Praxis and the Right Hemisphere

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We report our observations on praxis in a strongly right-handed man following a massive stroke that resulted in virtually complete destruction of the left cerebral hemisphere. Our patient was severely impaired in pantomiming transitive gestures with the left hand and in reproducing novel non-symbolic hand and arm movement sequences. However, overlearned habitual actions like actual object use and intransitive gestures were relatively spared. Performance of axial commands was intact. Gesture recognition and discrimination were also preserved. Based on these findings, we propose that the praxis system of the right hemisphere is strongly biased toward "concrete" or context-dependent execution of familiar, well-established action routines. The right hemisphere is critically dependent on transcallosal contribution from the left hemisphere for control of the left hand in "abstract" or context-independent performance of transitive movements and in learning novel movement sequences. At least in some individuals, the right hemisphere can recognize and discriminate gestures. Possible implications of our findings for the cerebral control of praxis and for recovery from apraxia are discussed. © 1993 Academic Press, Inc.

Introduction

Liepmann (1920) postulated that the left hemisphere of right-handed individuals contains the "space-time engrams" or "movement formulas" that control purposeful skilled movements of the limbs on both sides of the body. Liepmann's notion of left hemispheric dominance for praxis was based primarily on two sets of clinical observations. First, he noted that patients with left hemisphere lesions and right hemiplegia often demonstrated "sympathetic dyspraxia" of the left hand, while patients with right hemisphere lesions and left hemiplegia were not apraxic with the right hand (Liepmann, 1905). Second, he observed severe unilateral

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apraxia of the left hand to verbal command, imitation, and actual object use in a patient with an infarction that destroyed the anterior two-thirds of the corpus callosum (Liepmann & Maas, 1907). Based on these findings, Liepmann (1920) proposed that whereas the space-time engrams of the left hemisphere controlled movements of the right hand by direct activation of the left sensorimotor hand area via *intra*hemispheric association pathways, the execution of skilled movements with the left hand required additional *inter*hemispheric transfer of information from the hand center in the left hemisphere to the right sensorimotor hand area across the body of the corpus callosum.

Although Liepmann emphasized the role of transcallosal mechanisms in controlling the left upper extremity and suggested that left hand skills were for the most part "a property borrowed from the left hemisphere" (Liepmann, 1905), he was careful to point out that the right hemisphere may also have some intrinsic capacity to program and execute skilled movements: "We will note once and for all that the right hemisphere, too, is involved in praxis, especially for the left half of the body" (Liepmann, 1920). The possibility that the right hemisphere, at least in some right-handers, may possess praxic skills of its own has also been entertained by several other investigators as a likely explanation for the unexpected sparing of certain left hand praxic functions following left hemispheric or callosal lesions (Geschwind & Kaplan, 1962; Geschwind, 1975; Heilman, 1979; Heilman & Rothi, 1985; Graff-Radford et al., 1987; Kertesz et al., 1984; Kertesz & Ferro, 1984). However, attempts to define the extent to which the right hemisphere is capable of controlling skilled movements independent of left hemisphere participation have produced variable and at times inconsistent results. In apparent contradiction with Liepmann's hypothesis, neuropsychological studies in split-brain patients suggested that although some degree of left-sided apraxia was often present in the acute postoperative period (Gazzaniga et al., 1967), the only persistent praxic deficit following complete surgical sectioning of the corpus callosum was an impairment in carrying out skilled movements with the left hand to verbal command (Zaidel & Sperry, 1977). Since callosotomy patients performed well with the left hand on imitation and when handling actual objects, defective performance on verbal command was interpreted to reflect either the inability of the isolated right hemisphere to comprehend verbal instructions (Gazzaniga et al., 1967), or an impairment within the right hemisphere in associating verbal comprehension of commands with motor programming (Zaidel & Sperry, 1977). However, there is also the possibility that in callosotomy patients movements of the left hand in response to non-lateralized verbal commands were actually controlled by the language-dominant left hemisphere via ipsilateral motor pathways (Zaidel & Sperry, 1977). The observation that patients failed mostly on those commands that required distal movements supports this

hypothesis, since ipsilateral motor control of the upper extremity is generally thought to be less efficient for the distal hand musculature (Brinkman & Kuypers, 1973). Unfortunately, there is a more general problem with the interpretation of the split-brain data: most callosotomy patients have evidence of early brain damage and long-standing seizure disorder which may have led to anomalous lateralization of language and praxic functions (Sperry et al., 1969; Gazzaniga, 1983). Since these individuals are more likely to have bilateral representation of engrams for skilled movements than the average right-handed person, extrapolating from the callosotomy data may overestimate the right hemisphere's capacity for praxis.

Unlike split-brain patients, right-handed individuals with naturally occurring callosal lesions presumably had normal neurological development, and can thus be assumed to have a more standard pattern of premorbid cerebral lateralization for language and praxis. Observations in these patients have generally supported Liepmann's hypothesis for the cerebral control of skilled movements, since severe unilateral apraxia of the left hand has been repeatedly documented following lesions involving the body of the corpus callosum (Van Vleuten, 1907; Maas, 1907; Goldstein, 1908, 1909; Bonhoeffer, 1914; Sweet, 1941; Geschwind & Kaplan, 1962; Watson & Heilman, 1983; Goldenberg et al., 1985; Graff-Radford et al., 1987; Leiguarda et al., 1989). Consistent with the findings of Liepmann & Maas (1907), apraxia of the left hand in most cases was present on verbal command, imitation, and even when using actual objects, although there are some notable exceptions (Geschwind & Kaplan, 1962). It is of considerable interest that several patients with initially severe unilateral apraxia following partial callosal lesions demonstrated gradual improvement of left-hand praxis over time (Geschwind & Kaplan, 1962; Watson & Heilman, 1983; Graff-Radford et al., 1987). Unfortunately, it is not entirely clear whether this improvement reflected increasing right hemisphere capacity to program skilled movements of the left hand or whether it resulted from progressively greater and more efficient utilization of ipsilateral motor pathways by the left hemisphere. The finding that some patients with partial callosal lesions were better able to perform proximal than distal movements with the left extremity (Geschwind, 1975; Watson & Heilman, 1983; Leiguarda et al., 1989) suggests that they may have been using ipsilateral motor pathways. In patients with anterior callosal lesions, there is also the possibility that some of the improvement in left-hand praxis may have been related to the ability to utilize undamaged posterior callosal connections for interhemispheric transfer. That information relevant for the programming and execution of skilled movements with the left hand may cross from the left parietal region through posterior callosal pathways and subsequently gain access to the right premotor and motor areas was considered by several investigators (Liepmann, 1920; Kleist, 1934; Geschwind, 1975). Posterior callosal transfer may serve as an alternate route when anterior callosal pathways are rendered nonfunctional (Geschwind, 1975), and there is some evidence that the posterior callosum may be most efficient in mediating the transfer of nonverbal visual information relevant for praxis (Volpe et al., 1982).

Although neuropsychological studies of adults with dominant hemispherectomy might be expected to provide the most direct measure of right hemisphere praxic capacity, the ability to perform skilled movements has not been systematically investigated in these rare patients. While the claim has been made (Smith, 1966, 1974) that there is no evidence of "sympathetic dyspraxia" of the left hand following dominant hemispherectomy, the type of movements used for testing praxis were not described and the criteria used for scoring responses were not specified.

We now report our observations on praxis in a strongly right-handed man following a massive infarction that resulted in almost complete destruction of the left cerebral hemisphere. With the possibility of left hemisphere contribution to motor performance virtually eliminated, this case provided a unique opportunity to investigate the right hemisphere's intrinsic capacity to control the programming and execution of skilled movements.

CASE REPORT

GK is a 62-year-old man who was strongly right-handed for all skilled manual activities prior to his neurological illness. He does not have a history of early brain damage or a family history of left-handedness. In February, 1977, GK suffered a massive left hemisphere stroke that resulted in global aphasia, alexia, and agraphia. Additional neurological findings included dense right homonymous hemianopia, right hemiplegia, and right hemisensory loss. When GK was discharged from the hospital 2 months later, he was only able to produce occasional single spoken words, but demonstrated fair comprehension of conversational speech. The information available to us about the evolution of praxic skills in GK following his stroke is somewhat fragmentary. As far as we can tell, praxis was first formally evaluated approximately 2 months post-onset. At that time, a severe impairment of gestural performance was found with scores on the pantomime subtests of the Porch Index of Communicative Ability (Porch, 1971) only in the 28th percentile. Follow-up evaluations at irregular intervals by speech-language pathologists documented continued improvement of language and gestural abilities, reaching an apparent plateau at about 2 years post-onset. Unfortunately, the scope of the praxis evaluations was quite limited and little qualitative information about performance is provided.

Fifteen years after the stroke, GK's spontaneous speech remains effortful, non-fluent, and slightly dysarthric. His speech output is meaningful but agrammatical. Auditory comprehension is excellent for conversational speech, but it breaks down when formally tested with syntactically complex sentences. On the Western Aphasia Battery (Kertesz, 1982), GK's language profile was consistent with Broca's aphasia.

GK lives alone and is capable of handling his own affairs. He does not complain of any difficulty in utilizing tools and household objects, cooks for himself, and performs minor repairs around the house. In fact, his hobby is to build model cars and airplanes. He walks with the aid of a leg brace, but his right arm is essentially plegic with the exception of preserved proximal movements at the shoulder. Right homonymous hemianopia and right hemisensory loss are still present. On clinical examination, his left limbs appear to have normal strength and sensation.

A recent MRI scan revealed a massive old infarction, involving the distribution of all three major cerebral arteries supplying the left hemisphere (Fig. 1). The lesion resulted in virtually complete destruction of the cortex and white matter of all four cerebral lobes. Basal ganglia structures and posterior thalamus were also extensively damaged. Small scattered islands of cortical tissue in the primary visual cortex, peri-Rolandic sensorimotor region, paracentral lobule, uncus, and orbitofrontal area appear completely undercut and isolated. The left cerebral peduncle and the left side of the basis pontis are atrophied due to degeneration of the left hemisphere outflow tracts. The right hemisphere appears normal.

EVALUATION OF PRAXIS

Testing sessions were videotaped and subsequently scored according to the criteria described below. For all tasks involving the use of the nondominant hand, GK's performance was contrasted with the left hand performance of five age-matched normal controls (mean age = 63.6 years). Controls were strongly right-handed for all skilled manual activities and did not have a family history of left-handedness. Performance of axial commands, gesture recognition and discrimination were assessed in GK only.

Learned Skilled Limb Movements

Procedure

Transitive gestures. GK and controls were asked to demonstrate with the left hand the use of 20 common objects (Appendix) in the following four experimental conditions: on verbal command, on visual command (i.e., pantomiming the use of an object that they were allowed to see but not handle), imitating the examiner's gestures, and with the actual objects.

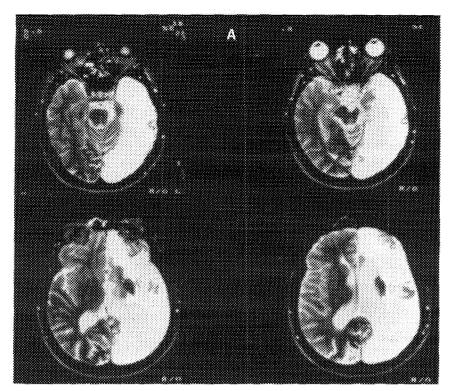


Fig. 1. (A,B) T₂-weighted MRI scan showing virtually complete destruction of left hemisphere cortex and white matter by the massive infarction. Basal ganglia structures and posterior thalamus are also extensively damaged.

Serial actions. In addition to evaluating the use of single objects, we also investigated performance of 6 serial action tasks requiring the use of several objects to achieve an intended goal (Appendix). All the necessary objects were placed on a table and subjects were verbally instructed to perform a given task using their left hand only (e.g., prepare a pot of coffee). Since some actions required bimanual performance (e.g., using a can opener, opening a bottle), the examiner held the tool or the recipient of the tool's action steady for the subjects when necessary, but otherwise offered no assitance.

Intransitive gestures. Subjects were asked to perform 15 symbolic gestures (Appendix) with the left hand to verbal command and imitation.

Scoring

Transitive and intransitive gestures were scored either as correct or incorrect. In addition, a qualitative analysis of apraxic errors was per-

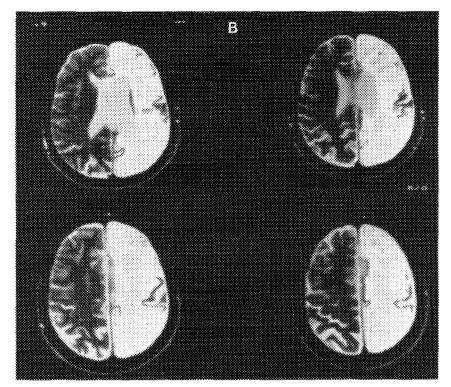


Fig. 1-Continued

formed using the classification system developed by Rothi et al. (1988). In scoring serial actions, emphasis was placed on conceptual knowledge of action rather than on the precision of the individual movements. Thus, we noted the number of component actions correctly performed in the sequence. Conceptually inappropriate use of individual objects, sequence errors and errors of omission were recorded, but errors due to "clumsiness" of the left hand in manipulating the objects were ignored. The maximum score for serial actions was 24.

Novel Non-symbolic Hand Postures and Limb Movements

Procedure

Static hand postures. Subjects were asked to reproduce 20 single static hand postures immediately after these were demonstrated by the examiner seated across the table. The hand postures were selected from the ones used previously by other investigators in studies of split-brain patients and subjects with focal brain damage (Gazzaniga et al., 1967; Kimura & Archibald, 1974; Jason, 1985). If subjects were unable to repro-

duce a hand posture correctly on the first trial, a second trial was administered and if they still failed, a third trial was conducted.

Non-symbolic hand and arm movement sequences. Subjects watched a videotape of the examiner performing meaningless hand and arm movement sequences with the left upper extremity, similar in complexity to the type of non-symbolic movements used in the studies by Archibald & Kimura (1974), Kolb & Milner (1981) and De Renzi et al. (1980, 1983). Immediately after viewing each movement sequence, subjects were asked to reproduce it. If they failed to perform correctly on the first trial, they were allowed to view the movement on the tape a second time and if they were still inaccurate, a third time. A total of 30 non-symbolic hand and arm movements were shown.

Scoring

The scoring procedure was identical for static hand postures and non-symbolic movement sequences. Correct performance on the first trial was given a score of 3 points, on the second trial 2 points, on the third trial 1 point and a score of 0 was recorded if subjects failed even on the third trial. Thus, the maximum score was 60 for static hand postures and 90 for non-symbolic hand and arm movements.

Axial Commands

GK was asked to perform 14 actions involving the axial musculature of the body (Appendix) to verbal command and imitation. Performance was scored either as correct or incorrect.

Gesture Recognition and Discrimination

Gesture recognition was evaluated by asking GK to identify 20 transitive gestures pantomimed by the examiner, either by naming the action or by selecting the appropriate object from foils. For testing gesture discrimination, the examiner performed the same 20 transitive gestures in a different order, but GK was now asked to select the correct pantomime for a given object from 3 foils that included pantomimes with body-part-as-object errors, spatial errors or content errors (i.e., a correctly performed gesture which, however, is not appropriate for the target object). Number of correct responses was recorded.

RESULTS

Learned Skilled Movements

Means and standard deviations for the control group are listed in Table 1. Although GK's scores fell 2SD below the means for the control group



TABLE 1
Group Means and Standard Deviations for Controls in Performing
Learned Skilled Movements

Transitive verbal	Transitive visual	Transitive imitation	Object use
15.2	16.2	16.0	18,2
0.83	1.30	1.00 0.4	
Serial actions	Intransitive verbal	Intransitive imitation	
24.0	14.0	14.6	***************************************
0	0.70	0.54	
	verbal 15.2 0.83 Serial actions 24.0 0	verbal visual 15.2 16.2 0.83 1.30 Serial actions Intransitive verbal 24.0 14.0 0 0.70	verbal visual imitation 15.2 16.2 16.0 0.83 1.30 1.00 Serial actions Intransitive imitation 24.0 14.0 14.6 0 0.70 0.54

on all tasks, some important dissociations were revealed in his performance. GK was severely impaired when performing limb transitive gestures with the left hand to verbal command and he did not improve significantly on visual command or imitation (Fig. 2). When pantomiming transitive gestures in these three experimental conditions, his errors were characterized predominantly by spatially incorrect or imprecise movements (i.e., internal and external spatial configuration errors and errors of movement timing and amplitude) and by body-part-as-object errors. Despite the spatiotemporal errors, the correct intent of the movement was virtually always apparent. Content errors and perseverations were not observed. GK's performance of transitive movements dramatically improved when handling actual objects with the left hand (Fig. 2), and the few minor spatial orientation errors were immediately corrected if the recipient of the given tool's action was also present (e.g., providing a nail to pound with the hammer or a sheet of paper to cut with the pair of scissors). As can be seen from Fig. 2, some "clumsiness" of the left hand was also evident in normal controls in all conditions, manifested mostly by spatially imprecise movements. In addition, controls made some body-part-as-object errors in pantomiming transitive gestures. Similar errors in normal subjects between the ages of 60-80 were also documented in other studies (Ska & Nespoulous, 1987; Rapcsak et al., 1989).

In performing serial actions, GK used all objects appropriately. He made only one sequence error (dialing a phone number prior to picking up the receiver) and a single error of omission (forgetting to pour the water from the pot into the coffee maker). A few seconds after he indicated to us that he had completed the task of making coffee, he spontaneously realized this omission and corrected it.

In contrast with his poor performance of limb transitive gestures, GK

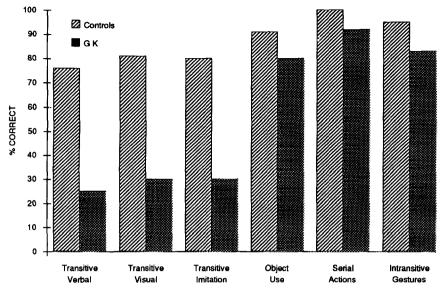


Fig. 2. Learned skilled movements. Verbal command and imitation scores for intransitive gestures were combined, since neither GK nor controls showed a significant difference in performance between these two conditions.

performed most limb intransitive gestures correctly on verbal command and imitation (Fig. 2).

Novel Non-symbolic Hand Postures and Limb Movements

Means and standard deviations for the control group are listed in Table 2. GK's performance was not significantly different from controls in reproducing single static hand postures (Fig. 3). However, in imitating non-symbolic hand and arm movement sequences with the left upper extremity, GK's score fell well below 2SD from the mean score for the control group (Fig. 3). In addition to spatiotemporal errors, GK's performance on this task was characterized by partial or complete omissions of certain movements in the sequence and by occasional perseverations.

Axial Commands

All axial movements were correctly carried out by GK both on verbal command and imitation.

Gesture Recognition and Discrimination

GK's performance on the gesture recognition task was flawless and he made only a single error on the gesture discrimination task by selecting a body-part-as-object foil as the correct gesture.

TABLE 2
Group Means and Standard Deviations for Controls in Performing Novel Non-symbolic
Hand Postures and Limb Movements

	Static hand		Movement sequences	
	postures			
Mean	57.4		65.6	
SD	2.30		3.20	

DISCUSSION

GK's left hemisphere was almost completely destroyed by the massive infarction; therefore, it seems reasonable to assume that all language and praxic functions are now mediated exclusively by the right hemisphere. Detailed evaluation of praxis in GK revealed that the right hemisphere's success in performing learned skilled movements with the left hand was both a function of the type of movement tested and the experimental condition under which it was elicited. GK was severely impaired in performing transitive gestures with the left hand to verbal command. The fact that his performance did not improve significantly on visual command or imitation suggests that the failure of the right hemisphere to carry out transitive gestures in this case could not be attributed to verbal comprehension defect or verbal-motor disconnection. GK's language

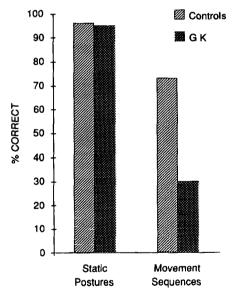


Fig. 3. Novel non-symbolic hand postures and limb movements.

comprehension is generally quite satisfactory, and he was able to carry out actions with objects, intransitive gestures and axial movements in response to verbal requests that were similar to verbal commands for transitive gestures in terms of linguistic complexity. That auditory comprehension defect was not a factor is also supported by the observation that the correct intent of transitive gestures was virtually always recognizable, and his errors consisted of spatiotemporal distortions of the required movements and body-part-as-object errors rather than content errors or failure to respond.

Spatiotemporal and body-part-as-object errors are the error types most frequently encountered in left-hemisphere damaged patients with ideomotor apraxia (Goodglass & Kaplan, 1963; Rothi et al., 1988; Poizner et al., 1990). Spatiotemporal errors, the predominant error type in GK, are thought to result from the destruction of the "space-time" (Liepmann, 1905, 1920) or "visuokinesthetic" (Heilman, 1979) engrams of the left hemisphere or, alternatively, may reflect a disconnection of these engrams from motor association areas. Heilman (1979) proposed that visuokinesthetic engrams for learned skilled movements were stored in the left parietal lobe. Without the information contained in visuokinesthetic engrams the motor system is unable to adopt the appropriate spatial positions of the relevant body parts over time (Heilman & Rothi, 1985). GK's numerous spatiotemporal errors in pantomiming transitive gestures with the left hand thus appear consistent with the notion of left hemispheric dominance for programming these actions, and suggest either that the right hemisphere has an impoverished store of visuokinesthetic engrams, or that intrahemispheric connections between the engrams and motor association areas are less well developed in the right hemisphere.

It has been known since the original study by Liepmann (1905) that left-hemisphere damaged patients with "sympathetic dyspraxia" of the left hand performed limb transitive movements significantly better with actual objects than on verbal command or imitation. Based on this observation, Liepmann (1905, 1920) concluded that the right hemisphere's inadequacy in programming transitive gestures with the left hand became strikingly apparent only when these movements had to be performed without the actual objects, either "entirely from memory" or on imitation. Liepmann (1905) believed that the combined tactile-kinesthetic and visual stimulation provided by handling objects might permit the right hemisphere to activate its store of motor learning. In a similar vein, Geschwind (1975) proposed that the right hemisphere's store of motor learning may be less accessible and might require the stronger multimodal stimulation afforded by manipulating objects to be released. In keeping with Liepmann's (1905) original observations, GK's left-hand performance dramatically improved when handling actual objects, and in fact completely normalized when the recipient of the particular tool's action

was also present. GK was also able to perform most serial actions requiring the use of several objects without significant difficulty. This is of course entirely consistent with the fact that he has no obvious problems in using objects in real-life situations. Our observations in GK suggest that the right hemisphere's capacity to program transitive movements with the left hand independent of left hemisphere contribution is a function of how closely the context of the task approximates natural performance. It appears that the right hemisphere can effectively program actions of the left hand in "concrete" object manipulation tasks designed to meet real-life demands. Conversely, the right hemisphere seems critically dependent on transcallosal transfer of information from the left hemisphere when pantomiming transitive movements with the left hand without actually manipulating objects (i.e., on verbal command, visual command, and imitation). Thus, consistent with Liepmann's (1905) hypothesis, the main limitation of the right hemisphere becomes apparent only when learned skilled limb movements are performed outside their natural context or "in the abstract". Based on our findings, we propose that the critical factor for releasing the right hemisphere's store of motor learning may not be the multimodal nature of the stimulation provided by handling objects per se, but rather the fact that the object manipulation task calls for the execution of well-practiced familiar actions, similar to performance in a natural setting. On the contrary, pantomiming the use of an object is an unfamiliar and "abstract" task that is unlikely to be performed outside the laboratory.

Similar to Hughlings Jackson's (1866) emphasis on the dissociation between "voluntary" versus "automatic" movements in apraxia, Goldstein (1948) made a critical distinction between "abstract" and "concrete" behavior and suggested that the failure of left-hemisphere damaged apraxic patients on pantomime tasks was due to their inability to assume the "abstract attitude". Such patients have "the greatest difficulty in pretending", due to a failure to assume an attitude toward the "merely possible" and to act symbolically (Goldstein, 1948). Our findings in GK are in agreement with Goldstein's formulation that the left hemisphere plays an indispensable role in "abstract" or context-independent performance of learned skilled movements. Although dependent on transcallosal contribution from the left hemisphere for control of the left hand in "abstract" performance of transitive movements, the right hemisphere has the potential for considerable autonomy in carrying out "concrete" actions with real objects.

The dissociation between "abstract" and "concrete" action in ideomotor apraxia is a fundamental one (Liepmann, 1905, 1920; Goldstein, 1948; Geschwind, 1975; De Renzi, 1985) and raises the question of whether or not the two types of performance are mediated by separate and even differentially lateralized neuronal systems in the normal brain. Specifi-

cally, it may be that although visuokinesthetic engrams are essential for controlling "abstract" performance of learned skilled movements outside their natural context (e.g., pantomiming transitive gestures), the more or less automatic execution of well-practiced "concrete" actions (e.g., the use of real objects) could be accomplished without the full participation of these engrams. Liepmann (1905, 1920) himself considered the possibility that certain well-established action routines may be executed without the activation of "space-time" engrams. He proposed that motor innervatory patterns or "kinetic engrams" represented in the sensorimotor cortical hand area might be sufficient to control these familiar overlearned actions. Liepmann (1905) also believed that the presence of such kinetic engrams in the right sensorimotor hand region might explain why some patients with "sympathetic dyspraxia" could manipulate objects well with the left hand. It may be that the visuokinesthetic engrams critical for "abstract" or context-independent performance of learned skilled movements are represented predominantly in the left parietal lobe, but the actual motor innervatory patterns for overlearned skills, like the habitual use of real objects, are more bilaterally represented. Cerebral representation and control of learned motor skills changes with continued practice and automatization and ultimately becomes independent from areas involved in the initial acquisition and performance of novel motor tasks (Paillard, 1960; Roland, 1984; Brooks, 1986). Bilateral cerebral representation for common everyday skills leads to a motor organization for these familiar actions that is largely independent of the neocortical commissures and may allow for control from either hemisphere (Zaidel & Sperry, 1977). Furthermore, several lines of evidence suggest that cerebral control for the initiation and automatic execution of well-established action routines does not require the full participation of higher-order parietal and frontal association cortices and is to a large extent relegated to the supplementary motor area (SMA), primary sensorimotor cortex, basal ganglia and cerebellum (Lauritzen et al., 1981; Marsden, 1982; Paillard, 1982; Roland, 1984; Brooks, 1986; Mazziotta et al., 1985; Goldberg, 1985).

In support of the hypothesis that automatic overlearned movements are more bilaterally represented is GK's relative success with intransitive gestures. Similar to actual object use, intransitive gestures are well-practiced actions that are performed in the testing situation much the same way as they are in a natural setting. The relative sparing of limb intransitive gestures in left hemisphere-damaged apraxics has in fact been noted by several investigators (Goldstein, 1948; Goodglass & Kaplan, 1963; Kertesz & Hooper, 1982; Haaland & Flaherty, 1984). The fact that GK's right hemisphere was successful in programming most intransitive gestures with the left hand to verbal command and imitation is consistent with the view that these overlearned movements may be more bilaterally represented and, consequently, depend less critically on left hemisphere

mechanisms than the pantomime of limb transitive gestures (Haaland & Flaherty, 1984).

Axial movements represent another class of automatized routine actions. Geschwind (1965, 1975) repeatedly emphasized the sparing of axial movements in left-hemisphere damaged patients with ideomotor apraxia. He proposed that axial movements did not depend on transcallosal integration, and could be controlled by the non-pyramidal motor system from either hemisphere via ipsilateral projections to brainstem centers. GK's normal performance of these actions provides empirical evidence that axial movements can indeed be effectively programmed by the right hemisphere alone.

Our conclusion that the praxis system of the right hemisphere is strongly biased toward context-dependent execution of familiar, wellestablished action routines is also supported by GK's striking difficulty in performing unfamiliar non-symbolic movement sequences. The fact that GK could reproduce single static hand postures adequately is consistent with the findings of Gazzaniga et al. (1967) that the isolated right hemisphere of split-brain patients is able to copy with the left hand static postures presented in the left visual field, and also with the study by Kimura & Archibald (1974) which failed to find evidence for left hemisphere specialization on this task in patients with focal brain damage. Kimura (1977) proposed that motor dominance of the left hemisphere becomes most apparent when actions require several changes in the spatial configuration of the hand and arm over time. Studies by various investigators (Pieczuro & Vignolo, 1969; Kimura & Archibald, 1974; Kolb & Milner, 1981; Kimura, 1982; De Renzi et al., 1980, 1983; Jason, 1983, 1985) have confirmed that left-hemisphere damaged patients, especially those with parietal lesions, were indeed severely impaired in imitating meaningless hand and arm movement sequences with the left upper extremity, although in several studies a deficit was also found when imitating static hand postures. It remains to be seen whether copying static hand postures and imitating non-symbolic movement sequences lie on a continuum of task difficulty or whether they in fact depend on distinct and differentially lateralized neuronal systems. Our findings in GK suggest that although the right hemisphere in some cases has the capacity to imitate single static postures with the left hand, transcallosal left hemisphere contribution to left-hand praxis becomes critical when performing novel non-symbolic movements requiring successive changes of hand and arm position.

Reproducing meaningless movements is an unusual task that proved relatively difficult even for our normal controls. Since the movement sequences were unfamiliar, performance could not have relied entirely on visuokinesthetic engrams and motor programs stored in long-term memory. Although it is conceivable that at least some unfamiliar movements are performed by analogy with familiar gestures using already ex-

isting programs, it would seem that copying unfamiliar non-symbolic movement sequences generally requires motor programs to be assembled de novo. Successful performance of this task also requires that the spatiotemporal aspects of the evolving movement be actively monitored in a "closed loop" fashion and compared with the image of the target movement held in working memory. In addition, compensatory modifications of the programs may become necessary on successive trials to correct errors. Our findings in GK and other investigations in patients with focal lesions (Pieczuro & Vignolo, 1969; Kimura & Archibald, 1974; Kimura, 1977, 1982; Kolb & Milner, 1981; De Renzi et al., 1980, 1983; Jason, 1983, 1986) suggest that left hemisphere damage severely disrupts the complex operations involved in learning to reproduce novel movement sequences. Kimura & Archibald (1974) presented some evidence that the impairment of left-hemisphere damaged patients on this task was not due to a failure to perceive the movements accurately. Whether the critical contribution of the left hemisphere is related to the mnestic (Jason, 1983) or motoric (Kimura & Archibald, 1974; Kimura, 1977) demands of the task, or both, remains to be determined. GK's poor performance despite repeated trials suggests that the right hemisphere has limited capacity for learning novel movement sequences. This finding is consistent with Liepmann's (1920) notion of left-hemispheric dominance for motor skill learning and with studies documenting impairments on a variety of motor learning tasks following left-hemisphere damage (Wyke, 1971; Heilman et al., 1975; Kimura, 1977; Jason, 1983).

Liepmann (1905) noted that gesture recognition was spared in his lefthemisphere damaged patients with "sympathetic dyspraxia". More recently, Heilman et al. (1982) proposed that there may be two different forms of ideomotor apraxia. They suggested that patients with apraxia following posterior left hemispheric lesions that presumably destroyed the visuokinesthetic engrams stored in the parietal lobe were also impaired in recognizing pantomimes and in discriminating correctly performed gestures from incorrect ones, while patients with apraxia from anterior lesions that disconnected visuokinesthetic engrams from motor association areas were impaired in gesture production only. However, recent models of praxis (Rothi et al., 1991) have argued that the system involved in the comprehension and discrimination of action pantomimes may be separate from the gesture production system. It is possible that gesture production and recognition abilities may in fact have somewhat different cerebral lateralization. Ferro et al. (1983) commented on the unexpected sparing of gesture recognition in some patients with large left hemisphere lesions or dominant parietal lobe lesions. These findings and our own observation of preserved comprehension and discrimination of action pantomimes in GK suggest that the right hemisphere, at least in some individuals, can mediate gesture recognition. It may be that neuronal systems involved in gesture recognition and discrimination are more bilaterally organized than the gesture production system. This model of cerebral organization for gesture would parallel the representation of language in the brain, where the right hemisphere is thought to have a considerable receptive vocabulary but only limited generative capacity for language production (Zaidel, 1985).

Our investigation of praxis in GK suggests that the right hemisphere in right-handed individuals may have the potential to program and execute familiar, well-established action routines with the left hand independent of left hemisphere contribution. However, this does not necessarily mean that under normal circumstances this potential for autonomy is utilized and control is shifted to the right hemisphere in an obligatory fashion when these actions are performed with the left hand. It is conceivable that in the intact brain the left hemisphere exerts control over all actions of the left hand by suppressing the right hemisphere's capacity to execute independently generated motor commands. A possible mechanism for maintaining left hemisphere control over the expression of the right hemisphere's praxic capacity might involve transcallosal inhibition. Transcallosal inhibition has already been implicated by several investigators as the putative neuronal mechanism by which the language-dominant left hemisphere exerts control over the expression of the right hemisphere's linguistic competence (Kinsbourne, 1974; Moscovitch, 1976; Zaidel, 1986). Left hemisphere damage or callosotomy may release the right hemisphere from inhibition and allow the expression of its intrinsic linguistic and praxic capacity. However, even following complete surgical sectioning of the corpus callosum the left hemisphere may still compete for motor control of the left hand through ipsilateral connections, and may continue to interfere with the execution of contralateral motor commands generated by the right hemisphere (Levy et al., 1971). It has been suggested that the release of right hemisphere processing following left hemisphere damage may be a function of lesion size (Landis et al., 1983). Consequently, in patients with smaller left hemisphere lesions control over motor performance may still be exercised by the damaged left hemisphere praxis system, and only following large left hemisphere lesion, as in GK, would control shift over completely to the right hemisphere.

Liepmann (1920) emphasized the right hemisphere's potential role in mediating recovery from apraxia following left hemisphere damage. As discussed previously, object use, intransitive gestures and axial movements are often preserved in left-hemisphere damaged patients with ideomotor apraxia. Based on our observations in GK, we propose that at least in some apraxic patients these spared functions may be mediated by the right hemisphere. Undoubtably, much of what the right hemisphere has accomplished in GK is the end-result of many years of practice and continued development made possible by his prolonged survival and

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by his strong motivation for functional independence. We believe that GK's case provides important clues about the range of praxic skills the right hemisphere may be able to mobilize in the process of recovery and, at the same time, it also demonstrates some inherent limitations. Since it is generally believed that there are significant individual variations in right hemisphere language and praxic skills (Liepmann, 1920; Geschwind & Kaplan, 1962; Sperry et al., 1969; Gazzaniga, 1983; Geschwind & Damasio, 1984; Zaidel, 1985; Heilman & Rothi, 1985), it is likely that the absolute level of compensation by the right hemisphere will vary from one person to another. The general implications of our findings will ultimately depend on whether patterns that are qualitatively different from that observed in GK will emerge in the process of recovery from ideomotor apraxia following left hemisphere lesions.

APPENDIX

Apraxia Battery

Transitive Movements Intransitive Gestures Toothbrush Shake fist at someone Screwdriver Salute Wave goodbye Key Hammer Scratch head Saw Snap fingers Comb Beckon "come here" Gesture "go away" Pencil Gesture "be quiet" Scissors Bottle opener Gesture "crazy" Fork Hitchike Gesture "OK" Flip a coin Gun Sign of victory Paintbrush Cross fingers for good luck Pour from bottle Pledge of Allegiance Signal "stop" Chalkboard eraser Glass Stir coffee with spoon Knife Razor

Serial Actions

Fold paper, place it in envelope, seal it, write address on envelope and put a stamp on it.

Prepare a pot of coffee using an electric coffee maker.

Put candle in a holder, light it with a match, then blow it out.

Open can of food with can opener, empty contents with spoon onto plate.

Open bottle with bottle opener, pour contents into glass and drink it. Look up a number in the phone book, pick up the phone and dial it.

Axial Commands

Shrug shoulders
Stand up
Take two steps forward
Take two steps backward
Bend forward
Turn head to the left
Turn head to the right

Look behind you
Turn around in a circle
Straighten up
Bend knees
Turn head up
Turn head down
Sit down

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