Apraxia in left-handers

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In typical right-handed patients both apraxia and aphasia are caused by damage to the left hemisphere, which also controls the dominant right hand. In left-handed subjects the lateralities of language and of control of the dominant hand can dissociate. This permits disentangling the association of apraxia with aphasia from that with handedness. Pantomime of tool use, actual tool use and imitation of meaningless hand and finger postures were examined in 50 consecutive left-handed subjects with unilateral hemisphere lesions. There were three aphasic patients with pervasive apraxia caused by left-sided lesions. As the dominant hand is controlled by the right hemisphere, they constitute dissociations of apraxia from handedness. Conversely there were also three patients with pervasive apraxia caused by right brain lesions without aphasia. They constitute dissociations of apraxia from aphasia. Across the whole group of patients dissociations from handedness and from aphasia were observed for all manifestations of apraxia, but their frequency depended on the type of apraxia. Defective pantomime and defective tool use occurred rarely without aphasia, whereas defective imitation of hand, but not finger, postures was more frequent after right than left brain damage. The higher incidence of defective imitation of hand postures in right brain damage was mainly due to patients who had also hemi-neglect. This interaction alerts to the possibility that the association of right hemisphere damage with apraxia has to do with spatial aptitudes of the right hemisphere rather than with its control of the dominant left hand. Comparison with data from right-handed patients showed no differences between the severity of apraxia for imitation of hand or finger postures, but impairment on pantomime of tool use was milder in apraxic left-handers than in apraxic right-handers. This alleviation of the severity of apraxia corresponded with a similar alleviation of the severity of aphasia as manifested by a lower proportion of left-handed patients with global aphasia.

Keywords: apraxia; handedness; imitation; pantomime; tool use; spatial processing

Introduction

Apraxia is a disorder of action on the border between cognition and motor control. It differs from other cognitive disturbances by its restriction to faulty motor actions and from other motor disturbances by the bilaterality of symptoms. In contrast with other motor symptoms of unilateral hemisphere damage, apraxia affects not only the contralateral but also the ipsilateral extremities.

For most manifestations of apraxia the crucial lesions are in the left hemisphere. The left hemisphere dominance for praxis coincides with left hemisphere dominance for language and in right-handed persons also with motor control of the dominant hand.

Theories of apraxia have placed emphasis either on its association with language or with handedness. A close link to language was postulated in the first printed use of the word ‘apraxia’ by the German linguist Chaim Steinthal. He described misuse of everyday
objects by an aphasic patient and concluded that ‘this apraxia is an obvious amplification of aphasia’ (Steinthal, 1881, p. 458). Finkelnburg (1870) postulated that defective production of communicative gestures and aphasia are both expressions of the same pervasive inability to use signs for communication. He named this basic disorder ‘asymbolia’. After Liepmann’s (1908) seminal writings on apraxia, defective production of communicative gestures was recognized as one of the manifestations of apraxia, but the idea of general asymbolia survived in a persistent tradition that regarded apraxia, at least when concerning communicative gestures, as being intimately linked to aphasia (Head, 1926; Pickett, 1974; Duffy and Duff, 1981; Wang and Goodglass, 1992; Goldenberg et al., 2003).

The emphasis on the link between the laterality of apraxia and handedness was introduced by Liepmann (1908). In a systematic group study of patients with unilateral lesions he observed that apraxia was present exclusively in patients with left brain damage. He argued that right handedness implies not only that the right hand is more skilful than the left but also that ‘what the left hand can is to a large part not it’s (respectively the right hemisphere’s) property, but is borrowed from the right hand (respectively, the left hemisphere)’ (Liepmann, 1908, p. 34–35). Liepmann believed that the superior motor competence of the left hemisphere explains why unilateral left sided lesions cause apraxia of both sides of the body.

The correspondence between the lateralties of dominant hand control and competence for language makes it difficult to decide which of them is more important for the laterality of apraxia. However, although this correspondence applies to the majority of right-handed subjects, it is not obligatory. Deviations are frequent in left-handers and exist also for right-handers (Alexander and Annett, 1996; Annett and Alexander, 1996; Knecht et al., 2000). Concerning right-handers there are observations of ‘crossed aphasia’ caused by right brain damage in right-handed patients (Alexander and Annett, 1996; Coppens et al., 2002; Bartha et al., 2004; Marien et al., 2004). In these patients, the right hemisphere is dominant for language although it does not control the dominant hand. The frequency of dissociations between the laterality of dominant hand control and of language increases when left-handed persons are considered. Indeed the majority of left-handed patients with aphasia have left hemisphere lesions, although their dominant hand is controlled by the right hemisphere. The number of patients with aphasia after right brain damage is, however, substantially higher than in right-handers, and there are indications that the brains of left-handers differ from those of right-handers also by an increased incidence of bilateral representation of language (Gloning, 1977; Hécaen et al., 1981; Kimura, 1983; Annett and Alexander, 1996; Knecht et al., 2000).

Dissociations between control of the dominant hand and dominance for speech offer the opportunity to decide empirically which of them determines the laterality of apraxia. On first perusal of the literature the response seems quite straightforward: neither the association with handedness nor that with aphasia is mandatory. Apraxia can dissociate from both. Dissociation from handedness has been amply documented in right-handed patients in whom crossed aphasia was accompanied by apraxia (Assal et al., 1981; Basso et al., 1985; Rapcsak et al., 1987; Selnes et al., 1991; Raymer et al., 1999; Bartha et al., 2004). The corresponding dissociation in left-handers, that is, apraxia accompanying aphasia from left-sided lesions, has been mentioned in reviews but apparently not found worthwhile for single case reports and in-depth exploration (Hécaen et al., 1981; Kimura, 1983; Hecaen, 1984; Frey, 2008). Indirect support for its existence comes from functional imaging studies of left-handed persons. They demonstrated a close correspondence between the asymmetries of neuronal activations induced by processing of speech and of communicative gestures (Królitzak et al., 2011; Vingerhoets et al., 2013).

The dissociation between apraxia and aphasia has engendered more single case studies. There are several detailed reports of left-handed patients in whom right brain damage caused apraxia without accompanying aphasia (Heilman et al., 1973; Valenstein and Heilman, 1979; Margolin, 1980; Poeck and Lehmkuhl, 1980), and also few reports of right-handed patients with ‘crossed non-aphasia’ in whom large left hemisphere lesions led to apraxia without aphasia (Junqué et al., 1986; Selnes et al., 1991; Alexander and Annett, 1996 (Case 2)). Finally there are rare reports of dissociation of apraxia from both language and handedness in right-handed patients with right brain damage who have apraxia but no aphasia [Alexander and Annett, 1996 (Case 9); Marchetti and Della Sala, 1997].

The conclusion that in left-handed patients the laterality of apraxia is completely independent from the laterality of aphasia and of control of the dominant hand is, however, not beyond doubt. The supporting evidence is deduced from single-case reports and methodically heterogeneous group studies. These studies permit to confirm the existence of dissociations between handedness, aphasia and apraxia, but do not provide a safe ground for comparing their frequencies. It is thus not possible to determine whether dissociations of apraxia from aphasia and from handedness are equally likely, or whether there are relative preferences for association with either aphasia or handedness. Moreover, studies rarely considered possible dissociations between different manifestations of apraxia beyond the traditional distinction between ‘ideational’ apraxia of real tool use and ‘ideomotor’ apraxia of manual gestures performed without an implement. A majority of studies probe the production of meaningful communicative gestures like the pantomime of tool use, either only on command (Hécaen et al., 1981) or first on command and, if this was failed, also in imitation (Heilman et al., 1973; Margolin, 1980; Rapcsak et al., 1987). Other studies concentrated solely on imitation that was examined either for a mixed set of meaningful and meaningless gestures (Basso et al., 1985; Marchetti and Della Sala, 1997) or for meaningless gestures only (Kimura, 1983). There is, however, evidence that production of meaningful gestures on command and imitation of meaningless gestures have different neural substrates even within the left hemisphere of typical right-handed subjects (Goldenberg and Karnath, 2006; Goldenberg et al., 2007). It is conceivable that their lateralization in left-handed patients follows divergent regularities that remain undetected because they are not analysed separately.

The aim of the present study was to explore systematically the relationships between the laterality of the neural substrates of
different manifestations of apraxia and the lateralities of handedness and of aphasia. To increase the chance of divergent laterality of dominant hand control and language, only left-handed patients were admitted in the study.

It has been proposed that the left-hander brain differs from the typical right-hander brain not only in greater variability of the assignment of functions to the left or right hemisphere, but also in the strength of asymmetry, and that functions that are clearly lateralized in the typical right-hander brain may be distributed across both hemispheres in the left-hander brain. The neural substrate of apraxia has been nominated a candidate for such bilateral distribution (Kimura, 1983; Hecaen, 1984). If the hypothesis of more bilateral organization of the neural substrate of apraxia in the left-hander brain is correct, apraxia should generally be milder in left-handers than in right-handers because in left-handers the undamaged hemisphere also contributes to the neural substrate of apraxia and thus reduces the consequences of its loss in the damaged hemisphere (Hecaen, 1984; Meador et al., 1999). Verification of this hypothesis was a further aim of the present study.

Materials and methods

Subjects
Subjects of this study were 50 consecutive left-handed patients admitted to the Department of Neuropsychological Rehabilitation, Bogenhausen Hospital, with unilateral lesions of either the left or the right hemispheres. Questions for handedness are part of the routine work-up at admission. If they provided indications that the patient might not be strictly right-handed, a handedness questionnaire was administered (Salmaso and Longoni, 1985). If the handedness quotient was negative, indicating a preference for the left hand, patients were eligible for the study. A further criterion for inclusion was the absence of bilateral or major diffuse brain damage on CT or MRI. There was no preselection concerning the intra-hemispheric localization of the lesion or the symptoms of patients, but as the department is specialized for neuropsychological rehabilitation, the incidence of neuropsychological disturbances like aphasia or hemi-neglect is likely to be higher than in unselected samples of patients with acquired brain damage. Detailed clinical examinations of neuropsychological impairments had been carried out for all patients admitted to the study. Otherwise, the demonstration was repeated and one point was given for correct imitation. Two points were given for swift performance and one for correct imitation. Otherwise, the demonstration was repeated and one point was given for a successful second trial. Imitation of these postures has been examined in several previous studies. Cut-off scores have been derived from examination of 60 control subjects, and inter-rater reliability has been found to be high (Goldenberg, 1996; Goldenberg and Strauss, 2002; Goldenberg and Kamath, 2006).

Pantomime of tool use was examined for 20 common tools. The examiner named the action and the tool (e.g. ‘show me how one cuts a sheet of paper with scissors’) and simultaneously showed a photograph of the tool. This photograph was hidden from view before subjects started miming. The test was preceded by practice items. Comprehension of instruction was assumed when subjects responded to the verbal commands with distinct gestures that were clearly different from beats synchronized with a stream of verbal utterances, from manual actions directed towards the presented picture, or from attempts to draw the outlines of the tool with the finger upon the table. If these conditions were not met or if patients perseverated at the same gesture across all items, testing was abandoned but repeated some weeks later after further speech therapy. Eventually the examination could be completed in all patients admitted to the study. For evaluation of the pantomimes, the examiner marked the presence or absence of predefined features of the pantomime on an examination sheet. For each item, one feature characterized grip and finger configuration, whereas the remaining one to three features concerned position and movement of the whole hand (e.g. screwing in of an electric bulb: spherical grip and rotation of the hand; cutting with scissors: bended fingers with opposition of thumb, opening and closing of hand or fingers, hand oriented perpendicular to table, and movement of whole hand parallel to table). Cut-off scores have been obtained from examination of 49 control subjects, and inter-rater reliability has been found satisfactory (Goldenberg et al., 2003, 2007).

Tool use was initially examined by handing to the patient one tool at a time with its corresponding recipient adapted for possible one-handed use (e.g. a hammer with a partially driven in nail) and asking them to execute its use (Goldenberg and Hagmann, 1998). Two points were given for swift performance and one for correct performance after hesitation or searching. During the course of the data collection, which spanned some 6 years, this test was replaced by a novel one presenting a rack with five recipients of tool actions fixed on it so that they can be manipulated. Patients were given one tool at a time and asked to select the corresponding recipient and demonstrate the use of the tool on it. Scores were given according to the same criteria as in the older test separately for selection and for application of the tool (Goldenberg and Spatt, 2009). Normal control subjects perform these tests virtually at ceiling. In addition, all patients had been seen by occupational therapists who reported whether patients had problems with tool use in everyday actions. Patients were classified as ‘normal’, ‘mildly impaired’ or ‘severely impaired’ from a synopsis of the test and the occupational therapists’ observations, but it turned out that in this patient sample there was no single patient with a severe impairment.

Results
There were 28 patients with left and 22 with right brain damage. They did not significantly differ with respect to age, gender distribution, time since lesion and the frequency of hemiparesis (see table 1). In accordance with established clinical knowledge (Hecaen et al.,
1981; Kimura, 1983), the incidence of aphasia after right brain damage was much higher than the usual incidence in right-handers with right brain damage but significantly lower than in left-handers with left brain damage. Hemi-neglect was more frequent in patients with right brain damage than left brain damage but this difference only approached statistical significance. A detailed breakdown of the frequency of individual combinations between laterality of lesion, presence of aphasia, hemi-neglect and hemiparesis is included in Supplementary Table 1.

CT or MRI had been available for all patients at the time of their inclusion in the study. At the time of evaluation only 40 could be retrieved. In view of the manifold of possible subdivisions of the patients and in absence of a priori hypothesis concerning the intra-hemispheric site of lesions in apraxic left-handers, there was no solid ground for voxel-based lesion symptom mapping (Bates et al., 2003; Rorden et al., 2007). For exploration of possible major effects lesions were classified as encroaching upon frontal, temporal and parietal lobes and scores on apraxia testing were compared between patients with or without a lesion. This was done separately for patients with right brain damage and left brain damage. None of these comparisons approached statistical significance.

Results are reported in two steps, looking first for single cases with complete dissociation of apraxia from either handedness or aphasia, and then for the distribution of impairments on single manifestations of apraxia and their relationships to clinical and demographic factors, to aphasia, to laterality of lesions, and to hemi-neglect. Finally, results are considered pertaining to the question whether apraxia in left-handers is generally milder than in right-handers.

### Complete dissociation of apraxia from handedness or aphasia

In several reported cases of dissociations of apraxia from aphasia in left-handed patients actual tool use was spared (Heilman et al., 1973; Valenstein and Heilman, 1979; Archibald, 1987; Marchetti and Della Sala, 1997). Accordingly the criterion for complete dissociations of apraxia from aphasia or handedness was impairment on pantomime of tool use and on imitation of hand and finger postures, but not necessarily on tool use. This criterion corresponds to the usual definition of ‘ideomotor’ apraxia (De Renzi, 1990).

There were three patients with apraxia without aphasia from right brain damage and three with apraxia and aphasia from left brain damage. The former constitute dissociations of apraxia from aphasia, and the latter from handedness. Tool use was mildly impaired in two of the patients with left brain damage and in one of those without aphasia. In this sample there was no case of a complete dissociation of apraxia from aphasia and from handedness as would be constituted by apraxia resulting from left brain damage without aphasia.

**Supplementary Fig. 1** displays the lesions of the six patients. Their distribution does not reveal consistent patterns underlying either apraxia from left brain lesions or apraxia without aphasia.

### Individual manifestations of apraxia

The following analyses consider individual manifestations rather than the global diagnosis of apraxia. The data from the six patients with global dissociation between apraxia and aphasia or handedness are included in these group analyses.

The splitting of apraxia into pantomime of tool use, actual tool use, imitation of hand and imitation of finger postures is justified by previous studies showing behavioural dissociations and different neural substrates between them in right-handed patients (Goldenberg, 1996; Goldenberg and Karnath, 2006; Goldenberg et al., 2007; Goldenberg and Spatt, 2009). It finds further support in cross tabulations of defective and normal performance comparing each of the seven possible pairings of the four tasks in the present study. They showed substantial proportions of patients who were classified as impaired on one but normal on the other test. The number of such dissociations was highest (16/50) for imitation of hand postures and pantomime, and lowest (9/50) for pantomime and real tool use.

### Laterality of lesion

Age was negatively correlated with the scores on pantomime ($r = 0.41, P < 0.003$), imitation of hand postures ($r = 0.31, P = 0.03$) and imitation of finger postures ($r = 0.42, P = 0.003$). There were neither significant correlations between the

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### Table 1 Demographic and clinical data

<table>
<thead>
<tr>
<th>Patients with left brain damage, n = 28</th>
<th>Patients with right brain damage, n = 22</th>
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</thead>
<tbody>
<tr>
<td>Female / male</td>
<td>10 / 18</td>
</tr>
<tr>
<td>Age, years</td>
<td>56.5 (23–75)</td>
</tr>
<tr>
<td>Handedness quotient</td>
<td>–0.74 (–0.3 to –1.0)</td>
</tr>
<tr>
<td>Weeks since lesion</td>
<td>15.0 (3–70)</td>
</tr>
<tr>
<td>Ischaemia / bleeding / trauma</td>
<td>16 / 11 / 1</td>
</tr>
<tr>
<td>Number of patients with:</td>
<td></td>
</tr>
<tr>
<td>Hemiparesis</td>
<td>12 (43%)</td>
</tr>
<tr>
<td>Aphasia</td>
<td>23 (82%)</td>
</tr>
<tr>
<td>Hemi-neglect</td>
<td>6 (21%)</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>7 / 15</td>
</tr>
<tr>
<td></td>
<td>58.3 (33–79)</td>
</tr>
<tr>
<td></td>
<td>–0.73 (–0.2 to –1.0)</td>
</tr>
<tr>
<td></td>
<td>12.6 (3–100)</td>
</tr>
<tr>
<td></td>
<td>16 / 5 / 1</td>
</tr>
</tbody>
</table>

Values in parentheses are ranges for age, handedness quotient, and week since lesions, and percent of patients for hemiparesis, aphasia, and neglect.

*P < 0.001 **P = 0.07; all other comparisons non-significant (X$^2$ test).
handedness quotient and any of the apraxia scores nor significant
differences between patients with or without hemiparesis (all P-
values > 0.15). Table 2 shows the influence of the laterality of
lesions. A substantial number of patients with left brain damage
scored below cut-off on one or more tests and was hence classi-
fied as apraxic for the manifestation of apraxia tapped by these
tests. As the patients were left-handers this indicates dissociation
between the laterality of apraxia and motor control of the dom-
inant hand. Imitation of hand postures was the only manifestation
of apraxia that was affected more often by right brain damage
than by left brain damage.

Aphasia

Table 3 compares patients with or without aphasia. The mean age
of patients with aphasia was higher than of those without
[(48) = 2.2, P = 0.035]. Aphasia was associated with significantly
higher incidences of disturbed pantomime of tool use and of actual
tool use, whereas apraxia for imitation of hand and finger postures
was approximately as frequent in patients with or without aphasia.
Age correlated negatively with pantomime and with both variants
of imitation but not with actual tool use. The selective influence
of aphasia on pantomime and on tool use thus cannot credibly be
referred to the slightly higher mean age of aphasic patients.

As a rule, all patients who had apraxia after left brain damage
were aphasic, and all patients who had apraxia without aphasia
had right brain damage. In other words, the laterality of apraxia
corresponded either with dominance for speech or with control of
the dominant hand. In five apraxic patients both associations
applied as they had right brain damage and aphasia. Two patients
with left brain damage who had apraxia but no aphasia provided
only weak grounds for doubting the regular concordance of the
laterality of apraxia with the laterality of either aphasia or domin-
ant hand control. In one of these patients the only manifestation
of apraxia was a score one point below the cut-off for imitation
of hand postures, and in the other a moderate impairment of imita-
tion of finger postures, whereas all other tests of apraxia were
passed normally by both.

Hemi-neglect

Table 4 shows the influence of hemi-neglect on apraxia. Imitation
of both hand and finger postures was disturbed more frequently
in patients with hemi-neglect than in those without, whereas the
proportion of patients with defective pantomime or defective
tool use was not significantly different. In a previous study exam-
imining imitation of the same hand and finger postures by right-
handers patients with right brain damage we also found a negative
influence of hemi-neglect on imitation (Goldenberg et al., 2009),
but a detailed analysis of the data of both studies suggests that
the mechanisms mediating the association of hemi-neglect with
defective imitation differ between left handers with right brain
damage, left handers with left brain damage, and right handers
with right brain damage.

Hemi-neglect in left- and right-handers

Table 5 combines the data from the present study with those
of the previous study of right-handed patients with right brain

Table 2 Apraxia and laterality of lesions

<table>
<thead>
<tr>
<th>Patients with</th>
<th>Patients with</th>
</tr>
</thead>
<tbody>
<tr>
<td>left brain</td>
<td>right brain</td>
</tr>
<tr>
<td>damage,</td>
<td>damage,</td>
</tr>
<tr>
<td>n = 28</td>
<td>n = 22</td>
</tr>
</tbody>
</table>

- Imitation of hand postures: 5 vs. 10*
- Imitation of finger postures: 8 vs. 9
- Pantomime of tool use: 11 vs. 8
- Tool use: 7 vs. 5

*P < 0.05; all other comparisons non-significant (X² test).

Table 3 Apraxia and aphasia

<table>
<thead>
<tr>
<th>Patients with</th>
<th>Patients with</th>
</tr>
</thead>
<tbody>
<tr>
<td>left brain</td>
<td>right brain</td>
</tr>
<tr>
<td>damage,</td>
<td>damage,</td>
</tr>
<tr>
<td>n = 29</td>
<td>n = 21</td>
</tr>
</tbody>
</table>

- Age (range): 60.6 (37–78) vs. 52.8 (23–79)*
- Imitation of hand postures: 7 vs. 8
- Imitation of finger postures: 10 vs. 7
- Pantomime of tool use: 16 vs. 3**
- Tool use: 10 vs. 2***

*P = 0.053; **P < 0.01; ***P < 0.05; all other comparisons non-significant (X² test).

Table 4 Apraxia and hemi-neglect

<table>
<thead>
<tr>
<th>Patients without</th>
<th>Patients with</th>
</tr>
</thead>
<tbody>
<tr>
<td>neglect, n = 34</td>
<td>neglect, n = 16</td>
</tr>
</tbody>
</table>

- Age (range): 58.5 (40–78) vs. 54.6 (23–79)
- Imitation of hand postures: 6 vs. 9*
- Imitation of finger postures: 7 vs. 10*
- Pantomime of tool use: 11 vs. 8
- Tool use: 6 vs. 6

*P < 0.01; all other comparisons not significant (X² test).

Table 5 Apraxia and hemi-neglect in right-handers and left-handers

<table>
<thead>
<tr>
<th>Finger:</th>
<th>Hand:</th>
</tr>
</thead>
<tbody>
<tr>
<td>mean (SD)</td>
<td>mean (SD)</td>
</tr>
</tbody>
</table>

- Left-handers LBD
  - 22 no neglect: 17.3 (3.5) vs. 18.3 (2.6)
  - 6 neglect: 15.0 (3.8) vs. 18.3 (1.6)
- Left-handers RBD
  - 12 no neglect: 17.5 (2.2) vs. 17.3 (3.3)
  - 10 neglect: 13.7 (5.2) vs. 13.7 (5.2)
- Right-handers RBD
  - 14 no neglect: 18.3 (1.4) vs. 19.0 (1.1)
  - 36 neglect: 15.5 (3.2) vs. 18.7 (1.8)

Maximum score for imitation of finger and of hand postures is 20, the fifth percent-
cile which constitutes the cut-off for classifying patients as apraxic is 18 for
hand and 17 for finger postures.

LBD = left brain damage; RBD = right brain damage.
damage. It shows that hemi-neglect is associated with a fairly uniform decrease of mean scores on imitation of finger postures in all groups. The picture is more complicated for imitation of hand postures. Scores on imitation of hand postures are generally poorer in right brain damage left-handers than in the other groups and drop massively in the presence of hemi-neglect. A multivariate ANOVA with the within subject variable body part (hand versus finger) and the between subjects variables group (left-handers with left brain damage, left-handers with right brain damage, right-handers with right brain damage) and hemi-neglect (present versus absent) confirms this impression largely, though not completely. There are significant main effects of body part \( F(1,93) = 15.8, P < 0.0005 \) neglect \( F(1,93) = 11.0, P = 0.001 \) and group \( F(2,93) = 5.5, P = 0.05 \) indicating that finger postures yield generally lower scores than hand postures, patients with neglect have generally lower scores than those without, and left-handed patients with right brain damage score generally lower than the other groups. A significant interaction between body part and group \( F(2,93) = 4.5, P = 0.013 \) confirms the selective impairment of hand postures in left-handed patients with right brain damage, whereas an interaction between body part and neglect \( F(1,93) = 6.3, P = 0.014 \) reflects the greater general vulnerability of finger than hand posture to the presence of hemi-neglect. However, the three-way interaction of body part, group and neglect that would correspond to a selective effect of neglect on hand postures in left-handers with right brain damage fails to reach statistical significance \( F(2,93) = 1.4, P = 0.3 \).

The selective effect of neglect on imitation of hand postures by left-handed patients with right brain damage does come to the fore when multivariate ANOVAs are computed separately for hand and for finger postures. They show effects of neglect for both kinds of gestures \( \text{hand: } F(1,93) = 4.4, P = 0.04; \text{finger: } F(1,93) = 14.1, P < 0.0005 \), but a significant effect of group only for hand postures \( F(2,93) = 11.7, P < 0.005 \); finger: \( F(2,93) = 1.1, P = 0.32 \). Importantly, there is a significant interaction between group and neglect for hand, but not for finger postures \( \text{hand: } F(2,93) = 3.1, P = 0.049; \text{finger: } F(2,93) = 0.28, P = 0.76 \) indicating that only for hand postures the influence of neglect is stronger in left-handers with right brain damage than in the other groups. Moreover, the difference between right brain damaged left-handers with and without neglect on hand imitation was strong enough to make the proportion of patients classified apraxic on this test significantly higher in patients with neglect than in those without (Table 4).

In sum it appears safe to conclude that imitation of hand but not of finger postures was less accurate in left-handed patients with right brain damage than in either left-handed patients with left brain damage or right-handed patients with right brain damage, and that the inferiority of right brain damage left-handers was most conspicuous in patients with hemi-neglect, although the statistical significance of this additional influence was insecure.

### Severity of apraxia in right- and left-handers

As outlined above, it has been postulated that the neural substrate of apraxia is more bilateral in left-handers than in right-handers, and that consequently apraxia in left-handers is milder and recovers more swiftly than in right-handers (Hecaen et al., 1981; Hecaen et al., 1984). To find out whether apraxia is generally less severe in left-handers the mean scores of the left-handed patients classified as apraxic for pantomime or imitation were compared with those of right-handers with left brain damage and aphasia who had been classified as apraxic by examination with the same tests in previous studies (Goldenberg and Karnath, 2006; Goldenberg et al., 2007). Mean scores were virtually identical for imitation of hand and finger postures (hand: mean 12.6 versus 12.4; finger: 12.0 versus 11.6) but significantly higher in left- than in right-handers for pantomime of tool use (35.5 versus 27.8; \( t(41) = 2.74; P = 0.009 \). It thus seems that impairment of pantomime of tool use is indeed generally milder in left-handers than in right-handers.

All but three left-handed patients with disturbed pantomime were aphasic (Table 3). Table 6 compares the distribution of types of aphasia and their influence on the pantomime scores between the right-handers of the previous studies and the left-handers of the present one.

The distribution of aphasia types differs significantly between left- and right-handers \( \chi^2 = 14.7; P < 0.01 \). This is mainly due to the higher incidence of global aphasia in right-handers, but the absence of any case of Broca’s aphasia in left-handers is also remarkable. Inspection of Table 6 suggests that the different severity of pantomime impairment in left- and right-handed patients is due to the poor scores of the right handed patients with global aphasia. Indeed, when they are omitted from the comparison, the

<table>
<thead>
<tr>
<th>Type of aphasia:</th>
<th>Left handers (14 patients)</th>
<th>Right handers (29 patients)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of patients</td>
<td>Pantomime mean (SD)</td>
</tr>
<tr>
<td>Global</td>
<td>2</td>
<td>38.5 (4.9)</td>
</tr>
<tr>
<td>Broca</td>
<td>0</td>
<td>30.5 (19.1)</td>
</tr>
<tr>
<td>Wernicke</td>
<td>2</td>
<td>35.0 (8.9)</td>
</tr>
<tr>
<td>Amnesic</td>
<td>3</td>
<td>38.6 (4.4)</td>
</tr>
<tr>
<td>Other</td>
<td>7</td>
<td></td>
</tr>
</tbody>
</table>

The total number of right-handed patients left brain damage examined in the previous studies was 44. This table includes only patients who have aphasia as well as apraxia for pantomime of tool use. The maximum score for pantomime is 55, the fifth percentile, which constitutes the cut-off for classification of patients as apraxic is 45.
difference of pantomime scores between left- and right-handers loses statistical significance \([t(22) = 1.13, P = 0.27]\).

The lower incidence of global aphasia in left- than in right-handers goes hand-in-hand with a higher general level of linguistic capacities as reflected in the five subtests of the Aachen Aphasia Test (Token Test, repetition, naming, written language, and comprehension). Their mean scores, expressed in percentiles, ranged from 55 to 62 in the aphasic left-handers but from 30 to 37 in the aphasic right-handers. However, the link between the severity of aphasia and of apraxia for pantomime is not mandatory. The pantomime scores of the three left-handers with right brain damage who had apraxia for pantomime but no aphasia were 25, 28, and 38, which is in the lower range of the distribution in the aphasic patients.

Discussion

The main findings of the study can be summed up as follows: in left-handed patients apraxia can be caused by lesions of the left hemisphere, which controls the non-dominant right hand and it can result from right brain damage without aphasia. In other words, the laterality of apraxia can dissociate from manual dominance as well as from language. There was in this sample of patients, however, no unequivocal dissociation of apraxia from aphasia and from manual dominance as would be constituted by apraxia from left hemisphere damage without aphasia.

Both kinds of dissociations were observed for all manifestations of apraxia, but their frequency varied between different manifestations. Defective pantomime and defective tool use occurred rarely without aphasia, whereas defective imitation of hand postures was more frequent after right than left brain damage. The higher incidence of defective imitation of hand postures in right brain damage was mainly due to patients who also had hemi-neglect.

There was partial support for the contention that in left-handed subjects the neural substrate of apraxia is more bilaterally organized than in right handers, and that therefore apraxia is generally milder in left- than in right-handers. There was no difference between mean scores of left- and right-handed apraxic patients for imitation of hand or finger postures, but those on pantomime of tool use were indeed higher in the left-handers. This alleviation of the severity of apraxia corresponded with a similar alleviation of the severity of aphasia and a lower proportion of patients with global aphasia.

Limits to the independence of apraxia

The associations between defective pantomimed or real tool use and aphasia and between defective imitation of hand postures and right brain damage confirm the suspicion that even in left-handers the lateralization of apraxia is not completely independent from the laterality of other functions. Possibly the deviations from anatomical independence reflect the functional importance of neural connections between the associated regions or functions, respectively. It may be speculated that such functional connections favour anatomical proximity and lowers the probability that the related functions are located in different hemispheres. The observation that different associations influence the laterality of different manifestations of apraxia endorses a concept of apraxia as a family of loosely connected symptoms rather than as a unitary syndrome resulting from damage to a coherent 'praxis system'. More specifically, they suggest that pantomime of tool use and actual tool use have close functional relationships to language, whereas imitation of hand postures depends on functional links with the right hemisphere that commands the dominant hand. The nature of these functional links are discussed below first for pantomime, actual tool use, and aphasia, and then for imitation and the right hemisphere.

Aphasia, pantomime of tool use and actual tool use

A simple explanation for the influence of aphasia on test performance would be insufficient understanding of the instructions by severely aphasic patients. This explanation does appear plausible for pantomime of tool use, because the instruction to pantomime the use of a tool is linguistically rather complex and lacks support by the communicative context. Rather than reacting to the presentation of a tool with a pantomime of its use, a more natural and habitual reaction would be to name it or to give a verbal comment on its properties (Goodglass and Kaplan, 1963). However, testing of pantomime took great care to ascertain the comprehension of the instruction. Moreover, the relationship to aphasia extended also to actual tool use. For testing actual tool use patients were given a tool and its recipient. The instruction to demonstrate the action of the tool upon the recipient does not appear exceptionally unusual or counter-intuitive. At any rate, it is hardly more difficult to understand than the request to imitate hand or finger postures, but imitation was not affected by aphasia.

A possible candidate for the unifying link between aphasia and pantomimed or actual tool use could be that both language and tool use require access to semantic memory. For language this is essential for comprehending the meaning of words and sentences. For pantomime of tool use semantic knowledge about features of tool use serves as the basis for their pantomimic demonstration. For actual tool use it provides a specification of the prototypical purpose of tools which is necessary to select the correct use out of the multitude of mechanically possible applications (Goldenberg and Hagmann, 1998; Goldenberg and Spatt, 2009; Osiurak et al., 2009). On this account, lesions that encroach upon the neural substrate of semantic memory are likely to affect the neural substrates of aphasia and of apraxia for tool use because the functional link between them promotes anatomical proximity of their substrates and partly overcomes the arbitrariness of their assignments to the left or right hemisphere.

The search for the link between aphasia and apraxia for pantomime of tool use is complicated by the observation that both apraxia for pantomime and aphasia were generally milder in left-handers than right-handers. The most likely explanation for this relative sparing is bilateral distribution of their neural substrates. For language it has been demonstrated that the distribution of linguistic capabilities across both hemispheres of left-handed persons respects functional divisions between components of language.
Handedness, hemi-neglect and imitation

As the right hemisphere controls the dominant hand, the higher incidence of defective imitation of hand postures after right brain damage than after left brain damage seems to support an association between apraxia and handedness, but the importance of motor control of the dominant hand is qualified by an association between defective imitation and hemi-neglect. Moreover, a crucial role of handedness is called into doubt by the restriction of the negative influence of right brain damage on imitation of hand postures. Imitation of finger postures was equally impaired in patients with right brain damage and left brain damage. It is difficult to understand why a loss of motor skills that are associated with control of the dominant hand should affect the placement of the whole hand in relation to parts of the face and the head that is required for imitation of hand postures more than the selective flexion and extension of individual fingers that is required for imitation of finger postures.

The association between hemi-neglect and poor imitation of hand postures in left-handed patients with right brain damage contrasts with the observation that hemi-neglect in left-handed patients with left brain damage as well as in right-handed patients with right brain damage affects predominantly finger postures and largely spares hand postures. Indeed, this common effect of hemi-neglect on finger postures was also present in the left-handed patients with right brain damage, but they were the only group in which patients with hemi-neglect scored lower than those without also on imitation of hand postures. It is difficult to find an explanation for the deviation from the common effects of hemi-neglect without assuming that the selective influence of hemi-neglect on hand postures in patients with right brain damage results from some other factor accompanying hemi-neglect in left-handed patients with right brain damage. To derive cues to the possible nature of such additional mechanisms we will recapitulate previous findings and theories concerning the differences between imitation of hand and of finger postures.

In right-handed subjects, imitation of hand postures is disturbed nearly exclusively after left brain damage (Goldenberg, 1996, Goldenberg and Strauss, 2002; Bekkering et al., 2005; Della Sala et al., 2006). Imitation of finger postures is impaired almost equally in left brain damage and right brain damage on condition that patients with right brain damage with hemi-neglect are included in the studies. In patients with right brain damage, the severity of impairment correlates with the severity of hemi-neglect (Goldenberg et al., 2009). It has been proposed that these asymmetries derive from different demands of hand and finger postures on two different aspects of spatial processing that are supported by left and right-sided brain regions (Goldenberg 2009; Goldenberg et al., 2009). Left-sided, in particular parietal, brain regions are necessary for body part coding that converts the perceptual multitude of demonstrated gestures into combinations of a limited number of defined body parts. Imitation of hand postures puts high demands on body part coding because determination of the spatial relationship between hand and face demands a selection from a multitude of very different body parts such as chin, lips, back and tip of the nose, cheek or ears. A right hemisphere contribution to imitation is needed when the perceptual analysis of demonstrated gestures demands simultaneous attention to spatially distributed elements. Finger postures are particularly vulnerable to narrowing and lateralized deviation of the attentional focus because perception of their configuration requires the distribution of attention across five spatially distinct but otherwise fairly uniform elements.

The different contributions of the left and the right hemisphere to imitation can be seen as manifestations of different general contributions to spatial processing. The left parietal contribution has been characterized as categorical apprehension of spatial relationships (Goldenberg, 2009) whereas the right hemisphere contribution concerns the maintenance and spatial distribution of attention (Husain and Rorden, 2003).

Generally, in the majority of left-handed subjects the right hemisphere is dominant for the spatial functions that are also supported by the right hemisphere in typical right-handers (Alexander and Annett, 1996; Floel et al., 2005). Taking into account the higher variability of lateralization in left-handers it might be speculated that in a substantial proportion of left-handed subjects the right hemisphere supports not only the usual right hemisphere contributions to spatial processing but also the categorical apprehension of spatial relationships that is a domain of the left hemisphere in the typical brain of right-handed subjects. This could explain why right brain damage in these patients impairs the imitation of hand postures, but leads to question why the severity of impairment increases when lesions cause also hemi-neglect. One might speculate that the concurrent damage to two, basically independent but functionally interacting, components of spatial processing affects even tests that are presumed to tap only one of these components more severely than the isolated damage to this component.

An important consequence of this speculation is denial of the importance of handedness for the laterality of lesions causing apraxia. The mechanisms that increase the likelihood of apraxia for imitation after right brain damage seem to be grounded in the laterality of spatial functions rather than in the laterality of dominant hand control.

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### Supplementary material

Supplementary material is available at *Brain* online.

### References


