Group and Movement Task had been observed for the mean score, this interaction was significant for the wrist angle component ($p = .02$; Figure 3D). Effect of Movement Task were only observed for the IMA group ($p < .001$) and control ($p = .04$) groups. However, the magnitude of difference between Posture and Grasp was greater ($p = .005$) for the IMA group (.87 vs. .95) than the control (.96 vs. .99) group.

The interaction between Group and Initiation was only significant for the hand configuration component ($p = .04$; Figure 3E). Effects of Initiation were only observed for the IMA group ($p = .001$), with hand configuration scores being lower in the delayed blindfolded than the delayed initiation condition (.80 vs. .87).

The interaction between Group and End Position was only significant for the hand orientation component ($p = .018$; Figure 3F). Although hand orientation scores were lower for body-relative than object-relative end positions in all groups, the difference was larger for the IMA group (.66 vs. .88) than the LCVA (.86 vs. .96, $p = .033$) and control (.85 vs. .96, $p = .042$) groups, which did not differ ($p = .86$).

Movement Matching

Results of the movement matching task are shown in Figure 4. Overall, all participants performed quite accu-

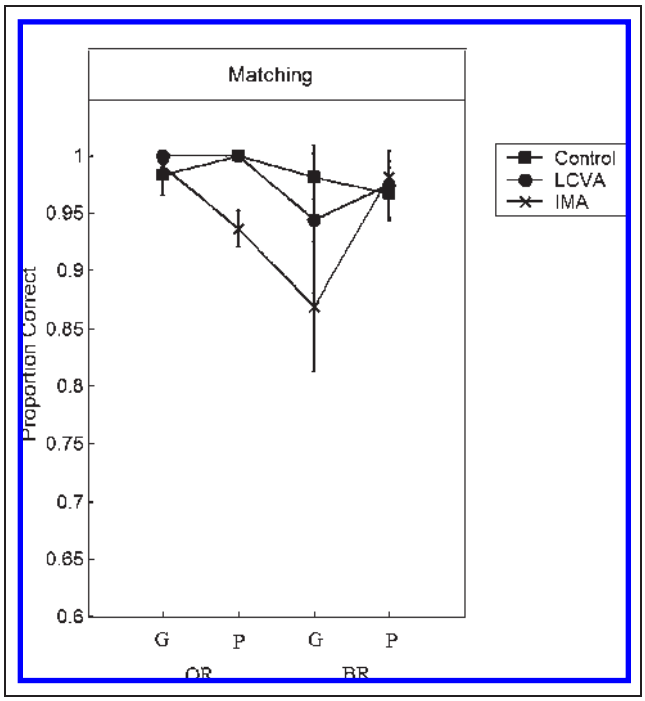

Figure 4. Mean proportion correct (±1 *SE*) for all movement matching tasks. Data are plotted separately for the grasp (G) and posture (P) video clips showing movements made to object-relative (OR) and body-relative (BR) end positions.

rately on this task. The results of a 3 (group: control, LCVA, or IMA) × 2 (Movement Task: grasp or posture) × 2 (End Position: object-relative or body-relative) ANOVA showed that the only reliable effect was a main effect of End Position, $F(1,18) = 4.43$, $p = .05$, with accuracy on matching body-relative movements being lower than object-relative movements (.95 vs. .99). The main effect of Group was not reliable, $F(2,18) = 2.28$, $p = .131$, nor were any interactions between Group and the other factors ($p = .21$).

Lesion Analysis

Finally, we explored the neuroanatomic substrates of patients' movement production deficits in two ways. First, we compared lesions in the IMA and LCVA groups to assess whether IMA in the present group could be ascribed to lesions similar to those previously reported (Buxbaum, Johnson-Frey, et al., 2005; Buxbaum, 2001; Haaland et al., 2000). Second, we compared lesion loci of high and low performers on the experimental task to explore the neuroanatomic structures mediating successful performance. Given the reliable behavioral differences between the IMA and LCVA groups, the two analyses would not be predicted to be vastly different. However, the second analysis allowed us to examine which neural structures were most strongly relied upon to successfully perform the imitation tasks we used.

Comparison of IMA and LCVA Groups

The left side of Figure 5 displays a lesion subtraction analysis comparing the IMA[3] and LCVA groups. Consistent with previous studies, IMA was associated with damage to the IPL (BAs 39 and 40) and portions of the middle frontal gyrus (BAs 6 and 46). In addition to these previously reported areas, damage to both cortical and subcortical areas of the superior temporal lobes (BAs 22, 41, and 42) was more common in the IMA group than the LCVA group. The preceding lesion subtraction analyses were confirmed statistically by comparing the average proportion of damage in the IMA and LCVA groups in the four a priori defined regions reviewed in the Introduction: (1) the superior parietal lobule, BAs 5 and 7, (2) the middle frontal gyrus, BAs 6, 8, 9, and 46, (3) the inferior prefrontal cortex, BAs 44 and 45, and (4) the IPL, BAs 39 and 40. Using a nonparametric hypothesis test,[4] we found that only in the IPL was damage significantly more extensive in the IMA group than the LCVA group (.42 vs. .08, $p = .021$; $p \geq .21$ for the other three regions). In addition to the a priori defined regions, damage to the superior temporal gyrus (BAs 22, 41, and 42) was greater in the IMA group than the LCVA group (.44 vs. .10, $p = .034$).

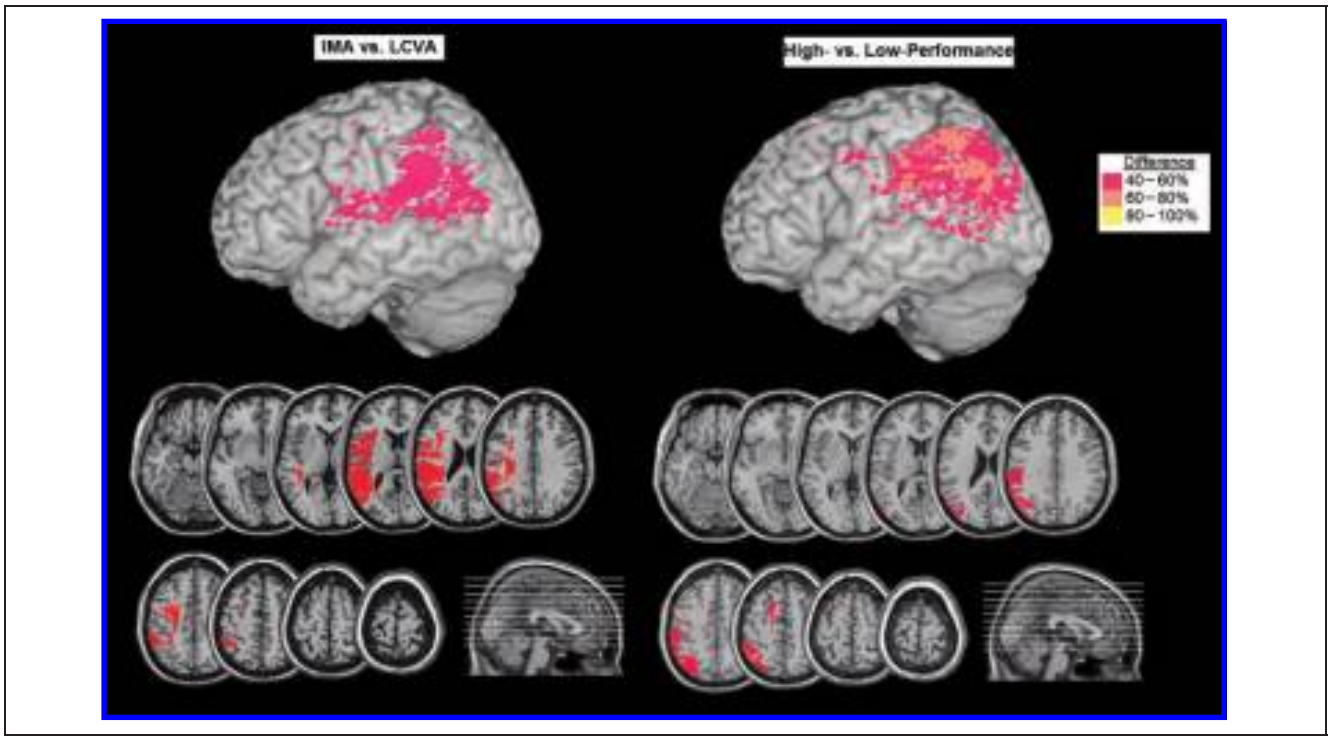

Figure 5. Results of lesion subtraction analysis comparing the IMA and LCVA groups (left) as well as the groups with low and high movement production scores (right). Colored voxels indicate areas where the percentage of participants with damage to a given voxel was greater in the IMA than LCVA group (left) or low-performance than high-performance group (right). For clarity, we only plot voxels where the percentage difference was between 40% and 60% (red), 60% and 80% (orange), and 80% to 100% (yellow).

Comparison of High- and Low-performing Groups

To examine the lesions associated with performance on the present tasks, we first examined whether lesion volume was predictive of overall performance. It was not ($r = -.19$, $p = .52$). Next, we classified all patients in the IMA and LCVA groups as exhibiting high or low production performance by using a permutation statistical approach (Goode, 2005). To do so, we first rank ordered all participants on their mean movement production across all tasks.[5] Next, we simulated dividing the patients into two groups along multiple points in the ranking (e.g., between the fourth and fifth best performing participants, between the fifth and sixth best performing participants, etc.), with the restriction that at least five patients be in a group. Finally, we determined which dividing point led to the greatest difference in behavioral scores across groups, as measured by the independent-sample t statistic.

The grouping resulted in a low-performing group ($n = 5$) consisting of the five lowest performing IMA patients and a high-performing group ($n = 9$) consisting of the remaining five IMA[3] patients and all four of the LCVAs. The difference between mean performance in these two groups was highly significant (.79 vs. .89, $p = .0002$). Finally, we used a lesion subtraction analysis to compare the lesion loci for patients in the high- and low-performing groups. As shown in Figure 5 (right), the IPL (BAs 39 and 40) most strongly differentiated the two performance groups. There was a small region within BA 40 in which the difference between the proportion damage in the two groups was between 80% and 100%. In addition to the IPL, damage to smaller regions of the premotor area (BA 6), primary sensory cortex (BA 2), superior parietal lobe (BA 7), posterior–inferior portion of the temporal lobe (BA 37), and anterior occipital lobe (BA 19) also showed differences between the two groups, although these difference were usually weaker (40–60% difference between groups).

Results of the lesion subtraction analysis were confirmed statistically by using a nonparametric hypothesis test[4] with the four a priori regions of interest as described earlier. Only in the IPL was the proportion of damage significantly more extensive in the low-performing group than the high-performing group (.50 vs. .19, $p = .049$). Damage to the other three areas, as well as all other Brodmann's areas, was not reliably different between the two groups ($p \geq .17$).

DISCUSSION

In this study we used two central issues in the study of motor control to frame a set of predictions about patients with IMA. IMA patients and two comparison groups performed grasp imitation and posture imitation movements to object- and body-relative end positions in the presence or absence of visual feedback. The intrinsic coordinate control account predicted that IMA patients would be more deficient in movements to body-relative end positions than object-relative end positions, more deficient with postures than grasping, more deficient on intrinsic coordinate frame movement components than extrinsic coordinate frame components, and show no effects of removal of vision. The correction-overreliance hypothesis predicted no end position, task, or movement component effects, but predicted that IMA patients would be disproportionately disrupted by the removal of visual feedback.

Several results deserve emphasis. First, patients with IMA showed a significantly greater disparity than the other two groups between movements made to body-relative and object-relative targets. Second, patients with IMA showed a greater disparity than the other groups between imitation of meaningless postures and grasping, as revealed in the wrist angle score. Third, both of these findings were observed whether or not online correction was possible. Fourth, the IMA group showed deficits in both intrinsic (hand configuration, wrist angle) and extrinsic (hand orientation, location) coordinate-frame movement components. Fifth, IMA patients were more disrupted than the other groups by the removal of vision. Sixth, the removal of visual feedback did not differentially affect tasks predicted to rely on intrinsic coordinate control (posture task, body-relative end positions) as compared to tasks predicted to rely on extrinsic coordinate control (grasp task, object-relative end positions). Finally, the results of the movement matching task, with no movement production component, showed that the deficits in movement production could not be explained by more elementary deficits in perception or working memory.

In summary, the pattern of results was not strongly predicted by either account under consideration to the exclusion of the other. IMA patients exhibit behavioral patterns consistent with *both* deficient intrinsic coordinate control and overreliance upon visual feedback. There are at least three possible explanations for these results. The first is that deficits in intrinsic coordinate-frame control and abnormal reliance on visual feedback are two independent deficits that sum to produce the observed behavioral pattern in IMA.

A second, more parsimonious, explanation is that preplanned and visual-feedback-informed aspects of movements preferentially rely on intrinsic and extrinsic coordinate control, respectively. For example, a grasping movement's hand configuration may be planned largely in intrinsic coordinates (e.g., a time-varying sequence of joint angles of the fingers and thumb), with correction at the end of the movement being more strongly specified in extrinsic coordinates (e.g., how the distance between the thumb and fingers compares with the size of the to-be-grasped object). On this hypothesis, IMA patients may compensate for deficient intrinsic coordinate control during planning with relative

reliance on intact extrinsic coordinate control during the correction phase.

The claim that visual-feedback-informed aspects of movements preferentially rely on extrinsic coordinate control is supported by data from neurologically intact individuals. For example, Newport, Rabb, and Jackson (2002) asked participants to match the orientation of two handheld bars in either extrinsic coordinates (make the bars parallel) or intrinsic coordinates (make the bars mirror images of one another, achieved by adopting similar configurations of the two arms). In both conditions, vision of the arms and bars was obscured by a barrier, and the participants' eyes were either open or covered with a blindfold. Even though vision provided no task-relevant information, participants were more accurate in the extrinsic task, but not the intrinsic task, with eyes open than when blindfolded. These results suggest that vision of the environment favors the representation of spatial relationships in extrinsic coordinates.

The claim that movement planning is accomplished primarily in intrinsic coordinates is less clearly supported. On the one hand, data supporting this claim were provided by Rosenbaum, Meulenbroek, and Vaughan (1999), who asked participants to make bimanual movements without visual feedback. When successive movements to the same spatial location were performed with different arms, analysis of the spatial errors indicated that the motor system transferred final arm configuration information (an intrinsic property), but not final spatial location information (an extrinsic property), across arms. This study, along with others (Jaric, Corcos, Gottlieb, Ilic, & Latash, 1994; Jaric, Corcos, & Latash, 1992; Martinuk & Roy, 1972), has been used to support models of motor control that plan movement in intrinsic coordinates (Rosenbaum et al., 2001; Feldman, 1986; Polit & Bizzi, 1978).

Other studies, however, suggest planning is at least sometimes accomplished in extrinsic coordinates. For example, Wang and Sainburg (2005) showed that generalization from learning a visuomotor rotation task occurs in extrinsic coordinates. In this study, a 30° directional rotation was introduced between a visually presented target and the movement to reach to that target. Generalization from training to later novel movements involved a remapping between the target and movement vectors (extrinsic coordinate properties) and not a remapping between the visual target location and the final arm posture (an intrinsic coordinate property). Similar conclusions about extrinsic coordinate planning have been drawn using other methodologies (e.g., Vindras et al., 2005; Krakauer, Pine, Ghilardi, & Ghez, 2000; Vindras & Viviani, 1998; Gordon et al., 1994; Rosenbaum, 1980).

These conflicting results suggest the need to expand our second explanation of the deficits in IMA to include planning in both intrinsic and extrinsic coordinate frames. Thus, IMA patients may have deficits in planning in both coordinate frames, with deficits in intrinsic planning being greater than deficits in extrinsic planning, along with intact online correction (which may occur primarily in extrinsic coordinates; Newport et al., 2002). This account has the merit of accommodating the persistent superiority of movements to object-relative as compared to body-relative end positions even in conditions that are highly reliant on planning (e.g., the delayed blindfolded conditions), something the previous explanation can not do. Directly testing these three explanations will be a challenge for future research.

Although deficits in intrinsic coordinate control with relatively intact extrinsic coordinate control (which may be preferentially used for online correction) can account for many of the behavioral patterns in IMA, several caveats are in order. First, the present results are based on a small sample of apraxic patients. Even though all of the critical main effects and interactions were significant, indicating that there was sufficient experimental power despite the small sample size, replication of the results are needed. Second, the proposal that apraxics have deficits in intrinsic coordinate control does not exclude additional deficits in some patients. For example, it is unclear how this hypothesis could account for the commonly observed difference between transitive (object related) and intransitive (symbolic) pantomime and imitation (Foundas et al., 1999; Haaland & Flaherty, 1984) without additional assumptions, namely, that transitive pantomime requires either more intrinsic control or allows for less online correction than does intransitive pantomime. This account also does not explain the deficits of many IMA patients in recognition of skilled movements (Gonzales Rothi, Ochipa, & Heilman, 1991). Such recognition deficits are usually ascribed to damage to or deficient access to stored representations of movements. (The intact performance on the movement matching task need not be inconsistent with these previous studies of movement recognition in apraxia because these stored representations are probably longer lasting than the short-term representations in working memory used to compare two meaningless movements separated by a delay.) It is clear that IMA is a complex syndrome, and it is unlikely that the entire behavioral profile of most patients can be explained without invoking several factors.

Finally, we reported two lesion analyses showing that damage to the IPL was associated with both IMA as well as poor performance on the present tasks. This result is consistent with previous studies of IMA (Buxbaum, Johnson-Frey, et al., 2005; Buxbaum, 2001; Haaland et al., 2000; Heilman et al., 1982) as well as a recent theory of motor control that postulates that movement planning and online corrections are subserved by the inferior and superior parietal lobules, respectively (Glover, 2004). The performance-based lesion analysis also suggests that the left IPL may be critical for intrinsic coordinate control. Additional studies will be required to confirm or

disconfirm this hypothesis. However, it is of note that several recent studies using functional magnetic resonance imaging (fMRI) (Parsons et al., 1995) and cognitive neuropsychological approaches (Schwoebel & Coslett, 2005; Schwoebel, Buxbaum, & Coslett, 2004) indicate the importance of the left IPL for body representation. Thus, the perceptual-motor system's representations of the body (e.g., the ''body schema'') may plausibly be related to intrinsic control processes.

In addition to IPL damage, we also observed significantly more damage to the left superior temporal lobe in the IMA group than the LCVA group (although damage to this area was not different in the second, performance-based lesion analysis). Even though reports of damage to the left superior temporal lobe have not been common in IMA, numerous neuroimaging studies have found significant activations in this area during movement planning (Johnson-Frey, Newman-Norlund, & Grafton, 2005; Gerardin et al., 2000), imitation of novel gestures (Rumiati et al., 2005; Peigneux et al., 2004), and perception of biological motion (Decety & Grezes, 1999), three functions that would be required to perform tasks that are often deficient in IMA. Thus, damage to the superior temporal lobe may contribute more to the deficits in IMA than previously thought. However, a second explanation for this result is that proximity of the IPL and superior temporal lobes leads to a high probability of co-occurring damage in both areas. Therefore, the superior temporal lobe may not play a functional role in IMA. Additional investigation with larger samples of patients may shed additional light on the substrates of action imitation (see Buxbaum, Kyle, et al., 2005).

In summary, we have presented evidence that patients with IMA have deficits in intrinsic coordinate frame control as well as an overreliance on visual feedback. The precise relationship between the two deficits is unclear and awaits further development. However, some combination of these deficits can account for many of the core behavioral features of IMA, including differences between pantomime and imitation with and without objects in hand, deficits in meaningless posture imitation, differences between imagined and actual grasping, and differences between grasping with and without visual feedback. Finally, results of lesion analysis suggest that damage to the left inferior parietal lobe (BAs 39 and 40) plays a key role in both deficits.

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Reprint requests should be sent to Laurel J. Buxbaum, Moss Rehabilitation Research Institute, Korman Building 213, 1200 W. Tabor Road, Philadelphia, PA 19141, or via e-mail: lbuxbaum@einstein.edu.

Notes

1. One previous study (Hermsdorfer, Blankenfeld, & Goldenberg, 2003) compared a reaching movement to the nose to reaching movements to objects in the environment and found no obvious difference between the two movement types. Critically, the authors tested only one body-directed movement, and therefore any conclusions drawn from this null result should be taken cautiously.
2. Although direct comparisons between the immediate and delayed blindfolded conditions were not appropriate (because they differed in both the presence of visual feedback and the delay between stimulus presentation and movement initiation), it is noteworthy that the introduction of the delay did not change production performance relative to the immediate initiation condition. This was confirmed using a 3 (Group: control, LCVA, or IMA) $\times$ 2 (Initiation: immediate or delayed) $\times$ 2 (Movement Task: grasp or posture) $\times$ 2 (End Position: object-relative or body-relative) ANOVA. The results of this ANOVA showed no main effect of Initiation ($p = .41$) and no interactions between Initiation or any of the other factors ($p \geq .32$).
3. One patient in the apraxic group (I6) was excluded from the lesion analysis because examination of her high-resolution CT scan showed no localizable lesion.
4. The statistic relied on a permutation, or resampling, hypothesis test that make no assumptions about the underlying population distribution from which the data were sampled (Goode, 2005). We chose to use permutation hypothesis tests rather than other nonparametric methods (e.g., Mann–Whitney/Wilcoxon test) because the former do not require ranking of data, which leads to loss of information about the magnitude differences between individuals and groups. As applied to the analysis of two independent samples, a permutation hypothesis test compares the observed overlap (as measured by the t statistic) between data in two groups (of sample size N1 and N2) to the overlap of all possible groupings of the pooled data into groups of size N1 and N2. This is done computationally by pooling the observed data values from both groups and selecting samples of size N1 and N2, without replacement, from the pooled data values. Next, the overlap of the two sampled groups is measured using the independent-sample t statistic. This process is repeated until t values are computed for all possible combinations of the pooled data into samples of size N1 and N2. From this repeated sampling, a distribution of t values is created. The p value reported describes the probability of observing such an extreme t value for the actual grouping of the data relative to the distribution of t values for all possible groupings of the data.
5. In addition to the analysis comparing the lesions associated with high- and low-performance on all tasks, we also explored the corresponding analyses of high- and low-performance in the tasks shown to be particularly deficient in the apraxic group (e.g., the posture tasks, tasks with body-relative end positions, the delayed blindfolded condition). Because grouping based on high- and low-performance on these different tasks resulted in nearly identical groups, we have chosen to not report these task-specific analyses.

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