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Hemispheric specialization in spontaneous gesticulation in a patient with callosal disconnection

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Abstract

This is an investigation of spontaneous gesticulation in a left-handed patient with a callosal disconnection syndrome due to infarction of the total length of the corpus callosum. After callosal infarction, the patient gesticulated predominantly unilaterally with the left hand despite left apraxia. Bilateral gesticulation occurred later on and was presumably achieved by an increase in ipsilateral proximal control. Movement analysis further indicated that the two hemispheres are specialized for certain gesture types. Gestures with emotional connotation and batons (emphasizing prosody) were generated predominantly in the right hemisphere whereas physiographics which picture the linguistic content concretely and deictics (pointing) were of left-hemispheric origin. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

In recent years scientific interest in gesticulation has increased, mediated by the appreciation of gesticulation as a means to monitor emotional and cognitive processes objectively. Numerous studies from diverse research fields have demonstrated that non-verbal behavior specifically reflects emotional states and psychopathology [1,7,9,14,15,18–20,33,44,45,51,52,55,57]. Moreover, psycholinguistic studies have shown that gesticulation can reveal important aspects of speech production processes because of the high informational and temporal coordination between speech production and the generation of co-speech gestures [11,31,32,38]. In addition, gesticulation that accompanies speech also influences receptive and memory processes [5,16].

Several analysis systems especially for hand gestures have been developed for research purposes [12,13,18,38]. There is considerable overlap between these different analysis systems and — despite terminology differences — a basic consensus on the existence of certain gesture types.

The different types of gesture can be distinguished by their function in the communicative context, i.e. give pictorial demonstrations of the linguistic content, illustrate the ideational process, emphasize the prosody, or substitute verbal expressions [10,12,13,38]. Apart from the communicative function, gestures such as self-touch in stressful situations can also express intrapsychic processes [9,14,19].

The differing nature of these gesture types suggests distinct neuropsychological functions and thus different loci of generation in brain. This assumption has been supported by several neuropsychological studies on handedness preference for certain gesture types that, for example, surprisingly revealed that right-handers do *not* prefer the right hand for all gesture types.

Kimura [29,30] differentiated between free movements as 'any motion of the limb which did not result in touching of the body or coming to rest', i.e. this category included all types of gestures as mentioned above, and self-touch, defined as 'any act resulting in the touching of the person's own body'. Her data showed clearly that there was a difference in hand preference for free movements and self-touch. Free movements were related to ear advantage and handed-

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ness. In contrast, this was not found for self-touch, which showed a slight tendency for left hand-preference. These data were supported by several studies [8,28,36].

Some studies applied finer categories for gesture types than the above mentioned studies (the findings are comparable despite different terminology). Pictorial gestures as a specific gesture type to illustrate the linguistic content are predominantly performed with the dominant hand. Souza-Poza [46] found right-hand preference for 'representational gestures', i.e. 'gestures that describe or depict objects', in right-handers. Stephens [48] also reported right-hand preference in right-handers for 'iconics' and 'metaphorics', i.e. pictorial demonstrations of concrete or abstract content, and left-hand preference for these gesture types in left-handers.

Gestures emphasizing the rhythm pattern of speech are apparently produced equally with both hands. No hand-preference for 'beats' in right- or left-handers was found [48] and equal frequencies for right and left hands for 'nonrepresentational movements', i.e. 'small vertical punctuating movements' in right-handers were observed [46]. Only Foundas [17] reported right-hand preference in right-handers for 'emphasis gestures'.

Some studies of self-touch differentiated between continuous types such as rubbing or scratching and short-lasting types which often imply a function such as adjusting hair. Significant left-hand preference occurred in continuous body-touching (>3 s) and no lateralization in discrete body-touching (<3 s) [46]. Stephens [48] found right-hand preference in right-handers in her category of self-adaptors, defined as skilled manual manipulations of body, clothing, etc., therefore reflecting a hand preference in the performance of functional motor actions. Analogously, the investigation of the self-touch pattern in a right-hander showed that the right hand was used for functional self-touch such as adjusting the hair, whereas the left hand was used for 'non-functional movements' such as rubbing or fidgeting [34]. In depressive states, an increase of continuous body-touching, especially with the left hand is reported [51].

As hand preference may reflect hemispheric specialization, studies suggest that most of the free movements while speaking are generated in the language-dominant hemisphere. This seems to apply particularly to the subcategory of pictorial gestures. The subcategory of batons is displayed with equal frequency in both hands.

In contrast to free movements, no such lateralization is found for the main category self-touch in right- or in left-hemispheric language dominant individuals. Finer classifications indicate that the left hand is preferred for 'primitive' types of self-touch having a repetitive, continuous character whereas there seems to be a right-hand preference for functional self-touch.

Concerning the question of hemispheric specialization in gesticulation, subjects with disrupted callosal transfer provide valuable information, as they give the opportunity to investigate the separate hemispheres. The rationale for investigating gesticulation in split-brain subjects is that due to callosal disconnection their hands are mainly controlled by the contralateral hemisphere [23,43,53,54] and therefore, the hemisphere that generates a gesture can be determined by the hand used to perform it.

However, it has to be taken into account that callosotomy patients develop a varying degree of ipsilateral motor control of the proximal limbs over time [2], as the supplementary motor area has bilateral direct efferent pathways to proximal muscles [23,43]. For two young callosotomy patients, it was reported that even ipsilateral control of the fingers was possible with the left hemisphere in 80–90% of the tasks and with the right hemisphere in about 25% [58]. In another case, the left thumb and index finger could be controlled rather efficiently via ipsilateral pathways, whereas fingers 4 and 5 had the least ipsilateral control and in the case of the right hand no ipsilateral control was possible [50].

However, the movement tasks were simple concerning the complexity of the desired motor action response, i.e. moving a finger or establishing a hand/finger posture in reaction to drawings. In the same patients, left dyspraxia was found for more complex tasks (complex movements to verbal command) [58]. Errors were predominant in movements requiring the use of single digits (despite 80–90% ipsilateral left finger control in the hand/finger posture imitation task).

Notwithstanding these few reports of ipsilateral finger control observed in special neuropsychological tests, in several studies on callosal apraxia apractic disturbances are evidenced especially in the distal part of the limbs, affecting fingers more than hands and arms gesture [3,21,56]. It seems likely, therefore, that in a spontaneous situation requiring more complex movements such as gesticulation during an interview, the 'naturally better' hand will be used. Hence, it is plausible that in a right-handed split-brain patient, the left hemisphere will use the right hand in gesticulation accompanying speech rather than the left hand for which the control is less developed. This will apply even more for the right hemisphere, which can achieve only 25% control of the ipsilateral hand when required in special test situations.

So far, there is one investigation by McNeill [38] on gesticulation in two right-handed patients L.B. and N.G. with complete callosotomy including the anterior and the hippocampal commissure. Following McNeill's transcript, Patient N.G. produced only right-hand gestures (iconics, metaphorics, deictics) and Patient L.B. produced 20 left-hand, 11 right-hand, and five bilateral gestures. Beats were only done with the left hand, iconics/metaphorics were done as unilateral right, left, and bilateral gestures, and deictics were done with right and left hands. Hence, McNeill's investigation indicated that deictics and iconics were generated in both hemispheres and beats in the right hemisphere.

This is a study of gesticulation in a patient with an ischemic infarction affecting the entire length of the corpus callosum. While McNeill's patients suffered from intractable epilepsy, a condition in which there are often atypical patterns of neural connection caused by the long lasting disease [22], this patient permitted the investigation of the disconnected hemispheres with neural patterns which were previously basically normal.

We wanted to test the hypothesis that the right and left hemispheres produce different nonverbal gesture types as suggested by the investigations on handedness preference and McNeill's observations. We were also interested in how the patient developed the competence to perform bilateral gestures despite his split-brain condition. If improvement in unilateral apraxia in split-brain patients can be explained by an increase in ipsilateral proximal control [53,54], our hypothesis was that bilateral gesticulation was achieved by one hemisphere controlling the contralateral hand and the ipsilateral proximal arm.

2. Method

2.1. Subject

The patient was a 54-year-old left-handed engineer, who had previously been healthy except for a long-standing insulin-dependent diabetes mellitus type II. The patient was left-handed with an Edinburgh Handedness Inventory laterality quotient of −64 [39]. He preferred the left hand for all manual activities except writing which he had been trained to do with the right hand in school and drawing which he used either hand for depending on the task, e.g. right hand for technical drawings with a ruler and left hand for quick sketches. The patient's maternal grandmother was left-handed.

The patient suffered an acute ischemic infarction damaging the total length of the corpus callosum except for some fibers in the middle of the splenium that might have been spared. Apart from that there was only a small lesion in the left parietal white matter.

The patient presented with an almost complete callosal disconnection syndrome [2] including left hemialexia, left visual anomia, left agraphia, predominantly right constructional apraxia, left apraxia to verbal command and imitation with impaired learning of new motor tasks, double hemianopia and dissociative phenomena.

Under tachistoscopic viewing conditions (2.4–4° from central fixation point) the percentage of correctly identified words were 45% for four letter, 25% for five letter and 10% for six letter words in the left visual field and 75, 85 and 90% in the right visual field (120 trials). Geometrical stimuli were named correctly in 33% and color in 40% in the left visual field as compared to 90 and 100% in the right visual field. With bilateral stimulation there was left neglect.

When motor responses to visual stimuli were required, double hemianopia was evident. Each hand responded correctly to stimuli in the ipsilateral visual field, whereas the correct response rate to stimuli in the contralateral visual field was near chance level.

The patient showed severe left agraphia with production only of neologisms and perseveration (score 0 of 9 possible points, according to Aachener Aphasie Test [27]). After 8 months, his left hand writing to dictation occasionally showed visual resemblance with the target word (score 4/9). When the patient had to compose cards with letters, syllables or words to form dictated words and sentences (composition to dictation), he scored 30/30 points with the right hand and 13/30 points with the left hand.

In a dichotic listening test [40], there was no auditory suppression. The accuracy of detecting the target digit was well above chance level on both sides. The task was to press a button when he heard the digit 'zero' in dichotic listening, tested for each ear with either hand.

In copying with the right hand, there were incoherence and disproportionate relationships between the parts and a loss of perspective. Copying with the left hand was often correct, with the exception of minor errors such as simplified versions with parts absent and slight faults in perspective. The patient attained 13 of 36 possible points with the right hand and 24 points with the left in the Taylor Figure [47].

The patient had severe left apraxia to verbal command. In a test battery derived from Poeck [41] with 22 meaningful and meaningless movement tasks, he showed substitution (in five out of 22 movement tasks), perseveration (5/22), augmentation of movements (4/22), hand configuration errors (3/22), no movement response (2/22) and correct response (3/22). After 8 months, motor reaction to verbal command was mostly correct (15/22), but errors in hand and finger configuration persisted (5/22), i.e. when the patient was asked to bring his index finger to his nose, he used his whole hand instead, or he was unable to perform such single-finger movements as bending his little finger. The other two remaining errors were substitution (1/22) and augmentation (1/22).

The patient also had apraxia to imitation with substitution (2/8), perseveration (1/8), hand configuration errors (3/8) and correct responses (2/8). There was clear improvement after 8 months with mostly correct responses (6/8). However, hand configuration errors persisted (2/8).

In learning a new visuo-motor task the patient took five times longer with his left hand than with his right. In a test design similar to Trail Making A on a computer screen, the patient had to hit each circle in ascending numerical order with the cursor of a computer mouse. The critical measure was the time needed to hit all 20 circles (Norm: after five trials, 16 s per course). The patient, who had never used a computer mouse before succeeded at once with his right hand and reached an asymptotic speed level within ten consecutive trials. In contrast, he took about five times longer to master the task with his left hand. After seven training sets (five trials each), the patient had reached asymptotic speed levels with both hands. At that point, his dominant left hand was slightly faster (16.5 s) than his nondominant right hand (18.0 s) in completing the course.

In contrast to the left apraxia in movement tasks, the patient was able to use his left hand for spontaneous routine motor actions such as catching a ball, throwing and even shaving himself, unless he did not attempt to control the motor action deliberately.

The patient showed dissociative phenomena such as intermanual conflict, e.g. if he lifted the toilet seat with his right hand, the left one closed it again. In clinical testing, e.g. token test, a correct right-hand reaction was often disturbed by an incorrect left-hand interference. There was an 'alien hand' phenomenon in the sense that the patient found the behavior of his left hand uncooperative. A further dissociative phenomenon was gesture-speech mismatch, e.g. the patient said 'No' when asked if he saw a stimulus in his left visual field but simultaneously nodded his head in affirmation.

Further examinations could not be pursued as the patient died due to dilated cardiomyopathy.

To summarize, the disconnection syndrome in this left-handed subject did not differ basically from right-handed split-brain patients. Left hemialexia, left visual anomia and left agraphia indicated left hemispheric language dominance. However, the presence of some right hemisphere language competence was suggested by the absence of auditory suppression and the ability to read 45% of the four letter words presented to the left visual field. It is noteworthy that despite his left-handedness, the patient displayed left apraxia even on imitation and that his right hand was more proficient in learning a new motor skill than his left hand. Hence, we assume that there was left-hemispheric dominance for praxis despite his left-handedness. Left apraxia on verbal command and imitation improved over time, but the remaining distal dyspraxia suggested that the improvement in left apraxia was achieved by an increase in ipsilateral proximal control. The persistent intermanual conflict also indicated to us that there was no recovery of callosal nor of extracallosal pathways for bilateral motor coordination [35].

2.2. Materials

The data source was videotaped interviews (46 min total length) of the patient at 2, 5, and 9 months after callosal infarction. The three interviews were conducted in a standardized setting with regard to place, camera, and interviewer. The patient was encouraged to report how he experienced the split-brain syndrome and how he coped with this impairment in daily life. As this was a retrospective evaluation the duration of the three interviews varied. At T1, the videotaped material lasted 302 s (5 min 2 s); at T2, 430 s (7 min 10 s); and at T3, 2040 s (34 min).

2.3. Measurements

A rating instrument for coding gestures was developed from the Efron classification of gestures [12], which also forms the basis of McNeill's classification of gestures [38] and as such allows comparison between McNeill's and our results. The Efron classification comprises the following categories: baton (emphasizing the beat pattern of the speech), ideographic (sketching a thought pattern), deictic (pointing to a real or imagined object or indicating a direction), physiographic (depicting a form or an action), and emblematic gestures (conventional signs having specific linguistic translation).

Since we aimed at an objective phenomenological classification of gestures based on their visual appearance alone (evaluation of videotapes without sound), we omitted the Efron category ideographic as this gesture type implies an interpretation of the linguistic context (thought pattern). Instead, we used the category physiographic for all gestures of pictorial demonstrations. As the patient frequently displayed two types of emblematics, shoulder shrugs and rise–fall gestures (rise–fall gestures appear to be 'vestiges' of the emblem of rotating the palms face up and shrugging the shoulders), we coded them as separate categories.

In addition, in order to examine specific questions of hemispheric specialization, the laterality of each unilateral gesture was coded as unilateral-right or unilateral-left. In order to understand how the patient managed to gesticulate bilaterally we specified the analysis of bilateral gestures. As suggested by the results from apraxia testing we assumed that the patient was able to perform bilateral gestures without intermanual conflict by activation of only one hemisphere. This hemisphere controls the contralateral arm/hand and the ipsilateral proximal arm. Contralateral (distal) control implies the ability to perform distinct hand and finger movements — here classified as the dominant hand — whereas ipsilateral proximal control does not enable to perform distal hand/finger movements resulting in rough, proximally initiated movements. Therefore, gestures were defined as bilateral left-dominant or bilateral right-dominant gestures.

Activation of both disconnected hemispheres was assumed to result in the disturbance of the distal 'synchrony' of bilateral hand gestures as defined by Condon [6]:

> If one body part moves or changes direction of movement, it does so concomitantly and in concert with the other body parts moving at the same time.... The 'process unit' is observationally defined as the initiation and sustaining of directionality of change of the body parts with each other (the *specific* directions being sustained by the individual parts may differ) across a given moment of time as contrasted with the preceding and succeeding sets of similarly sustained configurations of movement of the body parts [6, p. 224].

Self-dyssynchrony as the disturbance of this organization is not observed in normal subjects. Therefore, bilateral gestures with equal dominance of both hands were investigated as to whether they were distally synchronous or dyssynchronous.

In the case of bilateral gestures without distal hand movements a classification as right-hand/left-hand-dominant or synchronous/dyssynchronous was not possible by definition (noted as bilateral–not determined).

In addition, gesturing with folded hands was coded as a separate category.

2.4. Evaluation procedure

The three videotapes were observed and coded without sound. At the end of each gesture, which was defined as the return to a resting or 'homebase' position, the videotape was stopped and the exact time noted. The laterality and type of gesture was then recorded. Coding natural units of gesture was preferable to time sampling which may distort judgments of the phrasing of the gestures.

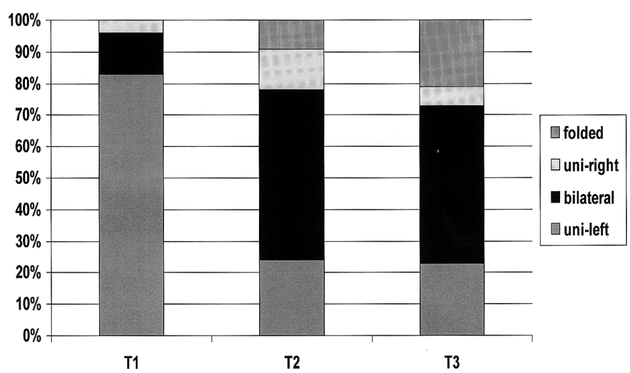

Fig. 1. Percentage of unilateral left (uni-left), unilateral right (uni-right), bilateral gestures (bilateral) and gesturing with folded hands (folded) at two (T1), five (T2) and nine (T3) months after callosal infarction.

Coding was done independently by two trained movement analysts. Rater training consisted of studying the definition catalogue, rating the training tape and checking the coding against a standard evaluation of the training sample.

Rater I was blind to the diagnosis, the specific hypothesis, and the chronology of the three videotapes. Rater II was aware of the diagnosis and the chronology, but the good interrater reliability (see below) indicated that her coding was not biased by this knowledge.

The interrater reliabilities for laterality and gesture type were 0.93 and 0.79 (Cohen's kappa). Since there was good interrater agreement only the results for Rater I are given.

In addition, context analysis as the evaluation of gestures in relation to verbal context was performed with sound. Owing to limited resources, this qualitative analysis was conducted by one rater alone.

3. Results

3.1. Lateralization

Since we were interested in the development of the patient's laterality pattern of gesticulation, we calculated the distribution over time of unilateral right, unilateral left, and bilateral gestures as well as gestures he made while keeping his hands folded. Surprisingly, shoulder shrugs as proximal movements were displayed in the same manner as distal hand gestures, i.e. they also occurred unilaterally right or unilaterally left. We have, therefore, included them in the calculation of the distribution pattern (Fig. 1).

Fig. 1 shows that there was a significant change in the patient's gesticulation pattern with regard to lateralization from T1 (2 months after callosal infarction) to T2 (5 months post infarction) and T3 (9 months post infarction) ($\chi^2 = 44.7$; $P = 0.000$). Two months after callosal disconnection (T1), our patient gesticulated predominantly with the left hand. Over time, there was a significant relative decrease in unilateral-left hand gestures from 83% at T1 to 24% at T2 and 23% at T3 ($\chi^2 = 37.7$; $P = 0.008$). At the same time, there was a significant relative increase in bilateral gestures from 12.5% at T1 to 53.7% at T2 and 50% at T3 ($\chi^2 = 25.64$; $P = 0.000$). In addition, the patient began to display significantly more gesticulation with folded hands with 0% at T1 to 9% at T2 and 21% at T3 ($\chi^2 = 9.6$; $P = 0.008$). No significant changes were observed for the unilateral-right hand gestures.

Since we were specifically interested in bilateral hand gestures, we performed an additional analysis for this gesture group. We analyzed if there was a dominance of

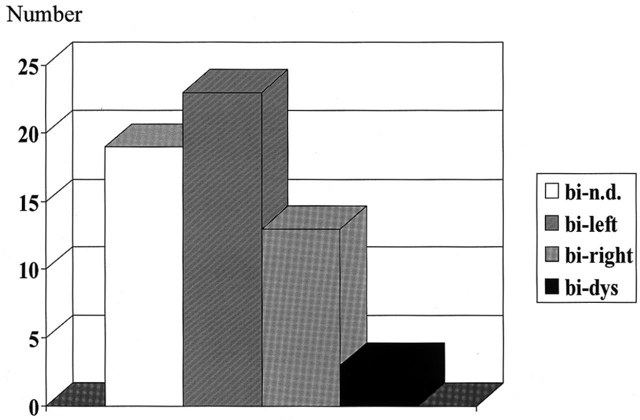

Fig. 2. Number of bilateral hand gestures with no distal motions (bi-n.d.), bilateral-left-dominant (bi-left), bilateral-right-dominant (bi-right) and bilateral-dyssynchronous (bi-dys) hand gestures, summed up across T1, T2, and T3.

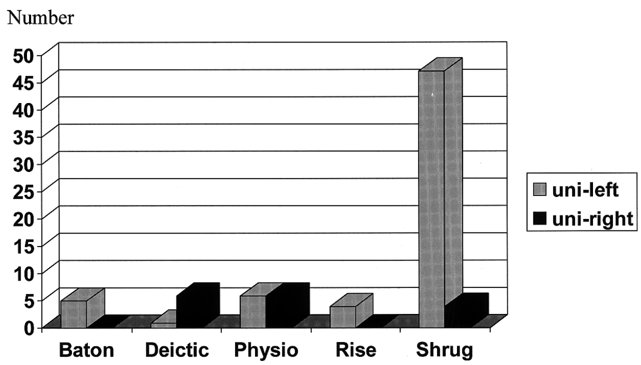

Fig. 3. Number of unilateral-left and unilateral-right gestures for each gesture type, summed up across T1, T2, and T3.

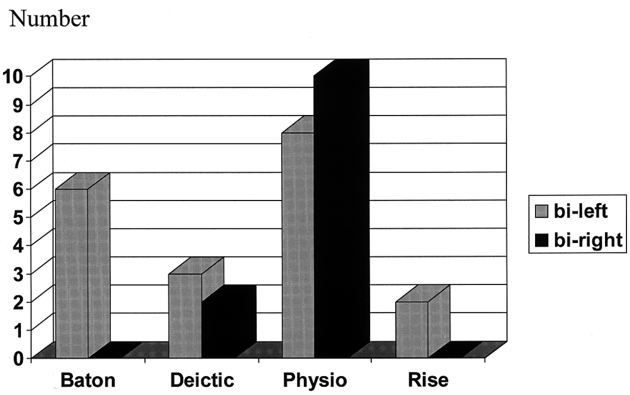

Fig. 4. Number of bilateral-left-dominant and bilateral-right-dominant hand gestures for each gesture type, summed up across T1, T2, and T3.

one hand or if the two hands acted synchronously (shoulder shrugs are not included in this calculation by definition of bilateral distal gestures) (Fig. 2).

Overall, for 19 bilateral gestures no subclassification was possible as no distal hand motions occurred [*bi-n.d.* in Fig. 2]. Twenty-three bilateral gestures showed a dominance of the left hand [*bi-left* in Fig. 2] and 13 of the right hand [*bi-right*]. There were three bilateral gestures in which right and left hand were equally dominant, but dyssynchronous [*bi-dys*]. No distally synchronous bilateral gestures were observed.

3.2. Gesture type differentiation

Secondly, we were interested in whether the two hemispheres produce different types of gestures. To be sure about the hemisphere in which each gesture was generated, the primary investigation focused on unilateral distal hand gestures since these are controlled solely by the contralateral hemisphere. As stated above, shoulder shrugs as proximal movements also occurred unilaterally and are therefore included in Fig. 3. Fig. 3 shows the distribution of gesture types for right and left hand, summed up across all three examinations.

Batons ($\chi^2 = 4$; $P = 0.05$), rise-fall motions ($\chi^2 = 4$; $P = 0.05$) and shoulder shrugs ($\chi^2 = 36.25$; $P = 0.000$) were done only resp. significantly more often with the left side than with the right. Physiographs were distributed equally between the right and left hand. There was a tendency for deictics to be performed more often with the right than with the left hand (n.s.).

For left-dominant and right-dominant bilateral hand gestures the distribution pattern was similar (Fig. 4). Here again, the gestures analyzed were summed up across all three examinations. Bilateral batons ($\chi^2 = 6.0$; $P = 0.025$) and rise-fall motions (n.s.) were only left-dominant. No significant differences in the frequency of left-dominant and right-dominant gestures were found for bilateral deictics and physiographics.

3.3. Context analysis

If one gesture type was observed for either hand (compare Fig. 3), we were interested in discovering whether the right and left hands were used in different contexts. It was striking to find that deictics with the right hand were used for external space, e.g. when the patient pointed to his wife who was present in the room or when he indicated imagined spatial relations such as his way to the hospital. In contrast, left-hand deictics occurred when the patient referred to himself. Physiographs that were displayed with the right hand directly accompanied speech and concretely pictured the linguistic content, such as depicting the motion of running or the form of a bathtub. Physiographs with the left hand sometimes occurred in speech pauses and generally reflected the ideational process, such as trying to find a word. Moreover, the qualitative analysis suggested that the two hemispheres can depict different aspects of the same message. Once, to depict a form, the patient simultaneously made two different gestures with the left and right hands: he traced a circle with his left hand and an arrow with the right. The rare right-shoulder shrugs occurred in the linguistic context of talking about the 'right side'. In contrast, the frequent left-shoulder shrugs occurred in the context of not knowing and resignation. The same was found for rise/fall gestures that occurred only in the left hand. Batons that were displayed only with the left hand were surprisingly found to be in synchrony with speech.

Although we did not evaluate head nods and shakes, we will give one qualitative description that elucidates the question of hemisphere generation of this nonverbal behavior. The patient was presented a visual stimuli to his right hemisphere. He negated the question of whether he saw anything, verbally with 'No' (as a correct answer of the disconnected left hemisphere) while he nodded his head in affirmation at the same time (as a correct answer of his right hemisphere).

4. Discussion

Two months after callosal infarction (T1), the patient predominantly gesticulated unilaterally with the left hand. This could be interpreted as an expression of his left-handedness. On the other hand, Kimura [30] found that left-handers with left hemispheric speech dominance as determined by auditory suppression showed equally distributed unilateral right and left hand use in gesticulation. According to Kimura's findings, our patient would be expected to display equal use of right and left hands in gesticulation as he had left hemispheric language dominance (and some right hemispheric language competence). Therefore, the almost exclusive use of the left hand in gesticulation after callosal infarction is probably due to callosal disconnection and suggests that gesticulation was predominantly generated in the right hemisphere. Following this assumption, the lack of right-hand gesticulation after callosal infarction would be effected by the callosal disconnection hindering the transfer from right hemispheric motor gesture patterns to the left hemisphere.

It is also noteworthy that 2 months after callosal infarction (T1), the patient's clear left-hand preference for gesticulation was in striking contrast to his left-hand apraxia. The latter made it almost impossible for him to use his left hand for volitional actions, i.e. he could not deliberately execute a specific motor action. In neuropsychological testing, left-hand apraxia was observed in verbal command and imitation tasks. In addition, the patient's right hand was more proficient in learning a new motor skill than his left hand (left apraxia for imitation was reported in several cases of patients with callosal lesions, suggesting that only the left hemisphere can translate a new movement idea into motor execution [23–25,35,37,56]). Therefore, we assume that the patient had left-hemispheric dominance for the performance of volitional motor actions despite his left-handedness. In contrast, spontaneous movements were performed in a meaningful way on the left side. We see this as related to the fact that the patient's left hand sometimes acted autonomously, i.e. in the sense of an 'alien hand' [2,4].

There was an obvious discrepancy between the incapability of using the left hand for volitional motor actions and the left hand's effective performance in spontaneous motor behavior and gesticulation. In general, gesticulation occurs without conscious control and there is an obvious alteration in the performance of gestures when they are initiated deliberately rather than spontaneously. We would like, therefore, to suggest tentatively a parallel between left-hand use in spontaneous praxis, such as catching an unexpectedly thrown ball or acting as an 'alien hand', and spontaneous gesticulation. Both types of motor actions might be the expression of a right hemisphere competence for spontaneous, maybe even emotionally motivated motor behavior. As a related phenomenon, the right hemisphere seems to be superior for response readiness compared with the left, because split-brain patients sometimes initiated action with the left hand in advance of the right when they intended to do something with the right hand [49].

The patient showed a significant relative increase in bilateral gestures (and a relative decrease in left-hand gestures) over time. The interesting question here was how the patient managed to gesticulate bilaterally despite his callosal disconnection. Clinically there was no evidence of the recuperation of callosal fibers or the development of extracallosal pathways as the disconnection syndrome persisted.

We strongly favor the explanation that the patient managed to gesticulate bilaterally by developing ipsilateral proximal pathways. This development was evidenced by the fact that the patient's apraxia improved significantly concerning proximal movements, whereas hand/finger configuration errors persisted. It is plausible that the increase in ipsilateral motor control was also manifest in gesticulation. This assumption is supported by the observation of an asymmetry of the two hands in those bilateral gestures in which distal hand movements occurred. One hand displayed distinct hand/finger movements whereas the other hand showed rather rough movements which were initiated by the proximal arm. This concurs with the hypothesis that the distinct hand was controlled by contralateral pathways and the non-differentiated hand by ipsilateral proximal pathways.

There were a few occasions in which the two hands seemed to act independently at the level of becoming dyssynchronous or even displaying two different complex gestures simultaneously suggesting bihemispheric activation. The observation that the patient began to display gesticulation with folded hands can be interpreted as a compensatory strategy to prevent intermanual conflict. In view of the limited data, our assessment of the distribution of gesture types in the right and left hand must be tentative. In particular, the observations of the context analysis are highly hypothetical as they were obtained by one rater alone.

The findings for gesture types based on unilateral gestures are supported by the fact that the distribution pattern was similar for bilateral gestures with dominance of one hand, i.e. left-dominant-bilateral gestures displayed the same gesture types as unilateral-left gestures as well as right-dominant-bilateral the same types as unilateral-right gestures.

As we assume that these bilateral gestures with dominance of one hand are controlled (similar to unilateral gestures) by the contralateral hemisphere, the findings of hand preference resp. hemispheric specialization for a certain gesture type are consolidated.

Our results concur with McNeill's findings in his two callosotomy patients.

Batons were performed by the left hand alone or in bilateral left-dominant gestures. This pattern agrees with McNeill's observation on the split-brain patient L.B. who performed beats only with the left hand. This might indicate that batons as gestures that are related to prosody are generated in the right hemisphere.

Physiographics were displayed by both the right and left hands. This also concurs with McNeill's observation that physiographs occurred in the right and left hands in L.B. and in the right hand in N.G. As compared with the assumptions derived from handedness preference studies suggesting that pictorial gestures are produced with the speech-dominant hemisphere, McNeill's and our findings indicate that physiographs can also be generated in the non-dominant hemisphere. The context analysis suggested that the right and left hemispheres generated different types of physiographics with the left hemisphere concretely picturing the linguistic content and the right hemisphere reflecting the ideational process. The observation that the patient displayed two different physiographs simultaneously with right and left hands even indicated that the two hemispheres can depict different aspects of the same message. Similarly, McNeill's patient L.B. was also reported to produce different gestures at the same time: 'One hand showed the character rushing to answer a phone (the left hand flicking off to the left), while the other hand depicted picking the phone up (grabbing something to the right)' [38, p.349].

Deictics occurred in both hands. Similarly, McNeill observed deictics in L.B. with the right and left hand and in N.G. with the right hand. It was striking to find that deictics with the right hand were only used for external space, whereas left hand deictics occurred when the speaker referred to himself.

Rise–fall gestures were displayed with the left hand (unilateral or bilateral left-dominant) and never with the right hand, so that right hemisphere generation should be assumed. As rise–fall gestures often have an emotional connotation of resignation, the assumption of right hemisphere generation could be seen as related to the findings that right hemisphere damage leads to reduction in emotional gesturing [42].

Shoulder shrugs as proximal movements can be controlled by contra- and ipsilateral pathways. Therefore, we cannot prove that the surprising number of unilateral left shoulder shrugs is generated in the right hemisphere. It is, however, plausible that the isolated left shoulder shrugs are the repeated right hemispheric expression of incomprehension (with emotional connotation) resulting from the disconnection from the speech area. Increase of shoulder shrugs to demonstrate incomprehension and head nodding or shaking as a sign of approval/disapproval also appears to be a communicative strategy in aphasic patients with left hemisphere damage [26] (in our patient head nods and shakes seemed to be generated in the right hemisphere). By contrast, unilateral-right shrugs were used in the verbal context of talking about the right-sided space.

The current data clearly show that the right hemisphere contributes to gesticulation and that the two hemispheres play different roles in gesticulation. In particular, we assume that gestures with emotional connotation and batons that emphasize prosody are produced in the right hemisphere whereas physiographs, which picture the linguistic content concretely, and deictics, which point to external space, seem to be of left-hemispheric origin. These data enhance the established, purely phenomenological gesture classification systems [12,13,18,38] by providing a neuropsychological basis. The gesture types thus far identified by their phenomenology do indeed seem to be generated in different hemispheres, reflecting specific cognitive and emotional processes.

There is, of course, a limit to the generalization of the data as this is a case study and the patient is a left-hander. Nevertheless, the patient — despite being a left-hander — had fundamentally the same hemispheric specialization pattern as right-handers. It can be assumed therefore that the finding of hemispheric specialization in gesticulation is generally representative. Moreover, the patient's data are consistent, e.g. concerning the similar development of ipsilateral control in apraxia and gesticulation and the corresponding distribution pattern for gesture types in unilateral and bilateral dominant gestures. In addition, the observations on gesticulation concur with the previous investigation by McNeill on two right-handed split-brain subjects.

Research on gesticulation has so far not focused on the question of hemispheric specialization. This preliminary approach to investigate the role of the two hemispheres in gesticulation offers some interesting and encouraging findings. We recommend that further studies be performed to test the assumptions raised by this investigation.

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