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Neuropsychologia xxx (2007) xxx–xxx

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

Speech-independent production of communicative gestures: Evidence from patients with complete callosal disconnection

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Received 31 January 2006; received in revised form 9 May 2007; accepted 28 May 2007

Abstract

Recent neuropsychological, psycholinguistic, and evolutionary theories on language and gesture associate communicative gesture production exclusively with left hemisphere language production. An argument for this approach is the finding that right-handers with left hemisphere language dominance prefer the right hand for communicative gestures. However, several studies have reported distinct patterns of hand preferences for different gesture types, such as deictics, batons, or physiographs, and this calls for an alternative hypothesis.

We investigated hand preference and gesture types in spontaneous gesticulation during three semi-standardized interviews of three right-handed patients and one left-handed patient with complete callosal disconnection, all with left hemisphere dominance for praxis. Three of them, with left hemisphere language dominance, exhibited a reliable left-hand preference for spontaneous communicative gestures despite their left hand agraphia and apraxia. The fourth patient, with presumed bihemispheric language representation, revealed a consistent right-hand preference for gestures. All four patients displayed batons, tosses, and shrugs more often with the left hand/shoulder, but exhibited a right hand preference for pantomime gestures.

We conclude that the hand preference for certain gesture types cannot be predicted by hemispheric dominance for language or by handedness. We found distinct hand preferences for specific gesture types. This suggests a conceptual specificity of the left and right hand gestures. We propose that left hand gestures are related to specialized right hemisphere functions, such as prosody or emotion, and that they are generated independently of left hemisphere language production. Our findings challenge the traditional neuropsychological and psycholinguistic view on communicative gesture production.

Keywords: Non-verbal communication; Split-brain; Gesture production; Handedness; Hemispheric specialization; Co-speech gestures

1. Introduction

The assumption that right-handers with left hemisphere language production prefer the right hand for gestures that accompany speech is an essential argument for neuropsychological, psycholinguistic, and recent evolutionary theories that propose a close association between language and communicative gesture production (Bernardis & Gentilucci, 2006; Corballis, 2002; Gentilucci, Stefanini, Roy, & Santunione, 2004; McNeill, 1992; Meister et al., 2003). While Kimura's seminal findings suggested a strong connection between speech and gesture at the level of motor output (Kimura, 1973a,b; Lavergne & Kimura, 1987; Lomas & Kimura, 1976), leading psycholinguistic theories (McNeill, 1992) postulate that gesture and speech are outcomes of a single temporally extended mental process. Others claim that these two processes are inherently inseparable such that the content of gesture is generated in one of the subprocesses of language production (Butterworth & Hadar, 1989; de Ruiter, 2000). Corballis (2002) argues that language evolved from manual gestures, gradually incorporating vocal elements. Meister et al. (2003) provide evidence for functional connec-

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0028-3932/$ – see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2007.05.010

tions between the hand motor area and the cortical network for language. More recently, Gentilucci, Bernardis, Crisi, and Volta (2006) argue that manual gestures and vocal language share the same control system located in Broca's area.

A dissociation of the gesture and language production systems has therefore rarely been proposed, except for Feyereisen (1987), who described dissociations between verbal and gestural output in aphasia as well as during language development in children. In the same line, gesture-speech mismatches are reported during learning and problem solving (Garber & Goldin-Meadow, 2002; Goldin-Meadow, Alibali, & Church, 1993). The authors provide evidence that the gesture-speech mismatches reflect two different cognitive strategies for a single problem.

The influential observation that right-handers with a right ear advantage in dichotic listening tasks prefer the right hand in free movements that accompany speech was first described by Kimura (1973a,b) and replicated in several studies (Dalby, Gibson, Grossi, & Schneider, 1980; Foundas et al., 1995). Among left-handers, those with a right ear advantage in dichotic examination used both hands for speech-accompanying gestures, with a slight left hand preference. Left-handers with a left ear advantage clearly favored the left hand (Kimura, 1973b).

Thus, Kimura proposed that hand preference for communicative gestures was determined by speech lateralization in the cerebral hemispheres. More explicitly, right-handers prefer the right hand for communicative gestures because their left hemisphere controls certain oral (i.e., speech) as well as brachial movements (i.e., communicative gestures) (Lomas & Kimura, 1976). However, in her theory, Kimura does not clearly distinguish between language comprehension, language production, and motor control of oral movements. She infers a lateralization of the control of 'certain oral movements' in right-handers from dichotic examination. However, this provides indirect evidence at best, since dichotic listening tasks usually measure phonetic perception, which, in turn, may be associated with auditory language comprehension more than with other language functions (Zaidel, Clarke, & Suyenobu, 1990). Kimura suggests that left-handers with a right ear advantage use both hands equally often for communicative gestures because in left-handers, expressive functions are more bilaterally organized. This implies that healthy left-handers really 'speak' with both hemispheres, but it does not explain her conclusion of a left hand preference in left-handers with a left ear advantage (Kimura, 1973b). In fact, Kimura does not consider handedness or manual dominance as a factor that could influence hand preference for communicative gestures. (For a detailed review of Kimura's experiments, see Lausberg & Kita, 2003.)

In several studies on hand use in communicative gestures, either right hand preference was not significant (Lausberg & Kita, 2003; Lavergne & Kimura, 1987), or an equally frequent use of the right and left hands was reported (Blonder, Burns, Bowers, Moore, & Heilman, 1995; Ulrich, 1980). Other researchers have demonstrated that right hand preference applies only to certain gesture types. For example, a right hand preference was found for physiographics, also termed iconics, i.e., gestures that concretely picture the verbal message (Foundas et al., 1995; Sousa-Poza, Rohrberg, & Mercure, 1979; Stephens, 1983). Furthermore, a right hand preference has been reported for deictics (pointing gestures) (Wilkins & de Ruiter, 1999). In contrast, no hand preference, or even a left hand preference has been found for batons, also termed beats, i.e., gestures that emphasize prosody (Blonder et al., 1995; Sousa-Poza et al., 1979; Stephens, 1983). Only Foundas et al. (1995) observed a right hand preference for 'emphasis gestures', while Moscovitch and Olds (1982) reported a decrease of right-hand preference in right-handers, when gestures were accompanied by a facial expression.

Thus, there is ample evidence against a generalization that right-handers prefer the right hand for communicative gestures, especially since a considerable number of left hand gestures has generally been reported. Even in those studies which report a statistically significant right hand preference for right handers, the percentage of left hand gestures in unimanual gestures ranges between 25 and 39% (Dalby et al., 1980; Kimura, 1973a; Lavergne & Kimura, 1987; Sousa-Poza et al., 1979; Stephens, 1983), a percentage not accounted for by Kimura's hypothesis.

Just as right hand gestures are assumed to reflect control by the left hemisphere, it can be assumed that left hand gestures are a sign of right hemisphere engagement. Thus, the substantial number of left hand gestures in communication, specifically, the left hand preference for batons that was established in several studies, suggest a right hemisphere contribution to the production of communicative gesture (Blonder et al., 1995; Lausberg, & Rothenhäusler, 2000; McNeill, 1992; McNeill & Pedelty, 1995; Sousa-Poza et al., 1979; Stephens, 1983). Hampson and Kimura (1984) observed a shift from right hand use in verbal tasks toward greater left hand use in spatial tasks and suggested that the problem-solving hemisphere will preferentially use the motor pathways which originate intrahemispherically. Consequently, the right hemisphere that primarily solves the spatial task employs the contralateral left hand. Indeed, in behavioral laterality experiments, when resources are sufficient for both decision and response programming, there is an advantage to responding with the hand controlled by the same hemisphere that performs the task (Zaidel, White, Sakurai, & Banks, 1988).

Exceptions to the rule that hand preference reflects the engagement of the contralateral hemisphere are left hand gestures that are performed with a semantic purpose, such as when talking about the left of two objects (Lausberg & Kita, 2003), or those determined by cultural conventions, such as when Arrente speakers in Central Australia use the left hand to refer to targets that are on the left (Wilkins & de Ruiter, 1999), or when the right hand is occupied with some other physical activity, such as a holding a cup of coffee.

Subjects with complete callosal disconnection offer a unique opportunity to examine the proposition that speech and gestures are controlled by a common motor system in the left hemisphere. Following callosal disconnection, each hand is mainly controlled by the contralateral hemisphere (Gazzaniga, Bogen, & Sperry, 1967; Lausberg & Cruz, 2004; Sperry, 1967; Trope, Fishman, Gur, Sussman, & Gur, 1987; Volpe, Sidtis, Holtzman, Wilson, & Gazzaniga, 1982). As a result, the actions of the right and left hands can reflect competence or incompetence of the contralateral hemisphere, as evidenced by the classical callosal

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disconnection symptoms of left hand apraxia to verbal command, left hand agraphia, or right hand constructional apraxia (Bogen, 1993).

Consideration should, however, be given to the fact that over time, callosotomy patients develop varying degrees of ipsilateral motor control of the limbs (Bogen, 1993; Gazzaniga et al., 1967; Volpe et al., 1982; Zaidel, 1998). Nevertheless, even under experimental conditions (i.e., when stimuli are lateralized to one hemisphere and the motor response of the ipsilateral hand is required), the ipsilateral motor control of the left hand achieved by the left hemisphere is limited (Gazzaniga et al., 1967; Lausberg & Cruz, 2004; Sperry, 1967; Trope et al., 1987; Volpe et al., 1982).

In an experiment with prolonged lateralized stimulus presentation of hand postures, N.G. and L.B., two patients with complete commissurotomy, were able to imitate on command with their ipsilateral left hand 80–90% of the tasks while they could only do so on 25% of the tasks with their ipsilateral right hand (Zaidel & Sperry, 1977). In the same session, the patients demonstrated a left hand dyspraxia when asked to perform non-lateralized tasks such as producing meaningful movements to verbal commands, suggesting that ipsilateral control is weaker in the absence of lateralized input. We are not aware of any report about split-brain patients using weaker ipsilateral control in spontaneous motor actions, such as communicative gestures. The only reports that deal with spontaneous motor behavior in split-brain patients describe disorders such as the autonomous syndrome (often mislabeled the "alien" hand syndrome, see Zaidel, Iacoboni, Zaidel, & Bogen, 2003), intermanual conflict (Zaidel et al., 2003), or "diagonistic dyspraxia" (Akelaitis, 1945). When occurring in patients with callosal disconnection, these phenomena imply that the right hemisphere spontaneously controls the left hand via contralateral pathways, independently of the left hemisphere (Bogen, 2000; Geschwind et al., 1995; Tanaka, Yoshida, Kawahata, Hashimoto, & Obayashi, 1996). Therefore, it seems plausible that when both hands are free to act in spontaneous communicative gestures, the more effective contralateral motor pathway will dominate. In the same vein, right-handed patients with callosal disconnection spontaneously use the left hand for visuo-constructive tasks (Graff-Radford, Welsh, & Godersky, 1987; Sperry, 1968; and in present study, see Section 2).

Up to now, in the patient group with complete callosal disconnection, communicative gesture types have only been analyzed in three subjects, N.G. and L.B. (McNeill, 1992; McNeill & Pedelty, 1995) and U.H. (Lausberg et al., 2000). The gesture type analysis of N.G. and L.B. showed that batons emphasizing prosody (in McNeill's terminology: beats) were performed mainly (N.G.) and exclusively (L.B.) with the left hand, whereas physiographics (in McNeill's terminology: iconics) that pictured the verbal content were performed exclusively (N.G.) and mainly (L.B.) with the right hand (McNeill, 1992; McNeill & Pedelty, 1995). Deictics (pointing gestures) were performed by N.G. almost exclusively with the right hand and by L.B. with both hands. However, while these are raw data deduced from McNeill's transcripts, McNeill did not interpret the hand preferences in relation to the generation of gestures in the contralateral hemisphere. He maintains that "non-imagistic beats" (batons) are generated in the "image-poor, language-rich left cerebral hemisphere" (1992, pp. 345–347). Further, his assumption that the left hemisphere is unable to generate iconics (physiographics) because they are based on imagery is contradicted by the split-brain patients' right hand preference for iconics and by the literature on visuo-spatial and mental imagery in split-brain patients which demonstrates a left hemisphere competence for generating mental images (e.g. Nichelli, 1999; Zaidel et al., 2003).

Similar hand preferences as in N.G. and L.B. were observed also in U.H. (Lausberg et al., 2000). According to Efron's (1941) gesture classification system, the left hand in U.H. performed exclusively batons, rise-falls (gestures with emotional connotation), and pictorial gestures that occurred in speech pauses and reflected the ideational process (ideographics). In contrast, the right hand was used exclusively for pictorial gestures, which matched the verbal utterance (physiographics) semantically and temporally, and for deictics (Lausberg et al., 2000). Despite the fact that shoulder shrugs can be controlled by contralateral and ipsilateral motor pathways, U.H.'s unilateral shrugs of the left shoulder occurred frequently (10 times more often than right shoulder shrugs) and in a context of lack of knowledge and resignation, whereas the rare unilateral shrugs of the right shoulder were performed when talking about the 'right side'. If the left hemispheres of the three patients had controlled the left hands via ipsilateral motor pathways, the gesture types displayed by the left hands should have been conceptually the same as those displayed by the right hands, perhaps executed in a deficient manner. This was not the case, as the left and right hands were each specialized for certain gesture types. It is noteworthy, that the hand preferences for gesture types observed in the three patients with complete callosal disconnection perfectly match the hand preferences for gesture types observed in the healthy subjects, i.e., a right preference for physiographics (Blonder et al., 1995; Sousa-Poza et al., 1979; Stephens, 1983) and deictics (Wilkins & de Ruiter, 1999), but a relative or absolute left hand preference for batons and gestures co-occurring with an emotional facial expression (Blonder et al., 1995; Moscovitch & Olds, 1982; Sousa-Poza et al., 1979; Stephens, 1983) (see review in Lausberg et al., 2000).

Kimura's findings and hypotheses concerning the link between speech and gesture at the level of motor output have been used by several researchers to argue that gesture and language production processes are obligatorily intertwined. However, the importance of the association of speech lateralization with hand preference in communicative gestures appears to be limited and it casts doubt on the proposition that speech and communicative gesture are necessarily controlled by a common motor system. The substantial number of left hand communicative gestures in healthy right-handers, and specifically, the left hand preference for batons suggest a right hemispheric contribution to gesture production. Case reports about patients with complete callosal disconnection point to the same direction.

Therefore, the present study aims to investigate Kimura's hypothesis of left hemispheric speech and gesture production in four patients with complete callosal disconnection. If, as

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predicted by Kimura's theory, speech and gesture production are controlled by a common motor system, then these patients should all show an exclusive right hand use for gestures insomuch as they have left hemisphere language production and motor control of speech functions. Secondly, the study aims to examine the hypotheses on hand preferences for specific gesture types which have been raised in a previous study on the patient U.H. with complete callosal disconnection (Lausberg et al., 2000). We hypothesize that the split-brain patients display a right hand preference for deictics and physiographs and a left hand preference for batons, ideographs, shrugs, and rise-fall gestures.

2. Methods

2.1. Sample

2.1.1. Subjects

We tested two patients with complete commissurotomy (A.A., N.G.), one patient with complete callosotomy (G.C.), and one patient with spontaneous complete callosal disconnection due to infarction of the total length of the corpus callosum (U.H.). As control groups, we investigated five right-handed patients with partial callosotomy (two females, three males; 23–59 years, mean age 38.6) and 10 right-handed healthy subjects (five females, five males; 18–54 years, mean age 41.4). The control subjects (partial callosotomy patients and healthy subjects) were chosen using the criteria of age, handedness, native language (English, French), and IQ rating in order to match the split-brain patients.

Table 1 shows the complete callosal disconnection patients' demographics relative to gender, age, handedness, level of intellectual function (WAIS-R or the short version of the Hamburg-Wechsler-Intelligenz-Testce Scales (WIP) and Coloured Progressive Matrices (CPM)). Also presented are extents of callosal disconnection, presence of extracallosal damage, and age(s) at surgery(ies) or infarction for the patients.

For U.H., details of the case history and neuropsychological examinations are given in Lausberg, Göttert, Münßinger, Boegner, and Marx (1999). For the others including the control subjects, the detailed descriptions are reported in Lausberg and Cruz (2004), Lausberg, Cruz, Kita, Zaidel, and Ptito (2003) and Lausberg, Kita, Zaidel, and Ptito (2003). For A.A. and N.G., the case histories can be found in Bogen (1969), Bogen, Schultz, and Vogel (1988), Milner and Taylor (1972) and Zaidel (1998). Because of their relevance to the present study, descriptions of the handedness, speech lateralization and hemispheric specialization for praxis are given in detail below for the patients with complete callosal disconnection.

2.1.2. Handedness

To establish handedness, we assessed the subjects in three modalities (verbally stated hand-preference, spontaneous hand-preference in pantomiming object use and in actual object manipulation) by administering two handedness questionnaires. One is used at the Montreal Neurological Institute and Hospital (Crovitz & Zener, 1962), the other is the modified version of the Edinburgh Handedness Inventory (Salmaso & Longoni, 1985). Both tests revealed that the three patients with complete commissurotomy/callosotomy were right-handed when the modalities of examination were verbally stated hand-preference and spontaneous hand-preference in pantomiming object use. With actual object manipulation, A.A. and G.C. were mildly ambidextrous.

The patient with spontaneous callosal infarction, U.H., was also given the Edinburgh Handedness Inventory (Oldfield, 1971). According to his verbally stated hand-preference, his laterality quotient was −64 (ambidextrous), while it was −100 on the modified Edinburgh Handedness Inventory, indicating left-handedness (for more details see Lausberg et al., 1999).

2.1.3. Hemispheric lateralization of language competence

A.A. and N.G. have left hemisphere language dominance. There is no evidence for right hemispheric speech production but some right hemisphere language comprehension (Nebes, 1971; Nebes & Sperry, 1971; see reviews by Gazzaniga, 1983; Zaidel, 2001; Zaidel et al., 2003).

G.C.'s performances on dichotic listening tasks were notable for right-ear suppression on digit identification (repeating the digits out loud) and left-ear superiority with the fused words task (visually recognizing the words and marking the appropriate ones) (Wexler & Halwes, 1983). The preferential processing of left ear input taken together with the presence of a right visual field scotoma suggests damage to the left cerebral hemisphere in G.C., although structural MRI examination was normal. The two hemispheres of G.C. often appeared to spontaneously react to verbal commands simultaneously and independently of each other, e.g., both hands started to pantomime tooth brushing when the command was given (Lausberg, Cruz, et al., 2003). Together with the dichotic listening results in G.C., this suggests bilateral language comprehension, with right hemisphere superiority. In keeping with the interpretation of bilateral language representation, G.C. only had mild left hand aphasic agraphia. In standardized examination of writing abilities, his score was 47 with the right hand and 35 with the left. In contrast, A.A. had a right hand score of 35 and a left hand score of 15, and N.G. had a right hand score of 47.5 and a left hand score of 15. (The minimum performance score in a healthy control group was 46 for the right hand and 41 for the left hand; the highest difference between the scores of the two hands being 4.5.) These data suggest that in G.C., language production is bilaterally organized, with greater left hemispheric representation. Tachistoscopic examination of language abilities was unreliable in this patient because of the visual field scotoma.

In patient U.H., left hemialexia and left visual hemifield anomia in tachistoscopic examination, as well as a left hand agraphia suggested left hemispheric language dominance. Under experimental conditions, limited right hemisphere speech production was demonstrated (for detailed results and discussion see Lausberg et al., 1999).

To summarize, A.A. and N.G. had left hemisphere language dominance with limited right hemispheric language comprehension and no right hemispheric speech production. U.H. had left hemisphere language dominance and,

Table 1
Patient data including gender, age, Wechsler Adult Intelligence Scales Revised (WAIS-R) Full Scale IQ rating, extent of callosal disconnection, presence of extracallosal damage, and age(s) at surgery(ies) or stroke

Subject	Sex	Age	WAIS-R Full Scale IQ	Etiology and extent of callosal disconnection	Extracallosal damage	Age(s) at surgery(ies) or stroke
A.A.	M	50	79	Single-stage complete commissurotomy	L fronto-parietal, R frontal	14
G.C.	M	46	78	Three-stage complete callosotomy	L auditory cortex, L optic radiations/visual cortex (based on functional defects)	33, 35, 38
N.G.	F	66	81	Single-stage complete commissurotomy	L posterior temporal, R central	30
U.H.	M	54	<90[a]; 108[a]	Infarction of corpus callosum; sparing of fibers in middle of splenium possible	L parietal white matter, probably due to diabetic microangiopathy	54

[a] For patient U.H., level of intellectual function was estimated with the Coloured Progressive Matrices (CPM) and the Hamburg-Wechsler-Intelligenz-Test—short version (WIP).

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under experimental conditions, very limited right hemisphere speech production. In G.C., both language comprehension and production were bilaterally represented. However, language production was better in the left hemisphere, whereas language comprehension was better in the right hemisphere.

2.1.4. Hemispheric lateralization of praxis

Left hand dyspraxia with conceptual errors in pantomime to visual presentation of objects was observed in the three split-brain patients, A.A., G.C., and most strongly N.G. (Lausberg, Cruz, et al., 2003). In addition, N.G. exhibited a left hand apraxia selectively for the imitation of hand-head positions (Lausberg & Cruz, 2004). After callosal infarction, the left-handed patient U.H. demonstrated a severe left hand apraxia, suggesting left hemispheric specialization for praxis despite his left-handedness (Lausberg et al., 1999). This is in keeping with the growing body of evidence showing that handedness and hemispheric specialization for praxis are dissociable (Frey, Funnell, Gerry, & Gazzaniga, 2005).

In contrast, if motor tasks contained spatial components, a superior left hand performance was observed in the patients with complete callosal disconnection (Lausberg, Kita, et al., 2003; Lausberg et al., 1999). Furthermore, in keeping with previous reports (Graff-Radford et al., 1987; Sperry, 1968), a spontaneous left hand preference was noted in A.A. and N.G. in two performance tests of the WAIS that required a motor response, i.e., block design and digit symbol.

To summarize, the patients with complete callosal disconnection show a left hemispheric specialization for praxis, which is more pronounced in U.H. and N.G. than in A.A. and G.C. In contrast, when spatial competence is required in motor actions the right hemisphere appears to be more involved.

2.1.5. Ipsilateral motor control

Based on previous experiments, the involvement of ipsilateral motor control in the four patients with complete callosal disconnection is subject to wide individual differences. The findings in N.G., A.A., and G.C. indicate that even if a minor degree of ipsilateral motor control can be used when required by experimental paradigms using lateralized input, its effectiveness in experiments with non-lateralized input is minimal as a severe left hand apraxia in different modalities occurs (Lausberg & Cruz, 2004; Lausberg, Kita, et al., 2003; Zaidel & Sperry, 1977).

U.H. exhibited a severe left hand apraxia to verbal command, to imitation, and in procedural learning of motor tasks at the time of interview 1, i.e., 2 months after callosal infarction (Lausberg et al., 1999). At the time of interviews 2 and 3, i.e., 5 and 9 months after callosal infarction, U.H. seemed to develop ipsilateral motor control, since in apraxia testing to verbal command and on imitation, the conceptual errors in the left hand were replaced by execution errors in distal finger movements and finger positions.

2.2. Materials and procedures

2.2.1. Materials

Data acquisition was based on three videotaped semi-standardized interviews of the four patients with complete callosal disconnection and on two interviews of the control subjects. The interviews were conducted at the beginning (interview 1), in the middle (interview 2)—only the patients with complete callosal disconnection—, and at the end (interview 3) of a neuropsychological examination on 2 successive days. Because patient U.H. had an acute callosal disconnection syndrome with ongoing recovery, the three interviews were conducted at 2, 5, and 9 months after callosal infarction.

The interviews were conducted in a standardized setting with regard to place, camera, and interviewer. The chair in which the subjects were seated had two arm rests. Care was taken to leave both hands free to act, i.e., subjects were asked not to hold anything in their hands. Interview duration varied. The first semi-standardized interview with the patients with complete callosal disconnection lasted an average of 15.3 ± 12.3 min ($M \pm$ S.D.), the second 17.2 ± 13.3 min ($M \pm$ S.D.), and the third (29.5 ± 23.7 min ($M \pm$ S.D.). The first semi-standardized interview with the control subjects lasted an average of 16.3 ± 9.06 min ($M \pm$ S.D.), and the interview at the end of the 2 days (termed interview 3 for comparison with the split-brain group) 14.5 ± 8.9 min ($M \pm$ S.D.).

The interview questions concerned medical history, professional career, social situation, and spatial relations, appreciation of test sessions, what kind of experiments they liked, etc.

The videotapes of the interviews were digitized in MPEG 1 format to permit use of the movement analysis program Media Tagger (Brugman & Kita, 1995).

2.2.2. Coding procedures

With the software Media Tagger, a segment of a movie can be selected and tagged with a value. In this study, each coding unit contained one gesture defined according to Davis (1991, rev. 1997) and McNeill (1992). A gesture unit was defined as the period of time between successive limb rests ('home base position'). Furthermore, the change of hand laterality – right hand, left hand, and both hands – within a gesture unit demarcated a gesture subunit. The tagging of the gesture units and, if applicable, the gesture subunits, was performed by an independent trained assistant.

The video recordings with tagged gesture units and/or subunits were given to two independent trained raters. Both raters were blind to the diagnoses and the research hypotheses, rater 1 coded 100% of the data and the second rater coded 25% of the data. Coding by the second rater was used only to establish interrater reliability. Thus, the statistical evaluation is based on the coding of the first rater. The videos were evaluated without sound in order to classify gestures based on their kinetic features alone.

The complete callosal disconnection patients' gestures were examined concerning gesture laterality and gesture types. In order to control for the effect of complete callosal disconnection on hand preferences for communicative gestures, the gesture laterality was examined in the control subjects (patients with partial callosotomy and healthy subjects).

2.2.3. Measurements

For coding gesture laterality and gesture types, the following criteria, proven effective in a previous study on communicative gestures in a patient with callosal disconnection (Lausberg et al., 2000), were used.

2.2.3.1. Gesture laterality. Gesture units and/or subunits were coded mutually exclusively as follows: 1, right-hand gesture; 2, left-hand gesture; or 3, bimanual gesture. The interrater agreement for the gesture laterality (Cohen's Kappa coefficient) was $\kappa = 0.998$.

Bimanual gestures were further classified as follows: (a) both hands equally dominant with temporal and semantic coordination; (b) both hands equally dominant, but lack of temporal and semantic coordination; (c) bilateral, with one hand dominant; (d) folded hands. The interrater agreement for bimanual coordination was $\kappa = 0.821$.

2.2.3.2. Gesture types. The coding system for gesture types used in the previous study (Lausberg et al., 2000) was substantially elaborated in order to be able to make more fine-grained distinctions and to test the assumptions that were raised in the previous study (see Section 1). Efron's classification of gestures (Efron, 1941) which comprises the categories batons, ideographics, deictics, physiographics, and emblematics remains the core of the present coding system. Furthermore, gesture types (tosses, palming) from Davis' Coding Manual (1991, rev. 1997) were adopted as well as categories from apraxia research, i.e., pantomimes (e.g. Liepmann, 1908) and body-part-as-object-presentations (e.g. Duffy & Duffy, 1989; Haaland & Flaherty, 1984; Lausberg, Cruz, et al., 2003; Ochipa, Rothi, & Heilman, 1994). In addition, based on observations in the previous and the present study, the following gesture types were defined: body-deictic, self-deictic, hand-showing, positioning, rise-fall gestures, tracing. Thus, the coding system used here comprises 15 gesture types.

Each gesture type is defined by a specific set of kinetic features, i.e., gestures are *not* interpreted with reference to the verbal context. The kinetic criteria are: (1) *hand shape* (McNeill, 1992; Ochipa et al., 1994: "internal configuration"); (2) *hand position* (Ochipa et al., 1994: "external configuration orientation"; Haaland & Flaherty, 1984: "orientation"; Hermsdörfer et al., 1996: "final position"); (3) *path* (Laban, 1988; Poizner, Mack, Verfaellie, Rothi, & Heilman, 1996; "spatial"; Hermsdörfer et al., 1996: "trajectory"); (4) *kinesphere* (Laban, 1988); (5) *gesture hemispace* (Lausberg, Kita, et al., 2003); (6) *levels* (Laban, 1988; McNeill, 1992); (7) *efforts* (Dell, 1979; Laban, 1988), (8)

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gaze (Gullberg & Holmquist, 2006); (9) involvement of body parts other than hands.

The 15 gesture types were defined briefly as follows (the extended coding manual that was used for training the rater can be obtained from the first author):

Deictic/direction: Finger or hand pointing to a visible or an invisible locus in the external space (Deictic); or indicating a direction (Direction).
Body-deictic: Finger or hand pointing to a body part, often accompanied by gaze at the respective body part.
Self-deictic: Finger or hand pointing to the sternum or chest, not accompanied by gaze.
Hand-showing: Showing one's hand.
Tracing: Drawing a path in the air; often the index leads the movement.
Positioning: Marking a place or a position in an imaginary space; often in relation to another position (opposition).
Baton: Up-down or circular movements with downward accent, often repetitive.
Tosses: Short outward/inward or supination/pronation movements of the hand with outward accent; either back (Back-toss) or palm (Palm-toss) of hand leading; can be enlarged to supination/pronation movements of lower arm; often repetitive.
Physiograph: Depicting a form (Iconograph) or a manner of movement (Kinetograph). (a) Iconograph: different modes of representation are possible: body-part-as-object/-subject, tracing a form, or shaping a form. (b) Kinetograph: body-part-as-object/-subject form of representation (in contrast to pantomime); depicting the manner of movement of an object/subject; can include directions and traces, but emphasis is clearly on the manner of movement.
Ideograph: Depicting abstract concepts, i.e., forms (e.g. a theoretical model), movements (e.g. a trend in society; trying to find a word), traces (e.g. 'path' of the thought patterns), positions (e.g. opinion), directions, and actions (e.g. the sweeping away gesture (Teßendorf, 2005)). The ideographic gestures have less distinct hand shapes and hand positions, and a less precise execution of paths as compared to their 'concrete' counter-parts, i.e., iconographs, kinetographs, etc. Furthermore, ideographs are performed at distinct locations in the gesture space (Ladewig, 2006).
Pantomime: Demonstrating an action, often referring to the use of an imagined object (tool use), to an imagined subject or surroundings; mode of representation (Müller, 1998): enacting, i.e., the gesturer him/herself pretends to act (in contrast to kinetograph). The configuration of the gesturer's hand (or other body parts) reflects the shape of the imagined object/subject/surroundings.
Emblem: Conventional sign having a specific linguistic translation (e.g. Johnson, Ekman, & Friesen, 1975; Kendon, 1992); in most cases interactive signs, more rarely pictorial signs, such as showing numbers or counting.
Palming: Rotation of the palms face up. Interactive sign (e.g. Beels & Ferber, 1989; Davis, 1991; Scheflen, 1973).
Shrug: Shoulder shrug. Interactive sign (e.g. Johnson et al., 1975).
Rise-fall: Single rise of lower arm, then drop. Interactive sign (Lausberg et al., 2000). Rise-fall gestures appear to be 'vestiges' of the palming and shrugs.

The interrater agreement for gesture types was $\kappa = 0.855$.

3. Results

3.1. Gesture laterality

Laterality was examined in three statistical analyses comparing the complete callosal disconnection patients and the two control groups on gesture variables calculated as described below. Mixed ANOVA with between-groups and repeated factors was used in all three analyses.

Table 2 gives for each patient in each interview the number/minute (and in brackets the absolute numbers) of total gestures, i.e., right hand gestures + left hand gestures + bimanual gestures, the number/minute of right hand gestures, the number/minute of left hand gestures, and the number/minute of bimanual gestures.

Table 3 gives the group means and standard deviations of the number/minute of total gestures, the number/minute of right hand gestures, the number/minute of left hand gestures, and the number/minute of bimanual gestures for the patient group with complete callosal disconnection (A.A., G.C., N.G., U.H.) in interviews 1, 2, and 3, and for the two control groups in interviews 1 and 3. Data submitted to statistical analysis consisted of total gestures/minute, gestures/minute for the right hand, left hand, and both hands (a repeated factor with three levels) for each interview (a repeated factor with two levels) and group (the between-groups factor with three levels). There were no statistically significant effects detected in the analysis for any factor or their interactions.

While the patients A.A., N.G., and U.H. consistently performed more communicative gestures with the left hand than with the right, the reverse was the case for patient G.C.

Table 2
Number/minute of total gestures (in brackets: absolute numbers of gestures), number/minute of right hand gestures, number/minute of left hand gestures, and number/minute of bimanual gestures for patients A.A., G.C., N.G., and U.H. in interviews 1–3

Patient	Interview	Total gestures/minute (absolute number of gestures)	Right hand gestures/minute	Left hand gestures/minute	Bimanual gestures/minute
A.A.	1	3.87 (90)	0.95 (22)	**2.19** (51)	0.73 (17)
	2	2.97 (49)	0.24 (4)	**1.69** (28)	1.03 (17)
	3	3.00 (48)	0.63 (10)	**1** (16)	1.38 (22)
G.C.	1	1.72 (11)	**1.41** (9)	0 (0)	0.31 (2)
	2	3.02 (108)	**1.54** (55)	0.53 (19)	0.95 (34)
	3	2.35 (13)	**1.99** (11)	0 (0)	0.36 (2)
N.G.	1	6.65 (188)	1.59 (45)	**4** (113)	1.06 (30)
	2	4.57 (53)	1.64 (19)	**2.07** (24)	0.86 (10)
	3	5.51 (326)	1.72 (102)	**2.35** (139)	1.44 (85)
U.H.	1	9.47 (32)	0.3 (1)	**8.28** (28)	0.89 (3)
	2	11.70 (57)	1.03 (5)	**2.46** (12)	8.21 (40)
	3	7.86 (292)	0.46 (17)	**2.45** (91)	4.96 (184)

In comparing the frequency of right gestures/minute with the frequency of left hand gestures/minute, the higher score is marked in bold print.

Table 3
Group means (M) and standard deviations (S.D.) for number/minute of total gestures, number/minute of right hand gestures, number/minute of left hand gestures, and number/minute of bimanual gestures for: (a) the patient group with complete callosal disconnection in interviews 1, 2, and 3; (b) the patient group with partial callosotomy in interviews 1 and 3; and (c) the healthy control group in interviews 1 and 3

Group	Interview	Total amount of gestures/minute ($M \pm$ S.D.)	Right hand gestures/minute ($M \pm$ S.D.)	Left hand gestures/minute ($M \pm$ S.D.)	Bimanual gestures/minute ($M \pm$ S.D.)
Complete callosal disconnetion (A.A., G.C., N.G., U.H.)	1	5.43 ± 3.37	1.06 ± 0.58	3.62 ± 3.51	0.75 ± 0.32
	2	5.56 ± 4.16	1.11 ± 0.64	1.69 ± 0.83	2.76 ± 3.63
	3	4.68 ± 2.52	1.20 ± 0.77	1.45 ± 1.17	2.03 ± 2.01
Partial callosal disconnection (N = 5)	1	5.19 ± 2.25	1.81 ± 0.97	1.73 ± 0.65	1.65 ± 1.30
	3	4.40 ± 2.97	1.51 ± 0.89	1.67 ± 1.31	1.22 ± 1.23
Healthy control (N = 10)	1	9.65 ± 2.94	2.92 ± 2.62	2.69 ± 2.71	4.04 ± 2.84
	3	8.19 ± 6.22	3.28 ± 3.88	1.95 ± 1.81	2.96 ± 3.07

The patients' bimanual gestures were characterized by deficient coordination and showed the same features that had been described previously (Lausberg et al., 2000). However, the bimanual gestures were excluded from further evaluation because the hemisphere from which they were generated, i.e., right, left, or both hemispheres, cannot be reliably determined.

In order to compare our data on hand preference for communicative gestures with Kimura's data, we calculated the subjects' asymmetry ratio scores according to Hampson and Kimura (1984), i.e. ([number of right hand gestures/minute − number of left hand gestures/minute]/[number of right hand gestures/minute + number of left hand gestures/minute]). Using these data in a mixed ANOVA with one repeated factor (interview, two levels) and one between-groups factor (three levels), there were no significant effects of interview, group, or their interaction for the asymmetry ratio scores.

Fig. 1 shows the asymmetry ratio scores in the four patients in the three interviews.

While U.H., A.A., and N.G. consistently showed a left hand preference, G.C. consistently displayed a right hand preference (In the interviews 1 and 3, G.C. even produced no left hand gestures).

3.2. Gesture types

The number of right hand gestures/minute and of left hand gestures/minute were explored separately for the gestures types (Fig. 2a and b).

In all four patients, batons were produced more often with the left hand than with the right hand (Fig. 2a, top left). G.C. produced this gesture type infrequently. Similarly, there was a left-hand preference for tosses in all four patients (Fig. 2a, top right). Furthermore, shrugs were displayed more often with the left shoulder than with the right (Fig. 2a, bottom left). G.C. produced only few shrugs with no side preference. In contrast to the previous types, pantomime gestures were displayed more often with the right hand in all four patients (Fig. 2a, bottom right). In G.C. und U.H., deictics/directional gestures were produced more often with the right hand, whereas N.G. produced them more often with the left hand (Fig. 2b, top left). Further analysis revealed that N.G. consistently used the right hand when pointing to the right and the left hand when pointing to the left. A similar trend as in N.G. was found in U.H., whereas G.C. used his right hand to point to either side. A.A. produced deictics/directional gestures infrequently with no hand preference. For physiographs (Fig. 2b, top right), there was a right hand preference in G.C., N.G., and U.H., whereas for ideographs (Fig. 2b, bottom left), there was a clear left hand preference in N.G. and U.H. Hand-showing occurred more often with the left hand in A.A., N.G., U.H., and with the right hand in G.C (Fig. 2b, bottom right).

For the gesture types body-deictic, emblem, palming, self-deictic, rise-fall gesture, tracing and positioning, the rate of occurrence was in three subjects 0.1 (number/minute) or less. Therefore, the data are not presented here.

In order to examine if the differences in hand preference (see Section 3.1) between the four patients, especially between G.C. and the other three patients, are related to differences in individual preferences for specific types of gestures, we examined the five most frequently displayed gesture types for each patient (Table 4).

A.A. often displayed one gesture type (emblems) that was not observed frequently in the others, while G.C. used two gesture types (tracing, positioning) not frequently seen in the others.

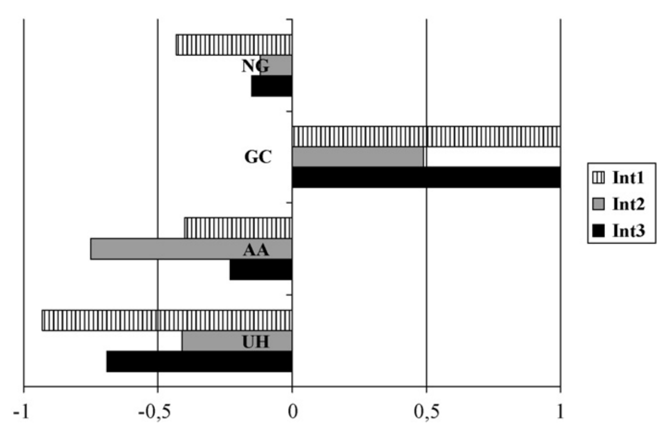

Fig. 1. Asymmetry ratio scores for the patients N.G., G.C., A.A., and U.H. at the interviews 1, 2, and 3.

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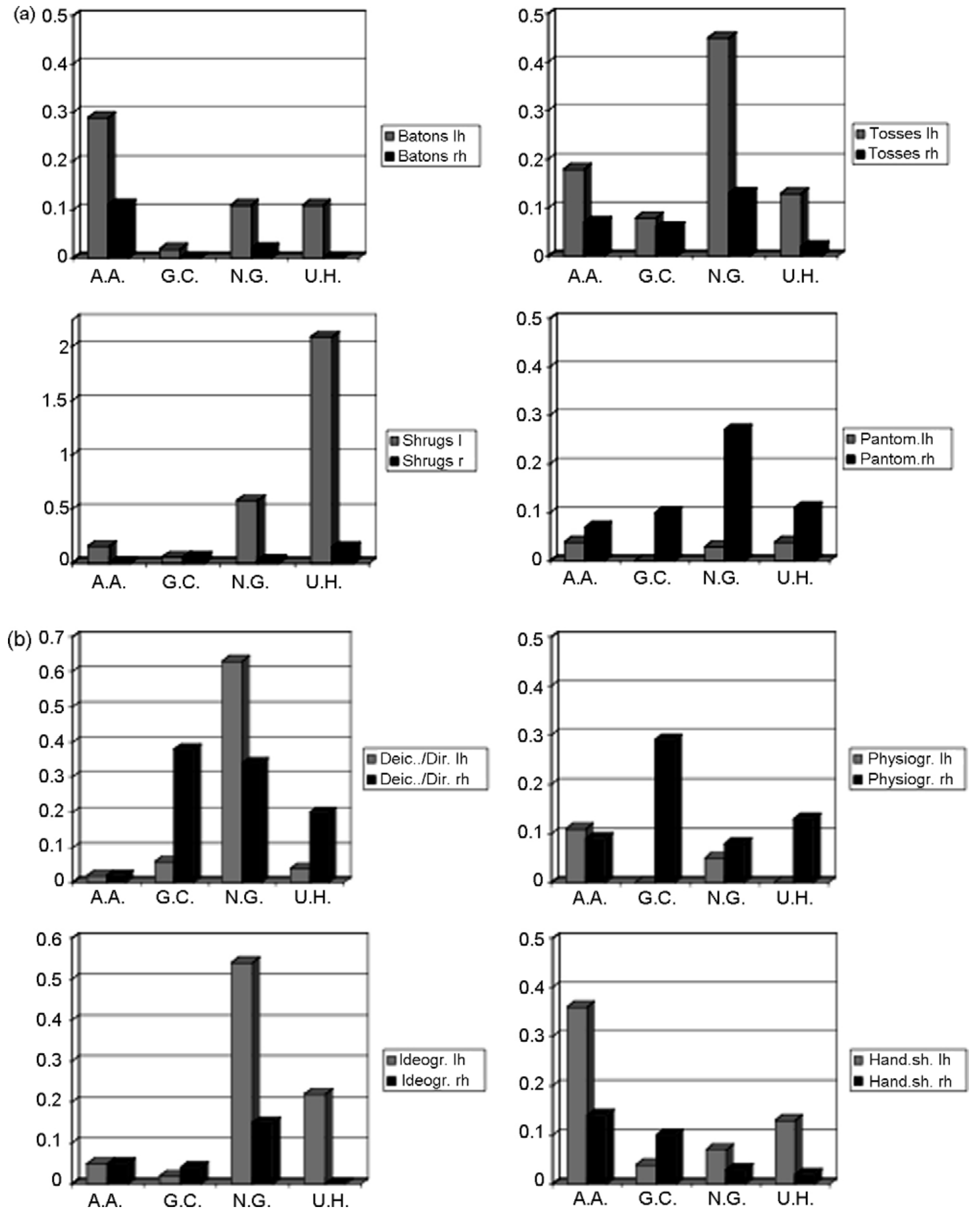

Fig. 2. (a) Batons (top left). Tosses (top right). Shrugs (bottom left). Pantomimes (bottom right): number of unilateral left hand gestures/minute (lh) and unilateral right hand gestures/minute (rh) in patients A.A., G.C., N.G., and U.H. (based on data from three interviews). (b) Deictics/directions (top left). Physiographs (top right). Ideographs (bottom left). Hand-showing (bottom right): number of unilateral left hand gestures/minute (lh) and unilateral right hand gestures/minute (rh) in patients A.A., G.C., N.G., and U.H. (based on data from three interviews).

Table 4
The five most frequently displayed gesture types by each patient (in brackets: number of gestures/minute)

Patient	Most frequent (number/minute)	Second	Third	Fourth	Fifth
A.A	Hand-showing (0.50)	Batons (0.39)	Tosses (0.25)	**Emblems** (**0.20**); Physiographs (0.20)	–
U.H.	Shrugs (2.25)	Ideographics (0.22)	Pantomimes (0.15); Deictics (0.15); Hand-showing (0.15); Tosses (0.15)	–	–
N.G.	Deictics (0.76)	Ideographics (0.69)	Shrugs (0.61)	Tosses (0.59)	Pantomimes (0.30)
G.C.	Deictics (0.36)	**Tracing** (**0.29**); Physiographs (0.29)	Hand-showing (0.15); **Positioning** (**0.15**); Tosses (0.15)	–	–

Gesture types that occurred only in a single patient among the five most frequent types are marked in bold print.

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4. Discussion

4.1. Hand preferences for communicative gestures

Left-hand preference for communicative gestures was found in the three patients with complete callosal disconnection who had left hemisphere language dominance and left hemispheric specialization for praxis, i.e., the two right-handed split-brain patients A.A. and N.G., and the left-handed patient with complete callosal infarction, U.H. Only the right-handed split-brain patient G.C. with presumed bilateral language representation displayed a right-hand preference for communicative gestures.

The left-hand preference in three of the four patients cannot be interpreted as an unusual pattern of hand preferences resulting from callosal disconnection because similar patterns of hand preferences were observed in the two control groups. The four patients with complete callosal disconnection did not differ from those with partial callosotomy and the healthy subjects with respect to number of total communicative gestures per minute, number of right hand gestures per minute, number of left hand gestures per minute, number of bimanual gestures per minute, and asymmetry ratio scores as a measure of hand preference.

According to Kimura's theory, namely that speech and gestures are controlled by a common motor system that in right-handers is located in the left hemisphere, A.A. and N.G. should have displayed a clear right-hand preference because of their left hemispheric speech representation. This was not the case. In fact, A.A. and N.G. demonstrated the opposite, a reliable left-hand preference for communicative gestures. Furthermore, Kimura (1973b) found that left-handers with left hemispheric speech dominance showed equally distributed unilateral right and left hand use in gesticulation. Thus, the left-handed patient U.H., with left hemisphere speech dominance, should have displayed equal use of the right and left hands in gesticulation. Again, this was not seen as he predominantly used his left hand in gesticulation. Further, following Kimura's logic, if ear advantage in dichotic examination was taken as an indicator of speech production, G.C., with his left ear advantage, should have displayed left hand preference for communicative gestures. In fact, he presented with a reliable right hand preference. Alternatively, it may be argued, in favor of Kimura's hypothesis, that G.C. had no right hand agraphia and a mild left hand aphasic agraphia in keeping with greater left hemisphere dominance for language production, which in turn would be compatible with his right hand preference.

Of all the subjects therefore, only G.C.'s pattern of hand preference is compatible with Kimura's prediction that communicative gestures are performed with the hand contralateral to the speech dominant hemisphere. The other three patients did not show the predicted hand preferences.

Should a stance be taken in favor of Kimura's theory, it could be reasoned that the patients with complete callosal disconnection and left hemisphere language dominance did not show the expected pattern of hand preference because they used ipsilateral motor pathways to control their left hand gestures. Some communicative gestures are kinematically simple and could be readily performed with proximal musculature.

Previous experiments suggest that some potential to exert ipsilateral control was only present in A.A., while for U.H., it was only noted in the course of ongoing recovery at the time of interviews 2 and 3. In experiments that explicitly required use of ipsilateral motor control, some meaningful left hand motor actions have been demonstrated by these two patients, but gesture execution was deficient (see Section 1). In fact, in separate testing at the time of the first interview when U.H. gesticulated almost exclusively with the left hand, there was a severe left hand apraxia with no evidence of ipsilateral motor control. Furthermore, the development of ipsilateral motor control in the months following infarction that was observed in the standard apraxia tests was not accompanied by an increase but rather by a decrease of left hand communicative gestures (see Lausberg et al., 1999, 2000). Indeed, U.H.'s potential to exert ipsilateral motor control on the left hand in apraxia tests did not correlate positively with unimanual left hand use for spontaneous communicative gestures. In addition, the literature provides no evidence that under free hand choice conditions, split-brain patients spontaneously make use of the weaker ipsilateral pathways to control motor actions.

Although it is likely that the four patients preferentially used the more efficient contralateral motor pathways during the interviews, it could be argued that they were prompted to use the left hand by some internal motivation to execute a gesture that was conceptualized in the left hemisphere. In healthy subjects, the use of the left hand can be semantically motivated (Lausberg & Kita, 2003), or it can be forced when the right hand is occupied. In our study, the latter condition was precluded by the study design, and no semantic determination of left hand use was observed during the interviews.

Another possibility that could be retained in favor of Kimura's theory is that callosotomy patients use compensatory cross-cueing strategies, as they do for ipsilateral motor control. However, this is unlikely since the choice of hand was free, and a physical or semantic reason to use the left hand was not evident.

In contrast, a strong argument for contralateral control of the left hand is that split-brain patients preferentially used the left hand to display specific gesture types while they preferred the right hand for other types of gestures (see below). In other words, if in the present study the patients' left hemispheres had controlled the left hands via ipsilateral motor pathways, the communicative gesture types would have been conceptually comparable for both hands. This was not the case.

To summarize, in addition to the fact that the potential to exert ipsilateral motor control is subject to wide individual differences, its use seems unlikely under free hand choice conditions. The same applies to cross-cueing strategies. In addition, left hand gestures differ conceptually from right hand gestures. Therefore, it is justified to attribute the spontaneous left hand communicative gestures in the patients with complete callosal disconnection to right hemisphere function.

Thus, we did not find support for Kimura's proposition that right handers prefer the right hand for communicative gestures because they have left hemisphere speech representation. However, speech production involves both the linguistic aspects of

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speech, such as semantics, phonology, and syntax that are lateralized to the left hemisphere, and non-linguistic aspects, such as prosody that are lateralized to the right hemisphere. Thus, in partial support of Kimura's hypothesis, our data are compatible with the view that gesture production involves a bilateral system that parallels the bilateral system for speech production. Thus, the links between gesture and speech may be more complex than Kimura thought, but might still exist. Furthermore, our results are in line with Kimura's statement (1973a,b) that hand-preference for communicative gestures cannot be primarily explained by 'handedness'. In the present study, the right-handed patients A.A. and N.G. reliably preferred the left hand for gesturing.

4.2. *Right hemispheric contribution to communicative gesture production*

The left hand preference for communicative gestures manifested by A.A., N.G., and U.H. stands in striking contrast to their left hand apraxia in the execution of verbal and motor tasks (see Section 2.1.4). This suggests that the production of spontaneous communicative gestures draws on resources other than those serving praxis. Rapcsak, Ochipa, Beeson, and Rubens (1993) provide an interesting hypothesis as to why the patients with complete callosal disconnection might be able to use their left hand for spontaneous communicative gestures (and actual object use), but not for executing motor tasks such as pantomime or imitation on command (Lausberg & Cruz, 2004; Lausberg, Cruz, et al., 2003; Lausberg, Kita, et al., 2003). Based on their comparisons of patients with left or right hemisphere damage, Rapcsak et al. suggested a strong bias of the right hemisphere toward 'concrete', context-dependent, familiar, well-established action routines. In turn, control of the left hand in 'abstract' tasks or context-independent performance would be critically dependent on a transcallosal contribution from the left hemisphere. In this view, the isolated right hemisphere might be able to perform left hand communicative gestures despite left hand apraxia because some communicative gestures represent over-learned motor patterns.

In the present study, however, the patients with complete callosal disconnection preferentially displayed batons, tosses, and shrugs with the left hand/shoulder, while they preferred the right hand for pantomimes and physiographs. We consider this as evidence of conceptual specificity of the left and right hand communicative gestures. Thus, left hand communicative gestures consist not only of over-learned patterns in the right hemisphere but also they are related to specific right hemispheric processes.

The left hand preference for batons, tosses, and shrugs is in line with our original hypothesis that split-brain patients prefer the left hand for these gesture types and supports the previous findings in healthy subjects and in the patients U.H., N.G. (and L.B.). As both gesture types, batons and tosses, are rhythmic gestures, it can be hypothesized that their production is associated with a right hemispheric specialization for the production of emotional prosody and a contribution to prosodic fundamental frequency (e.g., Schirmer, Alter, Kotz, & Friederici, 2001). Furthermore, the left side preference for shrugs, which are interactive signs with an emotional connotation (Johnson et al., 1975), is compatible with the right hemisphere superiority for emotional expression (Blonder, Bowers, & Heilman, 1991; Blonder, Burns, Bowers, Moore, & Heilman, 1993; Blonder et al., 1995; Fernandez-Carriba, Loeches, Morcillo, & Hopkins, 2002; Lausberg et al., 2000; Moscovitch & Olds, 1982; Ross & Mesulam, 1979) and for recognition of non-verbal emotional expression (Benowitz et al., 1983; Bowers, Blonder, Feinberg, & Heilman, 1991).

In contrast to the above gesture types, the four patients clearly preferred the right hand for pantomime gestures during the interviews. This finding matches the results of a previous study in which A.A., N.G., and G.C. displayed a left hand apraxia when pantomiming on command to visual presentation of objects (Lausberg, Cruz, et al., 2003) while the right hand pantomimes were correct. This indicates left hemispheric specialization for pantomiming, with no difference if the pantomimes were performed on command or if they occurred spontaneously in a communicative context. This left hemispheric specialization for pantomimes in callosal disconnection is in keeping with lesion studies demonstrating that patients with left hemisphere damage are more impaired in pantomiming object use on command than right hemisphere damaged patients (De Renzi, Faglioni, & Sorgato, 1982; Hartmann, Goldenberg, Daumueller, & Hermsdoerfer, 2005; Liepmann & Maas, 1907). In addition, recent fMRI (Choi et al., 2001; Lausberg et al., submitted for publication; Moll et al., 2000; Ohgami, Matsuo, Uchida, & Nakai, 2004) and PET-studies (Rumiati et al., 2004) demonstrate that independently of whether the right or left hand is used, pantomime is accompanied by left hemisphere activation.

In G.C. und U.H., deictics/directional gestures were produced more often with the right hand than with the left hand. This finding is in line with our hypothesis that the split-brain patients display a right hand preference for deictics. However, while A.A. produced only very few deictics, N.G. produced them more often with the left hand than with the right. It is noteworthy that N.G. consistently used the right hand when she pointed to the right, and the left hand when she pointed to the left, while the right-handed population in general prefers the right hand for deictics independently of the location they point to (Wilkins & de Ruiter, 1999). N.G.'s behavior seems to be associated with neglect of left personal space in right-handed gestural demonstrations (Lausberg, Kita, et al., 2003). Thus, N.G.'s right hand confinement to right personal space that was found in the previous experiment is also observed in the context of spontaneous communication, i.e., her right hand seems unable to point to the left space. Consequently, the left hand takes over this function.

For physiographs, there was a trend toward right-hand preference, while for ideographs a tendency to prefer the left hand was observed. These trends are in keeping with our original hypothesis that the split-brain patients display a right hand preference for physiographs and a left hand preference for ideographs.

However, further research is needed here to establish the potential difference between these two gesture types.

Concerning the individual preferences for certain gesture types, it is noteworthy that G.C. displays very infrequently all gesture types for which there is an overall left-hand preference in the patient group (batons, tosses, shrugs, and as a trend ideographs), i.e., not among his five most frequent types (except for tosses). In contrast, the other three patients prefer exactly these gesture types. G.C.'s "neglect" of batons, tosses, shrugs and ideographs may be related to the fact that he almost exclusively used the right hand for gesticulation and that the left hemisphere, which controls the right hand, is not specialized for the production of rhythmic and emotional gestures. Alternatively, G.C.'s right hand preference could merely reflect the fact that he prefers gesture types such as deictics or physiographs, which are predominantly generated in the left hemisphere. Thus, the difference between GC and the other three patients does not necessarily reside in the hand/hemisphere used to gesture, but could be related to the types of gestures they choose to make. Both interpretations are compatible with the fact that G.C. often displays the gesture types 'tracing' and 'positioning' which occur very infrequently in the other three patients (i.e., not among the five most frequently displayed gesture types). There appears to be a definite relation between the split-brain patients' overall hand preference for communicative gestures and the kind of gesture types they display but further research is needed to determine the direction(s) of influence between these two factors.

4.3. Conclusion

We do not dispute the possibility that a common motor control system for gesture and speech exists. However, our data are not compatible with the overly simplistic view that speech production is exclusively a left hemisphere function, so that right handers prefer the right hand for communicative gestures because they have left hemisphere speech representation. There is ample evidence indicating that the split-brain patients' left hand gestures are generated in the isolated right hemisphere. Thus, the links between gesture and speech may be more complex than Kimura thought in the sense that gesture production involves a bilateral system that partially parallels the bilateral system for speech production.

Furthermore, our data suggest that gestures can be generated independently of left hemisphere language production processes. Therefore, the results cast doubt on psycholinguistic theories that propose that communicative gesture production and left hemispheric language production are necessarily intertwined. The present findings support Feyereisen's proposition (1987) that gesture and language production are separate processes. The distinct hand preferences we observed for specific gesture types demonstrate a conceptual specificity of the left and right hand gestures, and they suggest that the production of left hand gestures reflects specialized right hemispheric non-linguistic functions, such as prosody or emotion.

The existence of independent language and gesture production systems and the association of specific communicative gestures with specific cognitive and emotional processes is theoretically interesting and has important implications for the rehabilitation of subjects with unilateral brain damage and subsequent communicative impairment.

Acknowledgements

This study was supported by the German Research Association grants LA 1249, and by the Language and Cognition Group of the Max Planck Institute for Psycholinguistics. In particular, we wish to thank Monique Lindeman, Sedinha Tessendorf, and Janina Beins for the tagging and coding of the extensive video material. Further, we wish to thank the patients and the controls for the participation in the study, and an anonymous reviewer for his/her valuable comments on the previous version of this paper.

References

Akelaitis, A. J. (1945). Studies on the corpus callosum. IV. Diagonistic dyspraxia in epileptics following partial and complete section of the corpus callosum. *American Journal of Psychiatry*, *101*, 594–599.

Beels, C. C., & Ferber, J. (1989). Context analysis of a family therapy session. In *Paper presented at the annual conference of the American orthopsychiatry association*.

Benowitz, L. I., Bear, D. M., Rosenthal, R., Mesulam, M. M., Zaidel, E., & Sperry, R. W. (1983). Hemispheric specialization in nonverbal communication. *Cortex*, *19*, 5–11.

Bernardis, P., & Gentilucci, M. (2006). Speech and gesture share the same communication system. *Neuropsychologia*, *44*, 178–190.

Blonder, L. X., Bowers, D., & Heilman, K. M. (1991). The role of the right hemisphere in emotional communication. *Brain*, *114*, 1115–1127.

Blonder, L. X., Burns, A. F., Bowers, D., Moore, R. W., & Heilman, K. M. (1993). Right hemisphere facial expressivity during natural conversation. *Brain and Cognition*, *21*(1), 44–56.

Blonder, L. X., Burns, A. F., Bowers, D., Moore, R. W., & Heilman, K. M. (1995). Spontaneous gestures following right hemisphere infarct. *Neuropsychologia*, *33*, 203–213.

Bogen, J. E. (1969). The other side of the brain. I. Dysgraphia and dyscopia following cerebral commissurotomy. *Bulletin of the Los Angeles Neurological Societies*, *34*, 73–105.

Bogen, J. E. (1993). The callosal syndromes. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (pp. 337–408). New York, Oxford: Oxford University Press.

Bogen, J. E. (2000). Split-brain basics: Relevance for the concept of one's other mind. *The Journal of the American Academy of Psychoanalysis*, *28*, 341–369.

Bogen, J. E., Schultz, D. H., & Vogel, P. J. (1988). Completeness of callosotomy shown by magnetic resonance imaging in the long term. *Archives of Neurology*, *45*, 1203–1205.

Bowers, D., Blonder, L. X., Feinberg, T., & Heilman, K. M. (1991). Differential impact of right and left hemisphere lesions on facial emotion and object imagery. *Brain*, *114*, 2593–2609.

Brugman, H., & Kita, S. (1995). Impact of digital video technology on transcription: a case of spontaneous gesture transcription. *Ars Semiotica*, *18*, 95–112.

Butterworth, B., & Hadar, U. (1989). Gesture, speech, and computational stages: A reply to McNeill. *Psychological Review*, *96*, 168–174.

Choi, S. H., Na, D. L., Kang, E., Lee, K. M., Lee, S. W., & Na, D. G. (2001). Functional magnetic resonance imaging during pantomiming tool-use gestures. *Experimental Brain Research*, *139*, 311–317.

Corballis, M. C. (2002). From hand to mouth: Gesture, speech, and the evolution of right-handedness. *Behavioral and Brain Sciences*, *26*, 199–208.

Crovitz, H. F., & Zener, K. (1962). A group test for assessing hand-and-eye dominance. *American Journal of Psychology*, *75*, 271–276.

Dalby, J. T., Gibson, D., Grossi, V., & Schneider, R. D. (1980). Lateralized hand gesture during speech. *Journal of Motor Behaviour*, *12*, 292–297.

Davis, M. (1991, rev. 1997). *Guide to movement analysis methods*. Behavioral Measurement Database Services, P.O. Box 110287, Pittsburgh, PA, USA.

De Renzi, E., Faglioni, P., & Sorgato, P. (1982). Modality-specific and supramodal mechanisms of apraxia. *Brain*, *105*, 301–312.

de Ruiter, J. P. (2000). The production of speech and gesture. In D. McNeill (Ed.), *Language and gesture* (pp. 284–311). Cambridge: Cambridge University Press.

Dell, C. (1979). *A primer for movement description using effort-shape and supplementary concepts*. New York: Dance Notation Bureau Press.

Duffy, R. J., & Duffy, J. R. (1989). An investigation of body part as object (BPO) responses in normal and brain-damaged adults. *Brain and Cognition*, *10*, 220–236.

Efron, D. (1941). *Gesture and culture*. The Hague: Mouton.

Fernandez-Carriba, S., Loeches, A., Morcillo, A., & Hopkins, W. D. (2002). Asymmetry in facial expression of emotions by chimpanzees. *Neuropsychologia*, *40*, 1523–1533.

Feyereisen, P. (1987). Gestures and speech, interactions and separations: A reply to McNeill (1985). *Psychological Review*, *94*, 493–498.

Foundas, A. L., Macauley, B. L., Raymer, A. M., Mahler, L. M., Heilman, K. M., & Rothi, L. J. G. (1995). Gesture laterality in aphasic and apraxic stroke patients. *Brain and Cognition*, *29*, 204–213.

Garber, P., & Goldin-Meadow, S. (2002). Gesture offers insight into problem-solving in adults and children. *Cognitive Science*, *26*, 817–831.

Gazzaniga, M. S. (1983). Right hemisphere language following brain bisection. *American Psychologist*, 525–537.

Gazzaniga, M. S., Bogen, J. E., & Sperry, R. W. (1967). Dyspraxia following division of the cerebral commissures. *Archives of Neurology*, *16*, 606–612.

Gentilucci, M., Bernardis, P., Crisi, G., & Volta, R. D. (2006). Repetitive transcranial magnetic stimulation of Broca's area affects verbal responses to gesture observation. *Journal of Cognitive Neuroscience*, *18*(7), 1058–1074.

Gentilucci, M., Stefanini, S., Roy, A. C., & Santunione, P. (2004). Action observation and speech production: Study on children and adults. *Neuropsychologia*, *42*, 1554–1567.

Geschwind, D. H., Iacoboni, M., Mega, M. S., Zaidel, D. W., Cloughesy, T., & Zaidel, E. (1995). Alien hand syndrome: Interhemispheric motor disconnection due to a lesion in the midbody of the corpus callosum. *Neurology*, *45*, 802–808.

Goldin-Meadow, S., Alibali, M. W., & Church, R. B. (1993). Transitions in concept acquisition: Using the hand to read the mind. *Psychological Review*, *100*(2), 279–297.

Graff-Radford, N. R., Welsh, K., & Godersky, J. (1987). Callosal apraxia. *Neurology*, *37*, 100–105.

Gullberg, M., & Holmquist, K. (2006). What speakers do and what addresses look at—Visual attention to gestures in human interaction live and on video. *Pragmatics & Cognition*, *14*(1), 53–82.

Haaland, K. Y., & Flaherty, D. (1984). The different types of limb apraxia errors made by patients with left vs. right hemisphere damage. *Brain and Cognition*, *3*, 370–384.

Hampson, E., & Kimura, D. (1984). Hand movement asymmetries during verbal and nonverbal tasks. *Canadian Journal of Psychology*, *38*, 102–125.

Hartmann, K., Goldenberg, G., Daumueller, M., & Hermsdoerfer, J. (2005). It takes the whole brain to make a cup of coffee: The neuropsychology of naturalistic actions involving technical devices. *Neuropsychologia*, *43*, 625–637.

Hermsdörfer, J., Mai, N., Spatt, J., Marquardt, C., Veltkamp, R., & Goldenberg, G. (1996). Kinematic analysis of movement imitation in apraxia. *Brain*, *119*, 1575–1586.

Johnson, H. G., Ekman, P., & Friesen, W. V. (1975). Communicative body movements: American emblems. *Semiotica*, *15*, 335–353.

Frey, S. H., Funnell, M. G., Gerry, V. E., & Gazzaniga, M. S. (2005). A dissociation between the representation of tool-use skills and hand dominance: insights from left- and right-handed callosotomy patients. *Journal of Cognitive Neuroscience*, *17*(2), 262–272.

Kendon, A. (1992). Some recent work from Italy on quotable gestures ('emblems'). *Journal of Linguistic Anthropology*, *2*(1), 77–93.

Kimura, D. (1973a). Manual activity during speaking. I. Right-handers. *Neuropsychologia*, *11*, 45–50.

Kimura, D. (1973b). Manual activity during speaking. II. Left-handers. *Neuropsychologia*, *11*, 51–55.

Laban, R. (1988). *The mastery of movement*. Worcester: Billing & Sons Ltd..

Ladewig, S. (2006). *Die Kurbelgeste—Konventionalisierte Markierung einer kommunikativen Aktivität*. Unpublished master thesis. Berlin: Free University.

Lausberg, H., & Cruz, R. F. (2004). Hemispheric specialisation in the imitation of hand positions and finger configurations. A controlled study in split-brain patients. *Neuropsychologia*, *42*, 320–334.

Lausberg, H., Cruz, R. F., Kita, S., Zaidel, E., & Ptito, A. (2003). Pantomime to visual presentation of objects: Left hand dyspraxia in patients with complete callosotomy. *Brain*, *126*, 343–360.

Lausberg, H., Davis, M., & Rothenhäusler, A. (2000). Hemispheric specialization in spontaneous gesticulation in a patient with callosal disconnection. *Neuropsychologia*, *38*, 1654–1663.

Lausberg, H., Göttert, R., Münßinger, U., Boegner, F., & Marx, P. (1999). Callosal disconnection syndrome in a left-handed patient due to infarction of the total length of the corpus callosum. *Neuropsychologia*, *37*, 253–265.

Lausberg, H., Heekeren, H., Kazzer, P., & Wartenburger, I. (submitted for publication). *Pantomime of tool use to visual presentation of tools and demonstration of tool use with tool in hand: A fMRI study*.

Lausberg, H., & Kita, S. (2003). The content of the message influences the hand choice in communicative gestures and in gesturing without speaking. *Brain and Language*, *86*, 57–69.

Lausberg, H., Kita, S., Zaidel, E., & Ptito, A. (2003). Split-brain patients neglect left personal space during right-handed gestures. *Neuropsychologia*, *41*, 1317–1329.

Lavergne, J., & Kimura, D. (1987). Hand movement asymmetry during speech: No effect of speaking topic. *Neuropsychologia*, *25*, 689–693.

Liepmann, H. (1908). *Drei Aufsätze aus dem Apraxiegebiet*. Berlin: Karger.

Liepmann, H., & Maas, O. (1907). Fall von linksseitiger Agraphie und Apraxie bei rechtsseitiger Lähmung. *Journal für Psychologie und Neurologie*, *X*, 214–227.

Lomas, J., & Kimura, D. (1976). Intrahemispheric interaction between speaking and sequential manual activity. *Neuropsychologia*, *14*, 23–33.

McNeill, D. (1992). *Hand and mind. What gestures reveal about thought*. Chicago: University of Chicago.

McNeill, D., & Pedelty, L. L. (1995). Right brain and gesture. In K. Emmorey & J. Reilty (Eds.), *Language, gesture, and space* (pp. 63–85). Hillsdale, NJ (USA): Lawrence Erlbaum Associates.

Meister, I. G., Boroojerdi, B., Foltys, H., Sparing, R., Huber, W., & Toepper, R. (2003). Motor cortex hand area and speech: Implications for the development of language. *Neuropsychologia*, *41*, 401–406.

Milner, B., & Taylor, L. (1972). Right-hemisphere superiority in tactile pattern-recognition after cerebral commissurotomy: Evidence for non-verbal memory. *Neuropsychologia*, *10*, 1–15.

Moll, J. D., de Oliveira-Souza, R., Passman, L. J., Cimini Cunha, F., Souza-Lima, F., & Andreiuolo, P. A. (2000). Functional MRI correlates of real and imagined tool-use pantomimes. *Neurology*, *54*, 1331–1336.

Moscovitch, M., & Olds, J. (1982). Asymmetries in spontaneous facial expressions and their possible relation to hemispheric specialization. *Neuropsychologia*, *20*, 71–81.

Müller, C. (1998). *Redebegleitende Gesten—Kulturgeschichte, Theorie Sprachvergleich*. Berlin: Arno Spitz.

Nebes, R.D. (1971). *Investigations on lateralization of function in the disconnected hemiphseres of man*. Unpublished doctoral dissertation. Division of Biology, California Institute of Technology.

Nebes, R. D., & Sperry, R. W. (1971). Hemispheric disconnection syndrome with cerebral birth injury in the dominant arm area. *Neuropsychologia*, *9*, 247–259.

Nichelli, P. (1999). Visuospatial and imagery disorders. In G. Denes & L. Pizzamiglio (Eds.), *Handbook of clinical and experimental neuropsychology* (pp. 453–478). Hove, East Sussex: Psychology Press.

Ochipa, C., Rothi, L. J. G., & Heilman, K. M. (1994). Conduction apraxia. *Journal of Neurology, Neurosurgery, and Psychiatry*, *57*, 1241–1244.

Ohgami, Y., Matsuo, K., Uchida, N., & Nakai, T. (2004). An fMRI study of tool-use gestures: Body part as object and pantomime. *Cognitive Science and Neuropsychology*, *15*(12), 1903–1906.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *64*, 236–247.

Poizner, H., Mack, L., Verfaellie, M., Rothi, L. J. G., & Heilman, K. M. (1996). Three-dimensional computergraphic analysis of apraxia. *Brain*, *113*, 85–101.

Rapcsak, S. Z., Ochipa, C., Beeson, P. M., & Rubens, A. B. (1993). Praxis and the right hemisphere. *Brain and Cognition*, *23*, 181–202.

Ross, E. D., & Mesulam, M. M. (1979). Dominant language functions of the right hemisphere? Prosody and emotional gesturing. *Archives of Neurology*, *36*, 144–148.

Rumiati, R. I., Weiss, P. H., Shallice, T., Ottoboni, G., Noth, J., Zilles, K., et al. (2004). Neural basis of pantomiming the use of visually presented objects. *NeuroImage*, *21*, 1224–1231.

Salmaso, D., & Longoni, A. M. (1985). Problems in the assessment of hand preference. *Cortex*, *21*, 533–549.

Scheflen, A. E. (1973). *Communicational structure: Analysis of a psychotherapy transaction*. Bloomington: Indiana University.

Schirmer, A., Alter, K., Kotz, S. A., & Friederici, A. D. (2001). Lateralization of prosody during language production: A lesion study. *Brain and Language*, *76*, 1–17.

Sousa-Poza, J. F., Rohrberg, R., & Mercure, A. (1979). Effects of type of information (abstract-concrete) and field dependence on asymmetry of hand movements during speech. *Perceptual and Motor Skills*, *48*, 1323–1330.

Sperry, R. W. (1967). Mental unity following surgical disconnection of the cerebral hemispheres. *The Harvey Lectures*, 293–323.

Sperry, R. W. (1968). Hemisphere deconnection and unity in conscious awareness. *American Psychologist*, *23*, 723–733.

Stephens, D. (1983). *Hemispheric language dominance and gesture hand preference*. Unpublished doctoral dissertation. University of Chicago, Department of Behavioral Sciences.

Tanaka, Y., Yoshida, A., Kawahata, N., Hashimoto, R., & Obayashi, T. (1996). Diagonistic dyspraxia—Clinical characteristics, responsible lesion and possible underlying mechanism. *Brain*, *119*, 859–873.

Teßendorf, S. (2005). *Pragmatische Funktionen spanischer Gesten am Beispiel des "gesto de barrer"*. Unpublished master thesis. Berlin: Free University.

Trope, I., Fishman, B., Gur, R. C., Sussman, N. M., & Gur, R. E. (1987). Contralateral and ipsialteral control of fingers following callosotomy. *Neuropsychologia*, *25*, 287–291.

Ulrich, G. (1980). Lateralization of hand-movements in patients with affective psychoses during an interview situation: An attempt at a physiological interpretation. *Psychological Research*, *41*, 249–258.

Volpe, B. T., Sidtis, J. J., Holtzman, J. D., Wilson, D. H., & Gazzaniga, M. S. (1982). Cortical mechanisms involved in praxis: Observations following partial and complete section of the corpus callosum in man. *Neurology*, *32*, 645–650.

Wexler, B. E., & Halwes, T. (1983). Increasing the power of dichotic methods: The fused rhymed words test. *Neuropsychologia*, *21*, 59–66.

Wilkins, D. P., & de Ruiter, J. P. (1999). Hand preference for representational gestures: A comparison of Arente and Dutch speakers. In V. Van Geenhoven & N. Warner (Eds.), *Annual report 1999* (pp. 51–52). Nijmegen: Max-Planck Institute for Psycholinguistics.

Zaidel, E. (1998). Stereognosis in the chronic split brain: Hemispheric differences, ipsilateral control and sensory integration across the midline. *Neuropsychologia*, *36*, 1033–1047.

Zaidel, E. (2001). Hemispheric specialization for language in the split brain. In F. Boller, & J. Grafman (Series Eds.) & R. Berndt (Vol. Ed.), *Handbook of neuropsychology: Vol. 2. Language and aphasia* (2nd ed., pp. 393–418). Amsterdam: Elsevier.

Zaidel, E., Clarke, J. M., & Suyenobu, B. (1990). Hemispheric independence: A paradigm case for cognitive neuroscience. In A. B. Scheibel & A. F. Wechsler (Eds.), *Neurobiology of higher cognitive function* (pp. 297–355). New York: Guilford Press.

Zaidel, E., Iacoboni, M., Zaidel, D. W., & Bogen, J. (2003). The callosal syndromes. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (4th ed., pp. 347–403). New York: Oxford University Press.

Zaidel, D., & Sperry, R. W. (1977). Some long-term motor effects of cerebral commissurotomy in man. *Neuropsychologia*, *15*, 193–204.

Zaidel, E., White, H., Sakurai, E., & Banks, W. (1988). Hemispheric locus of lexical congruity effects: Neuropsychological reinterpretation of psycholinguistic results. In C. Chiarello (Ed.), *Right hemisphere contributions to lexical semantics* (pp. 71–88). New York: Springer.

Please cite this article in press as: Lausberg, H., et al., Speech-independent production of communicative gestures: Evidence from patients with complete callosal disconnection, Neuropsychologia (2007), doi:10.1016/j.neuropsychologia.2007.05.010