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Pantomime to visual presentation of objects: left hand dyspraxia in patients with complete callosotomy

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Summary

Investigations of left hand praxis in imitation and object use in patients with callosal disconnection have yielded divergent results, inducing a debate between two theoretical positions. Whereas Liepmann suggested that the left hemisphere is motor dominant, others maintain that both hemispheres have equal motor competences and propose that left hand apraxia in patients with callosal disconnection is secondary to left hemispheric specialization for language or other task modalities. The present study aims to gain further insight into the motor competence of the right hemisphere by investigating pantomime of object use in split-brain patients. Three patients with complete callosotomy and, as control groups, five patients with partial callosotomy and nine healthy subjects were examined for their ability to pantomime object use to visual object presentation and demonstrate object manipulation. In each condition, 11 objects were presented to the subjects who pantomimed or demonstrated the object use with either hand. In addition, six object pairs were presented to test bimanual coordination. Two independent raters evaluated the videotaped movement demonstrations. While object use demonstrations were perfect in all three groups, the split-brain patients displayed apraxic errors only with their left hands in the pantomime condition. The movement analysis of concept and execution errors included the examination of ipsilateral versus contralateral motor control. As the right hand/left hemisphere performances demonstrated retrieval of the correct movement concepts, concept errors by the left hand were taken as evidence for right hemisphere control. Several types of execution errors reflected a lack of distal motor control indicating the use of ipsilateral pathways. While one split-brain patient controlled his left hand predominantly by ipsilateral pathways in the pantomime condition, the error profile in the other two split-brain patients suggested that the right hemisphere controlled their left hands. In the object use condition, in all three split-brain patients fine-graded distal movements in the left hand indicated right hemispheric control. Our data show left hand apraxia in split-brain patients is not limited to verbal commands, but also occurs in pantomime to visual presentation of objects. As the demonstration with object in hand was unimpaired in either hand, both hemispheres must contain movement concepts for object use. However, the disconnected right hemisphere is impaired in retrieving the movement concept in response to visual object presentation, presumably because of a deficit in associating perceptual object representation with the movement concepts.

Keywords: apraxia; split-brain; pantomime; object use; hemispheric specialization

Abbreviation: BPO = body-part-as-object

Introduction

Left hand apraxia in patients with callosal disconnection has been subject to controversial discussions concerning both its symptomatology and aetiology. Apraxia to verbal command has been found in the majority of patients with callosal disconnection, whether surgical or vascular (Liepmann and Maas, 1907; Geschwind and Kaplan, 1962; Gazzaniga *et al.*, 1967; Brion and Jedynak, 1972; Zaidel and Sperry, 1977; Volpe, 1985; Watson and Heilman, 1983; Goldenberg *et al.*, 1985; Degos *et al.*, 1987; Graff-Radford *et al.*, 1987; Starkstein *et al.*, 1988; Leiguarda *et al.*, 1989; Habib *et al.*, 1990; Kashiwagi *et al.*, 1990; Boldrini *et al.*, 1992; Buxbaum *et al.*, 1995; Tanaka *et al.*, 1996; Lausberg *et al.*, 1999; Goldenberg *et al.*, 2001) (see Table 1). Hence, there is some agreement that left hand apraxia to verbal command is a classical symptom of callosal disconnection (Bogen, 1993).

However, divergent findings arise if left hand apraxia is tested in modalities other than verbal command, such as imitation, object use with free vision or blind-folded, or pantomime of object use with visual object presentation. One group of investigators has reported only an impairment to verbal command, while other modalities such as imitation of movements with the left hand (Geschwind and Kaplan, 1962; Gazzaniga *et al.*, 1967; Brion and Jedynak, 1972; Zaidel and Sperry, 1977; Volpe, 1985; Degos *et al.*, 1987) or object manipulation (Geschwind and Kaplan, 1962; Gazzaniga *et al.*, 1967; Zaidel and Sperry, 1977; Degos *et al.*, 1987) are preserved. Apraxia of the left hand to verbal command with preserved imitation and object use has been convincingly explained by verbal–motor disconnection, i.e. left hemisphere language comprehension is disconnected from motor control of the left hand by the right hemisphere (Brion and Jedynak, 1972; Volpe, 1985; Bogen, 1993). Others state more generally that each hemisphere is able to exert volitional motor control if the task is not dependent on hemispherically specialized functions (Gazzaniga *et al.*, 1967; Zaidel and Sperry, 1977).

The verbal–motor disconnection explanation has been challenged by a number of reports of patients with spontaneous callosal disconnection in whom apraxia of the left hand not only occurred to verbal command, but also to imitation (Watson and Heilman, 1983; Goldenberg *et al.*, 1985; Graff-Radford, 1987; Starkstein *et al.*, 1988; Leiguarda *et al.*, 1989; Habib, 1990; Kashiwagi, 1990; Tanaka *et al.*, 1996; Marangolo *et al.*, 1998; Lausberg *et al.*, 1999; Goldenberg *et al.*, 2001), to manipulation of objects within sight (Liepmann and Maas, 1907; Watson and Heilman, 1983; Goldenberg *et al.*, 1985; Starkstein *et al.*, 1988; Leiguarda *et al.*, 1989; Buxbaum *et al.*, 1995), to manipulation of objects out of sight (Graff-Radford *et al.*, 1987; Goldenberg *et al.*, 2001) or to pantomime of object use with visual presentation of tools (Graff-Radford *et al.*, 1987; Boldrini *et al.*, 1992; Buxbaum *et al.*, 1995; Goldenberg *et al.*, 2001). These findings support Liepmann's hypothesis that the left hemisphere dominates motor behaviour and contains spatial–temporal movement concepts (Liepmann, 1908).

The divergence between reports of left apraxia restricted to verbal command and case reports of supramodal apraxia to verbal command, imitation and/or object use has, thus far, not been completely understood.

It is striking that apraxia restricted to verbal command has been found regularly in patients with complete callosotomy, whereas patients with spontaneous callosal disconnection tend to show more extensive forms of left apraxia. Within this context, it has been suggested that complete callosal section supports the development of autonomy between the two hemispheres more than spontaneous disconnection, in which some callosal fibres are often spared (Goldenberg *et al.*, 2001). Others (Graff-Radford *et al.*, 1987; Leiguarda *et al.*, 1989) have put forth the possibility that individual variation in brain organization resulting in different degrees of hemispheric specialization for praxis could explain the difference between the two groups. This is plausible especially for patients with severe epilepsy who often show substantial cerebral reorganization. Furthermore, surgical patients with apraxia restricted to verbal command have often been investigated years after surgery (Gazzaniga *et al.*, 1967; Zaidel and Sperry, 1977), whereas patients with spontaneous disconnection and supramodal apraxia have been examined earlier, within months after the cerebral infarction, haemorrhage or trauma (Liepmann and Maas, 1907; Watson and Heilman, 1983; Goldenberg *et al.*, 1985; Graff-Radford, 1987; Leiguarda *et al.*, 1989; Habib, 1990; Kashiwagi *et al.*, 1990; Boldrini *et al.*, 1992; Tanaka *et al*, 1996; Lausberg *et al.*, 1999). The time between occurrence of the disconnection and assessment is a relevant factor because apraxia of the left hand to imitation and object use improves in the first months after disconnection (Watson and Heilman, 1983; Graff-Radford *et al.*, 1987; Lausberg *et al.*, 1999).

In summary, there is substantial support for Liepmann's hypothesis that the left hemisphere is motor dominant. However, it is also evident that the right hemisphere has a certain aptitude for controlling movements independently from the left hemisphere when individual brain organization, time after disconnection, completeness of disconnection and the modus of the command to move are all taken into account.

The present study aimed to identify the specific modalities that elicit independent motor movements from the right hemisphere. Patients with complete callosotomy have usually been tested to verbal command, imitation and object use. We are not aware of any systematic investigation of pantomime to visual presentation of objects, which is of interest as different modalities of movement elicitation can be selectively impaired (see Table 1). Previous data have demonstrated that split-brain patients are not impaired on direct visual-motor imitation tasks (Gazzaniga *et al.*, 1967; Zaidel and Sperry, 1977; Volpe *et al.*, 1982; Volpe, 1985). Compared with imitation, pantomime to visual presentation of objects requires, however, the additional step of retrieving the instruction for object use. The clinical observation that preserved object use can co-occur with impaired pantomime of object use (Liepmann, 1908; De Renzi *et al.*, 1982) concurs with claims that different neural pathways are used for controlling pantomime and demonstrating with objects (Goodale *et al.*, 1994; Milner and Goodale, 1995; Westwood *et al.*, 2000). In addition, further examination of

Table 1 *Reports on investigations of apraxia in patients with callosal disconnection*

Authors	No. of patients	Extent of callosal disconnection	Aetiology	Time of examen post event	Verbal command	Imitation	Object use/tactile object presentation	Pantomime/visual object presentation
Liepmann and Maas, 1907	1	complete excl. splenium	infarction	3 months	+ (apra)		+	
Geschwind and Kaplan, 1962	1	anterior 2/3	tumor	<1 year	+	–	–	
Gazzaniga *et al*., 1967	9	complete	section	1 week post–op		–		
Gazzaniga *et al*., 1967	9	complete	section	'chronic'	+	–	–	
Gordon *et al*., 1971	2	anterior 5 cm (genu + truncus)	section	<1 year	–			
Brion and Jedynak, 1972	2 (cases 3+4)	complete, paracallosal	tumor, angioma	admission	+	–		
Zaidel and Sperry, 1977	2	anterior 2/3	section	4.5–5 years	–		–	
Zaidel and Sperry, 1977	6	complete	section	6.5–9.5 years	+	–	–	
Volpe *et al*., 1982	2	posterior truncus + splenium	section	~1–2 years		–		
Volpe, 1985	4	complete	section	~1–5 years	+	–		
Watson and Heilman, 1983	1	body	hemorrhage	3 d, 5 d, 5 months	+	+	+	
Goldenberg *et al*., 1985	1	anterior 2/3	hemorrhage	6 months	+	+	+	
Graff–Radford *et al*., 1987	1	genu + truncus	hemorrhage	4 weeks, 6 weeks, 4 months	+	+	+ (blind)	+
Degos *et al*., 1987		post. truncus + splenium	infarction	1–2.5 years	+	–	–	
Starkstein *et al*., 1988	1	'whole' corpus	hemorrhage	~1 months	+ (rh)	+ (rh)	+ (rh)	
Leiguarda *et al*., 1989	1 (case1)	genu + truncus	haemorrhage	~2 weeks	+	+	+	
Habib *et al*., 1990	1	post truncus + splenium	infarction	5 months	+	+	– (blind)	
Kashiwagi *et al*., 1990	1	post genu + truncus	infarction	~3 months	+	+	–	
Boldrini *et al*., 1992	1	middle + post truncus	trauma	10 weeks	+	–	– (blind)	+
Buxbaum *et al*., 1995	1	splenium	haemorrhage	6 weeks	+	–	+ (blind)	+
Tanaka *et al*., 1996	1	post truncus	infarction	2 months	+		–	
Tanaka *et al*., 1996	2	genu + truncus	haemorrhage, infarction	3 months; admission	+	+	–	
Marangolo *et. al*., 1998	1	left cingulate parallel to trunc + splenium	infarction	1 month		+		
Lausberg *et al*., 1999	1	complete	infarction	1 month, 5 months, 8 months	+	+		
Goldenberg *et al*., 2001	1	truncus + splenium	haemorrhage	2 years	+	–/+		+

+ = left hand apraxia; + (rh) = right hand apraxia; – = no apraxia; (blind) = blind-folded object manipulation

Liepmann's hypothesis in split-brain patients is of interest as functional MRI studies on pantomime of tool use show highly lateralized left hemisphere activation regardless of the hand used to pantomime (Moll *et al*., 2000; Choi *et al*. 2001).

Based on this information, we investigated whether patients with complete callosotomy show left hand apraxia in a pantomime task with visual object presentation. Further, we wished to gain insight into right hemisphere motor competence in order to test Liepmann's hypothesis. For this purpose, we wanted to ensure that the patients' left hand performances were generated in the right hemisphere and not controlled by the left hemisphere via ipsilateral pathways. Consideration should be given to the fact that, over time, callosotomy patients develop varying degrees of ipsilateral motor control of the proximal limbs (Gazzaniga *et al*., 1967; Volpe *et al*., 1982; Volpe, 1985; Bogen, 1993; Zaidel, 1998). In a number of studies on callosal apraxia, apractic disturbances are evidenced especially in the distal part of the limbs, affecting finger more than hand and arm gestures (Gazzaniga *et al*., 1967; Watson and Heilman, 1983; Boldrini *et al*., 1992). In an experiment with lateral tachistoscopic presentation of hand postures, N.G. and L.B., two patients with complete callosotomy, were able to imitate ipsilaterally with the left hand 80–90% of the tasks and with the right hand only 25% (Zaidel and Sperry, 1977). However, left hand dyspraxia for meaningful movements to verbal command has been documented in the same patients. Errors were predominant in movements requiring the use of single digits, suggesting that ipsilateral control was not sufficient without lateralized input. In another tachistoscopic experiment in which fingers had to be raised in response to a drawing, the left thumb and index finger could be controlled efficiently via ipsilateral pathways, while fingers four and five had the least ipsilateral control. Ipsilateral control for the right hand was very limited (Trope *et al*., 1987).

The emergence of ipsilateral motor control in split-brain patients is considered in the qualitative movement analysis that we performed here in order to understand individual differences in motor control in patients with disconnected cerebral hemispheres. We assumed that in the case of ipsilateral control, a patient's left hand would display distal errors of hand shape or hand orientation but the same movement concepts as in the right hand. Conversely, if the right hemisphere controlled the left hand, we expected the patient to display different movement concepts, some erroneous, in the left hand relative to the right, but with distinct distal control. We also investigated bimanual pantomimes based on the assumption that mirror movements of the left hand relative to the right would be indicative of ipsilateral control. In split-brain patients, synchronous symmetrical movements are unimpaired whereas interdependent or parallel movements are severely disturbed (Preilowski, 1975; Zaidel and Sperry, 1977). As mirror movements can be observed even after hemispherectomy (Zülch and Müller, 1969), it has been suggested that ipsilateral pathways are responsible for the patients' ability to perform symmetrical movements (Preilowski, 1975). In contrast, intermanual conflict (see review by Zaidel *et al*., in press) or diagonistic dyspraxia has been interpreted as a sign that the right hemisphere controlling the left hand is disconnected from the left hemisphere, which is dominant for volitional control of bimanual movements (Tanaka *et al*., 1996).

The current study investigated the competence of the isolated right hemisphere for pantomime in response to visual presentation of objects in three patients with complete callosotomy and compared it to the ability to demonstrate with object manipulation. For comparitive purposes, we also examined these abilities in patients with partial callosotomy and in healthy control subjects.

Methods

Subjects

We tested three patients with complete callosotomy (A.A., N.G., G.C.). As control groups, we investigated five patients with partial callosotomy (L.M., S.R., G.S., L.D., C.E.) and nine healthy subjects. The patients' case histories are summarized in Table 2. (Further details of the case histories for A.A. and N.G. can be found in Bogen, 1969; Milner and Taylor, 1972; Zaidel, 1998).

MRI examination verified the completeness of callosotomy in A.A., N.G. and G.C., but the status of the anterior commissures could not be evaluated (see Bogen *et al*., 1988, for further description of A.A. and N.G.). Except for fibres in the rostrum and ~1 cm of the midportion of the corpus callosum, the section was almost complete for L.M., while G.S. had a section of ~seven-eighths of the corpus callosum sparing the rostrum and splenium. S.R., L.D. and C.E. had a section of the anterior two-thirds of the corpus callosum. S.R. had an additional left fronto-temporal resection and a left amygdalo-hippocampectomy. The healthy controls were chosen from a cohort of 122 healthy adults tested neuropsychologically for a previous normative study at the Montreal Neurological Institute in 1993/1994.

The study was approved by the Ethics committee of the German Research Association, the Ethics committee of the Free University of Berlin Medical School, and the Ethics committee of the Montreal Neurological Institute. All subjects signed the Neuropsychology consent forms currently used at the Montreal Neurological Institute and Hospital. Concerning the special situation of video taping the pantomime demonstrations an additional form was given in which the subjects were asked (i) for their assent to the evaluation of the video tapes by two raters and colloborative researchers, and (ii) for their assent to show parts of the video tapes for educational purposes.

The three groups were matched as closely as possible according to gender ($\chi^2 = 0.154$; exact $P = 1.0$). There was no significant difference in mean age ($F = 1.503$; $P = 0.252$). All patients except C.E. had IQs within the low average range on the Wechsler Adult Intelligence Scales. C.E. had an average

Table 2 *Summary of patients' case histories*

Patient	Sex	Callosal surgery	Extracallosal damage	Age at surgery (years)	Age at testing (years)	WAIS IQ at testing
A.A.	M	Single stage complete callosotomy	L fronto-parietal, R frontal	14	50	79
G.C.	M	Three stage complete callosotomy	L superior temporal, L optic radiation/visual cortex (functional diagnosis)	33, 35, 38	46	78
N.G.	F	Single stage complete callosotomy	L posterior, temp., R central	30	66	81
L.M.	M	Two stage callosotomy, ~1 cm spared fibres in mid-truncus and rostrum	L temporal atrophy, bi-occipital lesions L>R	12, 13	23	76
G.S.	M	Single stage callosotomy (7/8), rostrum and splenium spared	bi-parieto-occipital	24	29	71
S.R.	M	Two stage anterior callosotomy	L fronto-temporal resection, L amygdalohippocampectomy	24, 25	37	84
L.D.	F	Single stage anterior callosotomy	(+ resection of craniopharyngioma)	40	59	88
C.E.	F	Single stage anterior callosotomy	–	36	45	92

IQ. The IQs of the healthy controls were distributed almost evenly within the average range. Handedness was established with a questionnaire currently used at the Montreal Neurological Institute and Hospital. All subjects were right-handed except for one healthy control, who was ambidextrous with a strong tendency towards right-handedness.

Sensorimotor testing included passive movement of the fingers, simultaneous sensory stimulation of the hands, pinch or grip strength, free and sequential tapping, and manual dexterity [Grooved Pegboard (Matthews and Kløve, 1964) and Purdue pegboard (Tiffin, 1968)]. A deficit in passive movement of the fingers was found in A.A. bilaterally (especially for the right hand) and in N.G. for the right hand only. For A.A., this deficit had been described before and attributed to his left hemisphere lesion (Milner and Taylor, 1970). Both patients also had astereognosis involving the right hand selectively (Zaidel, 1998). In the partial callosotomy group, L.M. showed a bilateral deficit in perceiving light touch and position sense. Sensory extinction for the left hand occurred only in two partial callosotomy patients (L.D., G.S.) and in one healthy control. No extinction errors were found in the patients with complete callosotomy.

There was no evidence of paresis in any participant as determined by pinch and grip strength examination. The pegboard and simple tapping tests showed some general slowing in all patients, a result likely associated with their anti-epileptic medication. Bimanual synchronous, symmetrical cooperation (Purdue pegboard) was not particularly disturbed in the patients with complete callosotomy. When age effects are considered, these results concur with previous examinations in 1967 and 1976 by Campbell and colleagues (Campbell *et al*., 1981). Bimanual synchronous, asymmetrical coordination (sequential tapping) was tested only in the partial callosotomy patients and the healthy controls; results were in the normal range. Overall, the motor tests results concur with those reported in a previous investigation on partial and complete callosotomy patients with a similar test battery (Zaidel and Sperry, 1977).

The patients with complete callosotomy were slightly better with the right hand than with the left hand in moving to command and were mildly dyspraxic with both hands when required to imitate hand and finger postures. In the imitation of hand postures, they performed worse with their left hands than with their right, whereas in the imitation of finger postures, they performed worse with their right hands than with their left. Copying drawings of meaningful objects, such as a cup, was slightly better with the left hand than with the right hand.

Materials and procedures

Pantomime of object use and actual demonstration with objects were tested with 11 objects (scissors, ball, glass, key, pen, comb, toothbrush, pitcher, screwdriver, cigarette and spoon; only 10 objects were tested for A.A., G.C., G.S. and two healthy controls), and with six pairs of objects (needle and thread, plate and dishcloth, knife and fork, hammer and nail, match and matchbox, cap and bottle).

On the first day, each single object and each object pair was presented visually to the participant who was asked to pantomime how s/he handles the object in everyday life. The investigator held the object 2 m in front of the participant who could start the pantomime at will. The participant was free to take as much time as needed to perform the pantomime task.

In the first phase of the pantomime experiment, 11 (10) single objects were tested with the spontaneously preferred hand. Subsequently, bimanual pantomime was tested with the six object pairs, allowing the participant to use the right and left hands according to his/her preference. The single objects were then tested again, but this time the participant was asked to use the 'other' (non-preferred) hand. This order enabled us to estimate hand preference effects.

On the second day, the same objects were presented to the participant who was again asked to demonstrate how s/he handled the objects in everyday life. But this time, the participant had to manipulate the objects. The objects were placed in neutral orientations centrally 50 cm in front of the participant on a table, e.g. the handle of the screwdriver was directed towards the participant's midline. The order of presentation of the tasks was the same as on the day before: unimanual execution with the preferred hand; bimanual execution with preferred distribution of the two objects to the right and left hands; and unimanual execution with the non-preferred hand.

Each participant's performances were taped with a video camera (Sony DCR TRV900E miniDV camcorder) placed 2.5 m in front of the participant. The video tapes were then digitized to MPEG format. This procedure permitted use of the movement analysis program Media Tagger (Brugman and Kita, 1995) for the evaluation of the video files. This software allows movement units to be selected and tagged with a value.

In our study, each movement unit contained the pantomime/manipulation response for one object and object pair, respectively, i.e. 28 (26) movement units per participant were coded 11 (10) responses with the preferred hand + six bimanual responses + 11 (10) responses with the non-preferred hand. For the evaluation of the pantomime experiment, the tagged videos were shown to two trained independent raters who were blind as to the subjects' diagnoses and research hypotheses. The videos were evaluated without sound to avoid procurement of clues by the subjects who may have been verbalizing while carrying out the task. As the demonstrations with actual object use were obviously normal, the evaluation procedure was reduced to a sample including the three patients with complete callosotomy, one patient (L.M.) with partial callosotomy and three healthy controls, and to a coding of the video data by one rater alone.

The criteria for the evaluation of apraxic errors were grouped into two main categories according to the theoretical distinction between concept and execution errors (Liepmann, 1908; Heilman and Rothi, 1993):

Concept errors

This main category refers to apraxic errors in which the correct concept is not retrieved, i.e. the target movement is not recognizable. The following error types are based on classical descriptions of apractic errors (Liepmann, 1908; Poeck and Kerschensteiner, 1975; Poeck, 1986).

Substitution

The correct movement is replaced by another definite movement and performed clearly and without hesitation. This could be: (i) another meaningful movement that is incorrect in the actual context, e.g. to pantomime eating when a ball is presented; or (ii) a non-meaningful movement, e.g. elbow flexion/extension or small, repetitive movements such as fidgeting, rubbing or grasping. If it turned out during the course of the experiment that a particular substitution, e.g. fist opening/closing, was performed repeatedly in different tasks, the first substitution was coded retrospectively as a perseveration.

Perseveration

The correct movement is replaced by another movement that has occurred in a previous task either correctly or as an error. The perseverating movement can be: (i) meaningful, e.g. when the pen is presented, the subject perseverates turning the key which was the correct response in a previous task; or (ii) non-meaningful, e.g. rubbing fingers, elbow flexion/extension.

Associative movement

The correct movement is replaced by another movement that shares one feature (e.g. the idea of rotation) with the target movement, e.g. instead of pantomiming how to screw a cap on a bottle, the hand is circling around the opening of the imagined bottle. The concept is not recognizable if the task is not known. This error type was added to the error classification as described in the literature.

Searching movements

The subject shows a clear effort to find the correct movement pattern. Different movements and hand shapes are tried out. The movements are usually slow and hesitant, and performed under visual control. If there is a successful stepwise approach to the target movement, this error type is the same as 'conduites d'approche' (Poeck and Kerschensteiner, 1975). If the correct concept was finally retrieved, two codes were given for the response (see below): (i) searching; (ii) correct concept (see Table 4: + = corrected in the course of the response).

Supplementary concept error types (coded only in the bimanual pantomimes)

Supplementary error types were used during the evaluation of the cooperation between the right and left hands in the bimanual pantomime tasks. The following error types refer to signs of mutual influence between the two hands (one hand affects the behaviour of the other hand in a non-meaningful manner).

Mirroring

One hand acts like the mirror image of the other hand. Zülch and Müller (1969) described 'identical associated movements', e.g. volitional flexion of the right index finger is accompanied by an involuntary flexion of the index finger of the left paralysed hand. As this phenomenon can even be observed after hemispherectomy, it has been suggested that ipsilateral pathways are responsible for the mirror movement. This assumption was supported by Preilowski (1975) who found that 'mirror movements' are as simple as single arm movements for split-brain patients (including N.G.), in contrast to their severe impairment for parallel movements.

Following

The pantomime movement of one hand is followed immediately by the same movement by the other hand, e.g. the right hand moves to the mouth to pantomime drinking and the left hand follows immediately so that both hands end up in front of the mouth. Judging from their examples, this feature is similar to what Tanaka and colleagues (Tanaka *et al.*, 1996) describe as the left hand making 'symmetric movements to the right', with the two hands possibly acting successively. Tanaka and colleagues propose that these abnormal movements result from bihemispheric activation, with the right hemisphere disconnected from the left dominant hemisphere for volitional control of movement.

Both hands unrelated

In bimanual pantomimes, concept errors in one hand imply that the bimanual coordination is neither meaningful nor complementary. The error type 'both hands unrelated' specifically refers to the case in which the right and left hands do not show concept errors, perform independently correctly and assume complementary roles, but in which the actions of the two hands are spatially (and temporally) unrelated to each other. Included here is the classical diagonistic dyspraxia or intermanual conflict in which one hand is acting at cross-purpose to the other hand (Akelaitis *et al.*, 1945; Bogen, 1993; Tanaka *et al.*, 1996; Zaidel *et al.*, 2003).

Execution errors (coded only in the unimanual pantomimes)

This error category refers to minor apraxic errors in which the correct movement concept is recognizable, but the execution of the target movement is deficient. At least one phase of the response needs to be conceptually correct to evaluate the execution. The following error types are based on categories from the Laban movement analysis (Dell, 1977; Laban, 1988), from computer-based kinematic analysis (Poizner *et al.*, 1990; Hermsdörfer *et al.*, 1996) and from other studies that focus on the qualitative analysis of apractic errors (Haaland and Flaherty, 1984; Ochipa *et al.*, 1994):

Effort error

This error type refers to movement dynamics (i.e. acceleration/deceleration, free/bound flow and lightness/strength). The inadequate quality is chosen, e.g. pantomiming bringing a glass to the mouth with acceleration and free movement flow (i.e. the hand 'shoots' to the mouth). Examples for this error type from computer-based kinematic analysis are hesitation at transition points between movement components (deceleration and bound flow) and irregularities in velocity with multiple peaks (Poizner *et al.*, 1990).

Spatial error

This error type refers to the invisible path drawn by the moving body part in three-dimensional space (on the video it is best assessed with 20% playback speed). This includes:

(i) A wrong movement path with inappropriate movement axes, e.g. when pantomiming bringing a glass to the mouth the arm raises vertically, making a break and then moving sagittally to the mouth instead of moving in a smooth curve to the mouth ('spatial errors', Poizner *et al.*, 1990; 'trajectory errors', Hermsdörfer *et al.*, 1996).

(ii) In repetitive movements, an irregular path with a big variance between the single movements, e.g. when brushing teeth, the single up-down movements vary in amplitude.

(iii) The use of wrong joints, e.g. when demonstrating the use of a screwdriver, performing an abduction/adduction of shoulder joint instead of supination/pronation of the lower arm ('distal joint control', Poizner *et al.*, 1990).

Hand position error

Errors in this category refer to the static position of the hand (i.e. its location and orientation) in relation to the external reference point, e.g. moving the imagined tooth brush to the forehead (location error) and with the back of hand oriented towards the forehead (orientation error) ('external configuration orientation', Ochipa *et al.*, 1994; 'orientation', Haaland and Flaherty, 1984; 'final position', Hermsdörfer *et al.*, 1996);

Hand shape error

This type refers to errors in the static hand shape, which is actively formed when the participant grasps and then holds the imagined or real object ('internal configuration', Ochipa *et al.*, 1994). Each object requires a specific grip that adapts adequately to the form of the object [precision grip, lateral grip, fist grip, V-grip (Mai *et al.*, 1993)]. An example for a hand shape error in the screwdriver pantomime is the display of a precision grip, which is normally applied for holding a needle.

Additional features (coded only in the unimanual pantomimes)

Body-part-as-object (BPO)

These features are pantomimes in which the hand is shaped as if it were the object, e.g. the hand does not pretend to hold the scissors, but is the scissors. This feature has been investigated in several studies (Haaland and Flaherty, 1984; Duffy and Duffy, 1989; Mozaz *et al*., 1993; Ochipa *et al*., 1994; O'Reilly, 1995). BPOs are not considered execution errors; our data suggest that BPOs cannot be generally classified as a pathological feature, but different types of BPOs have to be distinguished. This finding supports the position of Duffy and Duffy (1989).

Vocal augmentation

Vocal augmentations are meaningful and non-meaningful paralinguistic features such as clicking the tongue and smackering that accompany the motor actions (Poeck and Kerschensteiner, 1975). These features were noted only by the first author as the two raters evaluated the videos recordings without sound.

As the participants were free to take as much time as necessary to perform a pantomime or an object use task, some of them—especially those who had trouble performing the task—presented responses with several attempts to find a solution. Hence, for example, two different concept errors could occur during a response. Therefore, the raters had the option, when warranted, to code a maximum of two different types in each of the three main categories (concept errors, execution errors and additional features) per movement response. The qualitative analysis in Results below refers to all the errors that were observed. The statistical analysis of the data considered only one coding per main category (the first) and the response.

Results

Pantomime to visual presentation of objects

Statistical analysis was performed on the subjects' overall error scores (i.e. the number of responses with an error divided by the total number of responses) for concept errors, execution errors and, analogously, for additional features. The scores were calculated separately for the right and left hands, and for the unimanual and the bimanual conditions. Inferential statistics [mixed ANOVAs (analysis of variance)] were attempted with the three score categories as exploratory analyses, using group as a between subjects factor, and condition (unimanual or bimanual) and laterality (right hand or left hand) as repeated factors.

While statistically significant results were obtained for each analysis, evidence of satisfying assumptions regarding variances and multivariate normality could not be obtained. This was most likely due to the small sample sizes and the fact that patients with partial callosotomy and healthy subjects made very few errors. Thus, as a cautionary measure, we have chosen to primarily describe trends in the data. Descriptions of the types of gestural errors in each category—concept error, execution error and additional features—are presented in the second part of the results section.

The inter-rater reliability (Spearman correlation coefficient) in the unimanual pantomime tasks was: concept errors, $r = 0.91$; execution errors, $r = 0.76$; additional features, $r = 0.77$. In the bimanual pantomime tasks, inter-rater reliability for concept errors was $r = 0.83$. (Note that in the bimanual condition, execution errors and additional features were not evaluated and supplementary concept error types were examined that refer specifically to bimanual actions.)

Concept errors, execution errors and additional features (quantification)

Table 3 shows the scores for (i) concept errors, execution errors, BPO presentations and correct responses in the unimanual pantomimes and for (ii) concept errors in the bimanual pantomimes for all subjects for the right and left hands. Means for each subject group are represented by condition (unimanual versus bimanual) and laterality (right hand versus left hand).

Visual analysis of the means for concept errors (Table 3, first two and seventh/eighth columns) show that healthy subjects made no errors in either condition with either hand, patients with partial callosotomy committed very few errors across conditions and laterality, and patients with complete callosotomy showed the most errors. They made consistently more errors with the left hand than the right regardless of the pantomime condition, and they had the most errors in the bimanual condition with the left hand. Analogous mixed ANOVA results are significant main effects for group [F(1) = 35.80; $P < 0.0001$], laterality [F(1) = 45.30; $P < 0.0001$] and condition [F(1) = 6.37; $P < 0.024$], and the significant interactions of group × condition [F(1) = 4.37; df = 2; $P < 0.034$], group × laterality [F(1) = 33.97; $P < 0.0001$] and group × laterality × condition [F(1) = 4.31; $P < 0.035$].

For execution errors in the unimanual condition, visual ordering of the means presented in Table 3 (third and fourth columns) from smallest to largest for the left hand follows the pattern: healthy subjects, patients with partial callosotomy, patients with complete callosotomy. A different pattern is visible for the right hand with partial callosotomy patients making more errors than complete callosotomy patients. Further, the mean left hand execution error performance for the complete callosotomy patients was 10× greater than their mean performance with the right hand and 6× greater than the left hand performance of the partial callosotomy patients. This is analogous to significant effects for group [F(2) = 23.68; $P < 0.0001$], laterality [F(1) = 35.19; $P < 0.0001$] and the interaction of group × laterality [F(2) = 25.75; $P < 0.0001$] in mixed ANOVA.

Table 3 *Scores for all subjects and group means for concept errors, execution errors and correct responses in the unimanual pantomimes and for concept errors including supplementary concept errors in the bimanual pantomimes and for BPO presentations in the unimanual pantomimes*

	Unimanual pantomimes						Bimanual pantomimes		Unimanual pantomimes	
	Concept errors		Execution errors		Correct		Concept errors		BPO	
	Right hand	Left hand	Right hand	Left hand	Right hand	Left hand	Right hand	Left hand	Right hand	Left hand
Patients with complete callosotomy										
A.A.	0.10	0.20	0.10	0.60 (0.40)	0.80	0.20	0	0.83(0.25)	0	0
G.C.	0	0.20(0.20)	0	0.88*(0.13)	1.0	0.10	0	0.25	0	0
N.G.	0	0.63	0.09*	0.43*	0.91	0	0	0.67(0.33)	0	0.36
Mean	0.03	0.34	0.06	0.66	0.90	0.10	0	0.58	0	0.12
Patients with partial callosotomy										
L.M.	0	0	0.09	0.18	0.91	0.82	0	0	0	0
G.S.	0	0.10	0.20	0.30	0.80	0.70	0	0.08	0	0.10
S.R.	0	0	0	0	1.0	1.0	0	0	0	0
L.D.	0	0	0.09	0	0.91	1.0	0	0	0.18	0.18
C.E.	0	0	0.09	0	0.91	1.0	0.08	0	0	0.09
Mean	0	0.02	0.09	0.10	0.91	0.90	0.02	0.02	0.04	0.07
Healthy subjects										
1	0	0	0	0	1.0	1.0	0	0	0	0
2	0	0	0.09	0	0.91	1.0	0	0	0	0
3	0	0	0	0	1.0	1.0	0	0	0	0
4	0	0	0	0	1.0	1.0	0	0	0	0
5	0	0	0	0	1.0	1.0	0	0	0	0
6	0	0	0.09	0.18	0.91	0.82	0	0	0	0
7	0	0	0	0	1.0	1.0	0	0	0	0
8	0	0	0	0	1.0	1.0	0	0	0.09	0
9	0	0	0	0	1.0	1.0	0	0	0.09	0
Mean	0	0	0.02	0.02	0.98	0.98	0	0	0.02	0

Scores of responses in which two different error types of one main category occurred are given in brackets, e.g. a perseveration and an associative error in one response. *As execution errors can only be evaluated if in at least one phase of a pantomime response the correct concept can be recognised, the execution error scores in GC and NG are based on fewer tasks than in the other subjects, i.e. on 8 and 7 tasks, respectively.

The last two columns in Table 3 show the scores for BPO presentations. The scissor task was excluded because, in 56% of all subjects' scissors pantomimes, the hand represented the scissors instead of holding the imagined scissors. Because the display of BPO in pantomiming the use of scissors was the most common response in all three groups, it can be regarded as a cultural emblem for scissors. Therefore, only the BPOs in other pantomime tasks were scored. BPO use other than in the scissor task were displayed in all three groups, but N.G. was outstanding by displaying BPOs in four out of 11 unimanual tasks and only with her left hand (e.g. while the left hand represented a toothbrush with the index finger extended, the right hand showed the correct handgrip in the same task by forming around the imagined toothbrush). Not shown in Table 3 is the additional feature 'vocal augmentation', which was displayed by N.G. only. In three left hand pantomimes, she produced inadequate vocal augmentation; N.G. clicked with her tongue in the glass and spoon pantomimes, and smacked her lips in the cigarette pantomime.

Types of concept errors and execution errors (qualitative analysis)

The following qualitative analysis refers to the different types of concept errors and execution errors. Only those subjects in whom the respective types occurred are listed in Tables 4 and 5. Table 4 shows the scores for the different concept error types separately for the right hand, the left hand and the coordination between both hands (supplementary concept error types). The scores are based on the unimanual and the bimanual conditions, except for the scores of the supplementary concept errors types, which were coded in the bimanual condition only.

The three split-brain patients displayed different concept error types with their left hands. A.A.'s predominant left hand error type was searching, i.e. he tried out different hand shapes, hand orientations and movements under visual control, slowly and with bound flow. The associative error was performed in the cap and bottle task in which the subject has to pantomime screwing the cap on the bottle. A.A. circled his left hand at wrist level describing a circle around the opening of the imagined bottle, instead of screwing with the fingers. There was one concept error by the right hand, a meaningful perseveration (persistent key-turning in response to the presentation of a pen) that was repeated in an identical manner in left hand testing. This error repetition in left hand testing is particularly noteworthy. In the first two tasks of the bimanual condition, A.A. displayed mirroring, e.g. both hands threaded or wiped the dishes simultaneously. As the right hand started these activities, we can assume that the left hand mirrored the right hand.

G.C. showed some non-meaningful perseverations and errors, specifically in the coordination of the two hands. In the 'unrelated-error', the separate right and left hands each pantomimed the use of knife and fork correctly, but they acted

Table 4 *Scores in concept error types in the right and left hands, summed over the unimanual and the bimanual conditions, and supplementary concept error types concerning the coordination between both hands in bimanual condition*

	Right hand		Left hand					Both hands		
	Meaningful perseveration	Non-meaningful substitution	Associative	Meaningful perseveration	Non-meaningful perseveration	Searching	Non-meaningful substitution	Following	Mirroring	Unrelated
Patients with complete callosotomy										
A.A.	0.06–	0	0.06+	0.06+	0	0.25+	0	0	0.13+ (LH)	0
G.C.	0	0	0.06–	0	0.13–	0.06–	0.06+	0.06+ (LH)	0	0.06– (LH + RH)
N.G.	0	0	0.06–	0.18±	0.35–	0	0.12±	0	0	0
Patients with partial callosotomy										
G.S.	0	0	0.03+	0.06+	0	0	0	0	0	0
C.E.	0	0.05+	0	0	0	0	0	0	0	0

+ = errors corrected in the course of the responses; – = errors not corrected in the course of the responses; ± = in some responses, errors of this type were corrected. LH = left hand; RH = right hand.

Table 5 *Scores in execution error types in right and left hands in the unimanual condition*

	Right hand				Left hand			
	Effort error	Spatial error	Hand position error	Hand shape error	Effort error	Spatial error	Hand position error	Hand shape error
Patients with complete callosotomy								
A.A.	0.10	0	0	0	0	0.30	0.30	0.40
G.C.	0	0	0	0	0.38	0.50	0	0.13
N.G.	0.09	0	0	0	0	0	0.14	0.29
Patients with partial callosotomy								
L.M.	0	0	0.09	0	0	0	0.18	0
G.S.	0	0.20	0	0	0	0.20	0	0.10
L.D.	0.09	0	0	0	0	0	0	0
C.E.	0.09	0	0	0	0.09	0	0	0
Healthy subjects								
11	0	0	0	0.09	0	0	0	0
17	0	0	0.09	0	0.09	0	0	0.09

in a spatially and temporally unrelated manner. The left hand started alone to pantomime the use of the fork and, while it was moving towards the mouth, the right hand started to cut. Then the left hand went back to home base position while the right hand continued cutting. In the 'following error' that occurred in the bottle and cap pantomime, G.C.'s right hand moved to the mouth and was immediately followed by the left hand, which also moved up so that both hands ended up in front of the mouth.

N.G. displayed many substitutions and perseverations, mostly non-meaningful (e.g. fidgeting and waving), with the left hand.

Two patients with partial callosotomy, G.S. and C.E., displayed the following error types: non-meaningful substitution; meaningful perseveration; and associative error.

In several tasks, concept errors were displayed in the first phase(s) of the response and, after several attempts, the patients finally retrieved the correct concept and performed it either correctly or with an execution error (see + and – signs with scores in Table 4). Uncorrected concept errors occurred only in the complete callosotomy group. There were also clear differences between the three split-brain subjects. A.A. always ended up retrieving the correct concept, with or without execution error. G.C. and N.G. were able to overcome concept errors only in about one -third of the trials.

Table 5 shows the scores for the execution error types in right and left hands in the unimanual condition.

The three split-brain patients also differed in their patterns of execution errors. With his left hand, A.A. showed many hand shape errors (e.g. makes a fist instead of a lateral grip for holding the plate), hand position errors (e.g. his hand combed in front of the face) and spatial errors (e.g. in the screwdriver pantomime, he performed an ab/adduction of the upper arm instead of supination/pronation of the lower arm). Hence, A.A.'s execution errors, were mostly distal, i.e. hand shape errors and hand position errors. His spatial errors (subtype: use of wrong joints) were also indicative of a lack of distal control. G.C. showed predominantly effort and spatial errors in his left hand performances. In the ball pantomime, G.C.'s hand did not relax after having thrown (persistent bound flow) and, in the glass and the spoon pantomimes, the lower arm was 'thrown' to the mouth (inadequate acceleration and free flow). All spatial errors were characterized by a correction of the path from home base position to the target or locus of acting (e.g. in the comb pantomime, the left hand raised towards the breast, then the route was corrected and the hand continued in the direction of the head). N.G. showed a hand shape error, e.g. precision grip in screwdriver pantomime (this could likewise be coded as a BPO error with the hand functioning as a screwdriver) and hand orientation errors, e.g. in the drinking pantomime, the left hand ended above the head.

Demonstrations with object manipulation

In the demonstrations with actual object manipulation, no concept errors occurred in any of the three patients with complete callosotomy, or in the four representative subjects in the two control groups. Only some execution errors were observed in the split-brain group. It is further noteworthy that A.A. used his left hand for the fine graded movements of the bimanual tasks using the needle and thread, plate and dishcloth, cap and bottle (i.e. for threading, dishwashing and cap screwing) while his right hand held the needle, plate and bottle, respectively (retest-reliable). [In contrast, in the pantomime condition, A.A. spontaneously used the right hand for threading and dishwashing. Only in the cap and bottle pantomime, did he first hold the bottle with the right hand as in the object use task, but then, as he did not achieve the screwing movement with the left hand (see error type description), he switched hands and started to pantomime screwing the cap with the right hand.] G.C. showed a spatial error in the left hand, i.e. he moved the head more than the toothbrush when brushing teeth. No execution errors occurred with N.G. and with the four sample subjects.

Discussion

The patients with complete callosotomy showed a difference between the performances of their right and left hands in the pantomime condition. Whereas their right hand pantomimes were almost always correct, with the left hand, they displayed a broad range of responses with concept errors, execution errors, additional features and correct pantomimes. With their right hands, the patients with complete callosotomy showed a similar performance to that of the patients with partial callosotomy and the healthy controls, but their left hand performances differed from those of the two control groups. In the object use condition, the patients with complete callosotomy performed equally well with both hands and did not differ from the two control groups.

Hence, the most important result of this study is the observation of errors in the split-brain patients' left hand performances in pantomime to visual presentation of object while demonstration with object manipulation is preserved. Before we discuss these findings with respect to hemispheric specialization, we refer to the qualitative movement analysis to determine whether ipsilateral or contralateral pathways control the split-brain patients' left hand motor actions.

A.A.'s error pattern in the pantomime condition provides several strong arguments for ipsilateral (i.e. left hemispheric) control of the left hand. In contrast to G.C. and N.G., A.A. was more impaired with his left hand in the bimanual pantomime condition (83% of the tasks) than in the unimanual condition (20% of the tasks). This constellation is compatible with the assumption of ipsilateral control, as the left hemisphere can readily control unimanual left hand pantomimes via ipsilateral motor pathways, but has a very limited capacity to control bimanual, non-mirror movements (Preilowski, 1975; Zaidel and Sperry, 1977). In several bimanual pantomimes, A.A.'s left hand mirrored the right hand. In addition, a likely explanation for the occurrence of an identical meaningful perseveration error by the right and left hands is that the error originated solely from the left hemisphere rather than that the right hemisphere replicated the same error independently from the left. A.A.'s predominant concept error type was 'searching', suggesting that the movements of his left hand were motivated by the awareness of incorrect performance and the attempt to retrieve the correct concept. The searching movements were accompanied by an obvious attempt of visual control, which can be interpreted as a strategy used by the left hemisphere in order to compensate for deficient distal sensorimotor control by ipsilateral pathways. A plausible alternative explanation for the visual control is visual cross-cueing with the competent left hemisphere guiding the pantomime performance of the left hand, which is motorically still controlled by the right hemisphere. A.A. always ended up retrieving the correct concept, which he then performed correctly or with distal execution errors. In the demonstrations with object manipulation, A.A. demonstrated good right hemisphere competence, especially for fine-graded object manipulations. There was even a spontaneous and retest-reliable preference of the left hand for tasks that required fine distal motor control such as threading, indicating that in the object use condition contralateral pathways controlled his left hand. This finding is also compatible with his history of a sensory deficit in the right hand.

G.C.'s left hand concept errors in the pantomime condition suggest right hemisphere control. In contrast to A.A., G.C.'s left hand performance did not deteriorate in the bimanual pantomime condition, i.e. with simultaneous right hand activity. G.C. displayed pantomimes in which the right and left hands acted correctly independently but were spatially and temporally unrelated (supplementary concept errors types: unrelated and following). This behaviour indicates that the two hands are controlled by different hemispheres. Further concept error types displayed by G.C. consisted of non-meaningful perseveration, non-meaningful substitution and associative movement. These errors cannot be generated in the left hemisphere, as they essentially reveal an incompetence to retrieve a correct movement concept. In addition, G.C. was often unable to correct his left hand concept errors. G.C.'s object use was unimpaired with both hands. As his left hand was able to perform distinct distal movements such as threading and screwing, it is plausible that the right hemisphere controlled his left hand in the object use condition.

N.G.'s error type pattern suggests that, in the pantomime condition, the right hemisphere predominantly controlled her left hand. N.G. displayed concept errors in her left hand in about two-thirds of the tasks in both the unimanual and the bimanual conditions. These were mostly non-meaningful substitutions and perseverations. For about half of these concept errors, N.G. was unable to correct them. This constellation is in keeping with an incompetence to retrieve the correct movement concepts and, therefore, right hemisphere control. In addition to concept errors in the unimanual pantomimes, N.G. displayed four distally distinct BPO presentations with her left hand while, for the same objects, the right hand showed the correct handgrips for holding the imagined objects. The qualitatively different responses in the right and left hands are noteworthy and can be interpreted as the two hemispheres providing different movement concepts for the same tasks. The use of BPO presentations has been associated with early developmental stages, a reduced capacity for representational and abstract thinking (O'Reilly, 1995), and more with left hemisphere damage than with right hemisphere damage (see review by Mozaz *et al*., 1993). These propositions concur with the assumption that, in contrast, the BPO presentations in N.G.'s left hand were generated in the right hemisphere. (It should be noted that, in contrast, the performance of BPO presentations of the emblematic type, such as for pantomiming scissors, seems to be part of the normal cultural gesture repertoire, see Results.) Furthermore, only N.G.'s left hand pantomimes were accompanied by vocal augmentation. These types of non-linguistic vocal utterances *per se* are compatible with right hemisphere function. N.G.'s object use was unimpaired with both hands. As in A.A. and G.C., her left hand was able to perform distinct distal movements. Therefore, it is plausible that the right hemisphere controlled her left hand in the object use condition.

Left hand concept errors indicate a right hemisphere deficit in retrieving the correct movement concepts. As outlined above, BPO representations are also indicative of right hemisphere control. The interpretation of left hand execution errors coded only in the unimanual tasks, however, is ambiguous since execution errors can either indicate an underdeveloped concept in the contralateral right hemisphere or insufficient ipsilateral motor control by the left hemisphere. As pointed out by Hermsdörfer *et al.* (1996), kinematic abnormalities, i.e. execution errors, may be a direct indication of insufficient programming of the details of movement execution or an indirect sequel of conceptual errors. Therefore, the exact significance of execution errors warrants further investigation. Lateralized visual input would have been particularly useful to clarify the *post hoc* question of ipsilateral versus contralateral motor control, especially for execution errors. However, our original intention was to compare pantomime of object use to visual presentation of objects with demonstration of object use with object in hand. We also wished to compare unimanual with bimanual conditions. These data showed that the comparison of the four test variations was especially elucidating, i.e. A.A. was impaired in bimanual pantomimes but not in unimanual pantomimes, while G.C. and N.G. were impaired in unimanual and bimanual pantomimes to the same extent. All three patients were impaired in pantomime of object use to visual presentation of objects, but not in demonstration of object use with object in hand. The difference reveals that specific left hemispheric functions are required for pantomimes, but not for object use demonstrations. In this context, lateralized input could only have been realized for the unimanual pantomime condition. Testing bimanual pantomime with bilateral tachistoscopic presentations with one object of a pair to each hemisphere may not have induced the desired intermanual cooperation. For the demonstration of object use with object in hand, lateralized tactile input would not have been methodologically efficient as, at least for A.A. and N.G., substantial ipsilateral tactile projections (to the left hemisphere more than to the right) have been described (Zaidel, 1998).

The unlateralized object presentation implied that both hemispheres were able to see the object and the involved effector. This raises the possibility of visual cross-cueing. However, as outlined above, only A.A. seemed to effectively use visual control for left hand pantomimes. The possibility of visual cross-cueing with unlateralized stimulus presentation might have influenced the performance, but did not prevent left hand concept errors, execution errors and BPO presentations in the split-brain group.

To summarize, the performances of the three split-brain patients suggest that the right hemisphere is less specialized than the left hemisphere in controlling pantomimes to visual presentation of objects. Furthermore, the degree of right hemispheric incompetence is subject to wide individual differences. In contrast, in all three patients, the right hemisphere successfully controlled the demonstrations with object manipulation. The patients showed distinct distal motor control and A.A. even preferred his left hand for fine object manipulation.

Similar findings of dyspraxia in pantomime to visual object presentation co-occurring with preserved object use have been reported previously. De Renzi *et al.* (1982) investigated 150 patients with left hemisphere damage and found significantly better performance in demonstration of object use without sight than in pantomime to visual object presentation. As their sample included two cases with a reverse disturbance pattern, i.e. preserved pantomime and impaired demonstration to tactile presentation (see also Motomura and Yamadori, 1994), De Renzi and colleagues concluded that these types of apraxia result from a disconnection between the areas where information is processed and the areas where the movement is programmed. Interestingly, a patient with spontaneous partial disconnection of the middle and posterior truncus of the corpus callosum (Boldrini *et al.*, 1992), who displayed the same pattern of disturbance as callosotomy patients (i.e. left apraxia to verbal command, intact imitation and intact object manipulation) presented with a clear left apraxia when tested with pantomime to visual presentation of objects.

Before we discuss Boldrini's hypothesis concerning the discrepancy between impaired pantomime and preserved object use, possible confounding factors other than apraxia that might have caused the right hemisphere's incompetence to perform pantomimes should be considered. The left hand concept errors in pantomime to visual presentation of objects could be secondary to right hemispheric deficits in visual perception, motor execution, associative visual object agnosia or in the use of visual feedback. However, concerning the ability to perceive objects, A.A. and N.G. have shown superior tactual–visual performances with their left hand in palpating geometric figures and pointing to the matching picture on a multiple choice card (Zaidel, 1998). The fact that these patients' right and left hands show equal levels of performance in the imitation of hand and finger postures (Zaidel and Sperry, 1977) demonstrates that the right hemisphere is not inferior to the left in the aptitude to transfer visual stimuli directly into direct motor action. A deficit in the motor execution is also excluded, as the patients were able to perform correct motor response if the objects were held in the hands. Previous studies on object recognition have demonstrated that the right and left hemispheres perform equally well in interpreting the meaning of tachistoscopically presented objects, e.g. matching a picture with a tool to a picture with a scene such as a picture of a shovel with a picture of a car stuck in the snow (Gazzaniga, 1983). Zaidel (1979) and Cronin-Golomb (1986) tested, among others, our subjects A.A. and N.G., and found both hemispheres to be equally competent in matching tachistoscopically presented pictures of objects that are associated on an abstract level (e.g. 'calendar' and 'clock' share the abstract concept of time). Trevarthen (1990) reported that, in commissurotomy patients, both hemispheres were able to perform conceptual matches, e.g. a tachistoscopically presented photo of a dollar bill was matched with a coin felt in the hand. Furthermore, in the present study, the left hand BPO presentations indicate that the right hemisphere recognized the meaning of the object (e.g. that the function of a comb is to comb the hair), but the movement concept was deficient (e.g. the hand was used as if it were the comb). A right hemispheric deficit in using visual feedback for online movement control is an unlikely explanation for the left hand deficit in pantomiming. Goodale and colleagues demonstrated that pantomimed reaching for objects was driven by stored perceptual information about the object while real grasping of the object utilizes the normal visuo-motor online control system (Goodale *et al*., 1994). In the present study, no left hand deficit occurred in the condition with visuo-motor online control, i.e. with actual object manipulation.

Furthermore, functional MRI studies show that predominant left hemisphere activation in pantomime tasks occurs not only with visual (Choi *et al*., 2001), but also with auditory (Moll *et al*., 2000) object presentation. In the latter study, activation was found in the intraparietal cortex and the dorsalateral cortex, and could be distinguished from activation due to the verbal task. Hence, there is little reason to assume that the pantomime deficit would depend on a deficit in processing visual information. We tentatively predict that if the separate right hemisphere were exposed to acoustic object presentation, e.g. object noises, a similar deficit in pantomiming the object use would occur.

In the following discussion, we differentiate between two phases in the pantomime and object use demonstration performances. In the first phase, in the object use condition, the real object is grasped and in the pantomime condition, the mental representation of the object is grasped. Different neural pathways are used for these two actions (Goodale *et al*., 1994). In our study, the second phase (i.e. after having grasped the real or imagined object) is similar in the two conditions, as performance had to rely on stored knowledge. The object use demonstrations are partly based on imagination just as the pantomimes, e.g., the screw or the keyhole has to be imagined when demonstrating the use of the screwdriver or key, respectively.

Boldrini *et al*. (1992) explained their findings of impaired pantomime and preserved object use by the left hand by proposing that only pantomime to visual presentation of objects required the left hemispheric semantic analysis of the object. In contrast, pantomiming to tactile object presentation would not require semantic elaboration and could rely on tactual–motor transformation by the right hemisphere alone. The idea of tactual–motor transformation can be related to Liepmann's notion (Liepmann, 1908) that apractic patients were able to actually use objects because the objects guided their hands. Goldenberg and Hagmann (1998) demonstrated that the ability to actually use an object depends not only on the retrieval of instructions of use from semantic memory, but also on the direct inference of the functional movement from the structure of the tool. In their study, corresponding objects such as the padlock for the key and novel objects were provided. The tactual–motor explanation by Boldrini and colleagues (Boldrini *et al*., 1992) can, however, apply only for the first phase of the object use demonstration, i.e. the actual grasping and holding of the object. In this phase, the object-specific tactual information could induce a corresponding motor action, e.g. if the scissors are grasped correctly, there is no other option than opening and closing. In addition to inference of the functional movement from the structure of the tool, another aspect seems noteworthy. The tactual information could provide enough information to avoid performing an initial apractic error. The actual grasping and holding of the object could simply inhibit the performance of apractic patterns in hand and fingers (e.g. perseverative fidgeting is eliminated if the object is held in the hand). In addition, the tactual input could be sufficient to block the immediate execution of an erroneous pattern and give time to find a solution. (In the pantomime condition, several concept errors were only performed as a first response and then corrected.)

Tactual–motor transformation cannot explain the successful performances in the second phase of the object use condition. Like our patients, Boldrini's patient was not tested with actual use of the objects in real context, but he had to demonstrate how he would use them on the basis of imagining the corresponding content (Boldrini *et al*., 1992). Hence, after the initial actual grasping of the object, there was no more tactual feedback, e.g. such as that provided by a keyhole, a paper or by teeth (in actual toothbrushing). There are some further limitations to the proposition that the motor response is based on tactual information. In our study, the patients did not display tactual exploration behaviour, but grasped the objects immediately in the correct manner. In addition, the tactual information that the patients could infer from the handles of the tools was not very specific for the function, e.g. spoon and toothbrush provide similar facilities for the hands to hold them. Therefore, we suggest that the tactual information does not sufficiently enable accomplishment of an object use demonstration. Object use performance must rely on a stored instruction of object use.

The effect of familiarity might play a role in the better performance with object in hand than with pantomiming, because acting with the object is more familiar than acting with an imagined object. Familiar motor actions, including those involving the left hand, reportedly remain intact after callosotomy (Akelaitis *et al*., 1942; Gazzaniga *et al*., 1967). However, for several reasons familiarity is of limited value for the object use condition in our study. The execution of familiar movements is strongly facilitated by the appropriate context in apractic patients (De Renzi, 1999), e.g. a patient with callosal disconnection with left hand apraxia to visual and tactile object presentation showed clear improvement of left hand use in a natural context (Buxbaum *et al*., 1995). In our study, however, the patients' performances in the object use condition could hardly profit from the familiarity of the movements: First, the object use had to be performed in the laboratory. Secondly, the absence of concrete counterparts (corresponding objects or body parts), e.g. toothbrushing is performed without touching the teeth, drinking without touching the mouth with the glass, naturally changes the kinematics of object use demonstration relative to everyday life actions. Thirdly, the object use also has to be demonstrated with the non-dominant hand, a motor action that is unlikely to be automatic. Therefore, the object use task does not primarily tap over-learned patterns and does not differ substantially from the pantomime task with respect to the novelty of the required movements. This holds especially for the examination of the left hand.

We therefore suggest that in the object use conditions, the patients with complete callosotomy rely on right hemispheric instructions for object use. The right hemisphere seems to be able to associate efficiently the tactual object information with the instruction of object use. The assumption is supported by the fact that the right hemisphere has a superior non-verbal memory for tactual information (Milner and Taylor, 1972). The study by Milner and Taylor included A.A. and N.G., and tested with objects similar to the ones used in our investigation. It is plausible that the efficient right hemisphere storage of tactual object information entails a strong connection to the motor instructions for object use.

In contrast, the competence of the split-brain patients' right hemispheres to pantomime is limited and subject to wide individual differences. Hence, in the separated right hemisphere, the retrieval of the instruction for object use based on visual object presentation is deficient. It is noteworthy that in 34% of the unimanual pantomime trials with the left hand, the split-brain patients did not display the correct movement concept. This indicates that the right hemisphere failed to access the correct concept. In the remaining 66% of left hand unimanual trials, the pantomime demonstration revealed a correct concept of how to use the object. However, only 10% of the left hand pantomimes were actually correct as execution errors were prevalent in the other responses. The broad range of left pantomime responses in the split-brain patients with concept errors, execution errors, BPO presentations and correct pantomimes raises interesting questions, which warrant further investigation. For example, for which objects in which pantomime tasks do subjects not have movement concepts at all? When do they show execution errors? Further, for which objects do they show underdeveloped movement concepts as revealed by BPO presentations? Our study was not designed to identify groups of objects for which the three split-brain patients showed correct responses, concept errors, execution errors or BPO presentations. Further studies should test factors such as object familiarity, since the different degrees of familiarity of the objects might explain why the concept of object use can be found for some objects but not for others. Likewise, the understanding of execution errors and BPO presentations as compensatory strategies would be helpful for analysing the faculties that are necessary to pantomime the use of certain objects.

In the following section, we relate the development of the competence to pantomime in the disconnected right hemisphere to Piaget's theory of symbolic play development in children (Piaget, 1962). Several studies demonstrated that children first acquire the ability to actually use objects, then to demonstrate with similar substitute objects, then with dissimilar substitute objects, then to use body parts as substitutes (BPO representations), and finally to perform pantomimes with holding of imagined objects (Overton and Jackson, 1973; Elder and Pederson, 1978; Ungerer *et al*., 1981; O'Reilly, 1995). It has been suggested that unless children are able to abstract the movement concept from the tactile experience of the object and to rely on a mental representation of the objects, they are not able to perform pantomimes. A similar hierarchy could apply to patients with apraxia for pantomime of object use but not for demonstration with object manipulation. Graham and colleagues described a patient who was unable to pantomime to visual object presentation, but able to demonstrate the object use with the object in hand, and with a neutral object in hand, e.g. to pantomime combing with a toy truck in hand (Graham *et al*., 1999). This ability could be compared with the children's ability to demonstrate with dissimilar substitute objects. The display of (non-emblematic) BPO presentations by N.G.'s left hand is compatible with the assumption that the right hemisphere could not connect the motor instruction for object use with a stored perceptual representation of the object; rather the connection was made with a body part representing the object. BPO presentations similar to the ones displayed by N.G.'s left hand are reported for children at ages between 3 and 6 years (Overton and Jackson, 1973) [However, it should be noted that, in general, it is not the case that either the disconnected left or right hemisphere represents some consistent development stage in Piaget's sense (Zaidel, 1978)]. Hence, we suggest that the pantomime dyspraxia results from a right hemispheric deficit in associating perceptual object representation with the motor instruction for object use.

As outlined in the Introduction, different positions are maintained concerning the right hemisphere motor competence in patients with callosal disconnection. According to Liepmann's hypothesis, only the left hemisphere contains the movement concepts and, therefore, is motor dominant. Others propose that both hemispheres contain movement concepts and that callosal apraxia is primarily a verbal–motor disconnection apraxia. A modified version of the latter hypothesis proposes that each hemisphere is able to exert volitional motor control if the command is given in a modality that can be processed in the addressed hemisphere.

Our data show that left hand apraxia in split-brain patients is not limited to verbal commands, but also occurs in pantomime to visual presentation of objects, i.e. callosal apraxia is not a mere verbal–motor disconnection apraxia. The present study demonstrates that modality-specific left apraxia for pantomime, which had been reported only in patients with spontaneous callosal disconnection, can also be found in patients with surgical section. Split-brain patients are similar to patients with spontaneous callosal disconnection in that they display left hand apraxia for pantomime, but they also differ from many patients with spontaneous callosal disconnection because they show no apraxia with actual object use. As suggested in the literature, this constellation demonstrates that spontaneous callosal disconnection can yield a more severe disruption of gesture execution than surgical callosotomy in epileptics. Severe epilepsy often results in neural reorganization leading to bihemispheric representation of cognitive functions. In addition, the period of time after disconnection and the completeness of disconnection represent factors that favour the development of right hemispheric motor competence. The present data show that the right hemisphere is even able to develop movement concepts. The split-brain patients were able to execute the correct movement in object manipulation with either hand in keeping with the hypothesis that both hemispheres contain movement concepts for object use. The ability to pantomime to visual presentation of objects was clearly subject to hemispheric specialization. While the left hemisphere was able to react to this modality, the right hemispheric competence to do so was deficient. We suggest that the right hemispheric impairment to pantomime is related to a deficit in associating perceptual object representation with the movement concepts for object use. In that sense, our findings are consistent with the general proposition that, in split-brain patients, each hemisphere is able to perform meaningful movements if the task is not dependent on hemispherically specialized functions.

A word of caution is appropriate in drawing inferences from the present findings in split-brain patients. The left hand ability for actual object use in split-brain patients does not argue against Liepmann's concept, which refers to the organization of motor competence in the normal brain and not to the condition of a brain with substantial neural reorganization such as in epileptic patients with complete callosal section. In contrast, the left hand apraxia to pantomime even gives some support for Liepmann's proposition as, in the split-brain patients, the left hemisphere is motor-dominant compared with the right hemisphere in the sense that it is capable of retrieving movement concepts in response to different modalities of commands.

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