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# PRAXIS AND LANGUAGE ORGANIZATION IN LEFT-HANDERS

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## SUMMARY

### Background:

The performance of learned manual gestures (praxis) and the production of speech are thought to depend on related neural processes. If this relationship is not invoked by an unknown, third variable then shifts in their laterality, including dissociations of these two functions, would be unlikely unless the sharing of some neural resources with other functions is advantageous. This could be the case in lefthanders, in whom actions requiring manual precision are controlled by their right hemispheres, and whose representations could *attract* the control of skilled gesture.

### Material/Methods:

Functional neuroimaging (fMRI) was used to study praxis and language functions. Their lateralization indices were measured in 56 consecutively tested lefthanders (28 females), with the mean age of  $23.3 \pm 4.9$  years (range 18.4 – 47 years), and an Edinburgh Handedness Inventory quotient between –100 and –55.6 (with the mean of  $-83.8 \pm 14.2$ ).

### Results:

We show that atypical, bilateral organization or right-lateralization of praxis is more common than atypical organization/lateralization of language, observed, respectively, in 23 (41%) vs. 15 (26.8%) of cases. Specifically, we found: (a) seven cases (12.5%) of clear, and an additional three cases (5.4%) of less pronounced dissociations of atypically represented praxis from typically represented language; (b) 13 cases (23.2%) with atypically organized praxis also associated with atypically organized language, and (c) only two cases (3.6%) of rather strongly atypical lateralization of language, yet with quite typical lateralization of praxis.

### Conclusions:

These outcomes are consistent with an idea that, in some lefthanders, the guidance of skilled manual actions can profit from tighter links with the right hemisphere, whose motor specialization is linked in this particular population to manual precision, but in general to attentional resources, visuo-spatial processing and even bimanual coordination. Because of the presumed links of praxis with productive language, such transfers are often, and unsurprisingly accompanied by the reorganization of the latter. Yet, the very rare cases of reversed language functions, without any pronounced shifts in representations of praxis, indicate that such a pattern of segregation – or inverse dissociation – of these two functions could be maladaptive.

**Keywords:** tool use gestures, verbal fluency, lateralization, interrelations, asymmetries, segregation of functions, functional dissociations

## INTRODUCTION

One of the first reports with the use of functional magnetic resonance imaging (fMRI) investigating interrelationships between such fundamental cognitive abilities as the control of skilled manual gesture (praxis) and language production was published in 2011 (Króliczak, Piper & Frey, 2011). Interestingly, this neuroimaging research also included one of the most neglected populations of volunteers, namely lefthanders. This was so because the study premises were contingent on the identification of as many atypical cases of laterality of functions as possible and, at least in the case of productive language, they are most often found in strongly left-handed individuals (Knecht et al., 2000).

A hypothesis that a shift in language organization, i.e., its more balanced representation or even right lateralization, should be associated with a shift in the organization of praxis, was well supported in this early report (Króliczak et al., 2011). Not only were significant correlations between the laterality indices (LIs) of these two functions observed but the majority of atypical cases involved reorganization of both of them. Put simply, atypical lateralization of one of the studied faculties somehow allowed one to predict the laterality of the other function. While these results are consistent with a notion that both of these abilities utilize a common cortical processing specialization – such as the brain’s competency to symbolically represent complex movements, and to organize the multifaceted hierarchies of their sequences (e.g., Kimura & Archibald, 1974) – they also indicate that, counterintuitively, its location has little to do with handedness. Ultimately, all participants were left handed, and the majority of them (67%) had relatively typical, left-sided organization of both praxis and language.

Although an independent report was published which showed comparable results and reached similar conclusions (Vingerhoets et al., 2013; cf. Goldenberg, 2013a, and a chapter in Goldenberg, 2013b; for a review devoted exclusively to praxis skills in lefthanders, see Króliczak, 2013), the studied samples were rather small and – given the reproducibility crisis (Open Science, 2015; see also Anderson et al., 2016), this mere fact calls for a replication. Importantly, not even a single case of mirror-reversed organization of any of these two functions in which language and praxis would clearly dissociate was then identified. Given the postulated common evolutionary origins of their representations (e.g., Corballis, 2003; Arbib, 2005; see also Corballis, 2017), such dissociations are quite unlikely. Indeed, any shifts in the neural underpinnings of praxis and language would be unexpected, unless other essential processes or mechanisms could also support their representations. Put simply, sharing neural resources could be a trigger for the partial or complete reorganization of functions, and evidence for this should be easiest to find in lefthanders (e.g., Vingerhoets, 2019; see also Króliczak, Piper & Frey, 2016; for reviews see Willems, Van der Haegen, Fisher & Francks, 2014; and Króliczak, Gonzalez & Carey, 2019).

Testing the left-handed population of individuals, with no history of brain injuries or seizures, is critical here because it is most likely that in their brains the

mechanisms underlying hand preference may attract, or in extreme cases perhaps even engulf, the mechanisms mediating manual praxis (a tentative model for such shifts was proposed in Króliczak et al., 2018; cf. Begliomini et al., 2018; see also Constant & Mellet, 2018; Ochando & Zago, 2018). Yet, there is no obvious reason why such a reorganization should be limited only to language.

## METHODS

Data from a group of 56 healthy lefthanders tested in three consecutive projects by Króliczak and collaborators (starting from Króliczak et al., 2011; Biduła, Przybylski, Pawlak & Króliczak, 2017; and the present cohort, not yet described before) were used in this report. The tested sample included 28 females and 28 males, with mean age of 23.3 years, and standard deviation (SD) of  $\pm 4.9$  years (range = 28.6, min. 18.4 and max. 47) at the time of their testing. As indicated by the revised Edinburgh Handedness Inventory (EHI, Oldfield, 1971), most of these participants were rather strongly left-handed: the mean LI =  $-83.8$ , SD =  $14.2$ ; range =  $44.4$ , min. =  $-100$ , max.  $-55.6$ ; with the assumption that scores  $\leq -50$  denote lefthandedness (cf. Whitehouse & Bishop, 2009, where scores  $\leq -40$  denote lefthanders,  $\geq +40$  denote righthanders, and ambidexterity or mixed handedness is located in between). Each volunteer signed written informed consent for participation in these projects, approved by the Ethics Committee for Research Involving Human Subjects at the University of Oregon, and the Bioethics Committee at Poznań University of Medical Sciences (Ethical Approval No. 63/12), and consistent with the principles of the 2013 WMA Declaration of Helsinki.

For clarity and full disclosure, it should be emphasized that in the first study by Króliczak and collaborators (Króliczak et al., 2011) the calculation of praxis LIs also involved neural activity from planning intransitive (“communicative”) gestures – i.e., their LIs were collapsed across two disparate praxis tasks. In the current report, for consistency with later projects, only tool use pantomimes (transitive gestures) are included, and LIs based on these results alone were not identical with Króliczak et al. (2011). Indeed, they have not been utilized in any analyses of praxis-language correlations, yet. For further disclosure, it should be also stated that, in an earlier study devoted exclusively to language functions, Biduła et al. (2017) computed LIs for task-related neural activity only in a subset of 21 left-handed individuals (also included here) as in the – more threshold-dependent – method of Jansen et al. (2006). As this approach is actually more liberal, the identification of typical vs. atypical participants in that sample would slightly differ. This is offset by the additional use of dispersion as a criterion, which indicates that a participant with language LI of  $+50.11$  does belong to a typical group. Notably, the assignment of participants would not differ substantially if the ranges described earlier by Króliczak et al. (2011) were used, wherein values from  $+100$  to  $+33.3$  reflect a strong to weak left-hemisphere dominance, whereas from  $-33.3$  to  $-100$  indicate a weak to strong right-hemisphere dominance.

In the current work, cerebral processing asymmetries, identified independently in the brain of each participant, were in fact computed as in Króliczak et al. (2011). Moreover, both the spatial extent of neural activity linked to task performance, and the related changes in signal amplitudes of the identified active voxels, i.e., based on beta weights, but then converted to percent signal change (%SC) values were considered. Importantly, only voxels located within the independently defined anatomical left and right hemisphere regions of interest (ROIs), and showing positive Z values in unthresholded activity maps (similarly to Jansen et al., 2006), were used in LI calculations. Consistent with a few earlier projects from our group (cf. Biduła & Króliczak, 2015), the following two sets of ROIs, depicted in Figure 1, were used: for manual gestures – the supramarginal gyrus (Brodmann area (BA) BA40, approximated by two subdivisions [PF and PFm] of the inferior parietal lobule [IPL], as defined by Caspers et al., 2006), and for productive language – Broca’s area (approximated by BA45 and BA44, defined earlier by Amunts et al., 2004). While using the spatial extent of task-related neural activity, we simply counted the number of voxels that exceeded six percentage of the maximum (POM) activity thresholds (namely: 90, 80, 70, 60, 50, and 40%), relative to the maximum Z value identified (separately for each individual Zstat image) within a given pair of ROIs. While using amplitudes of neural activity, here (unlike in Króliczak et al., 2011), we also averaged percent signal changes from all the voxels whose activation exceeded the same six, pre-defined activity thresholds.

The described methodological approach to the calculation of values that will then be entered to the LI equation brings substantial improvements for three reasons: it is directly inspired by one of the approaches with the highest correlation to the Wada test (Chlebus et al., 2007), it lets us base our conclusions on two complementary methods, and it also guards against biasing these conclusions

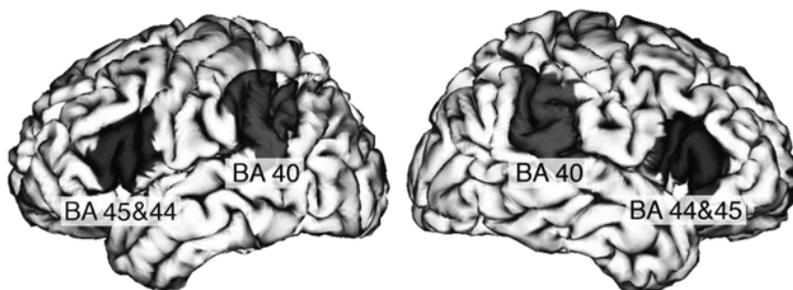


Figure 1. Regions of interest (ROIs). The maps of Broca’s area, and its right-hemisphere counterpart (Brodmann areas [BAs]44-45), as well as the left and right supramarginal gyrus (SMG, approximating BA40 by combining divisions PF and PFm), obtained from the Juelich histological atlas (implemented in the neuroimaging software of our choice, i.e., FSL). Before the addition of their subdivisions, all these maps were thresholded at the 50th percentage of their respective maximum probability values for their voxels. These ROIs are shown on a pial surface of the cerebral cortex of the template brain implemented in Connectome Workbench imaging software

on the use of a particular – just one, and in some cases too liberal – threshold (for more details, see Króliczak et al., 2011). As before, in each participant, hemispheric dominance was then assessed with the use of the following formula:  $LI = [(L-R)/(L + R)] \times 100$ , where L and R stands for relevant values obtained separately from the left-, and right-hemisphere ROI, and these values are either the number of suprathreshold voxels, or the average percent signal change, first observed separately for all six thresholds, in the respective ROI. The final individual LI is then, in both approaches, collapsed across the six LIs.

### **Praxis tests**

In a “tool use gesture” task utilized at the University of Oregon (UO), and a “grasp and tool use gesture” task employed at Adam Mickiewicz University and the Nencki Institute of Experimental Biology, participants planned and then executed tool use pantomimes, either in response to action words (presented in gerundive form), or tool images displayed on a screen for 1.5 s or 2 s. The control task involved either the linguistic processing of words related to abstract actions (for details, see Króliczak et al., 2011), or counting parts of non-tool objects (for details, see Przybylski & Króliczak, 2017). Despite such methodological differences, the obtained outcomes – i.e., the identified networks underlying tool use pantomimes – were very similar, and typically organized at a group level. Therefore, we had no concerns about them being used in one project.

### **Productive language tests**

In a cued verbal fluency test, with five or six 30-s task blocks, interchanged with five or six 30-s rest blocks, participants silently generated as many words as possible, starting with a pseudorandomly displayed letter (A, E, G, H, K, L, M, or T) shown above the fixation cross watched via a coil-mounted mirror on the monitor behind the scanner. These letters were selected based on English and Polish language studies which had earlier demonstrated that most of the words people spontaneously generate in their native languages begin with such letters.

### **Acquisition of fMRI data, pre-processing, and analyses**

The experiments were performed using one of the two Siemens scanners: a 3-Tesla Allegra at the Robert and Beverly Lewis Center for Neuroimaging at UO in Eugene, and a 3-Tesla Trio scanner, in the Laboratory of Brain Imaging at the Nencki Institute in Warsaw. Both the pre-processing, and data processing steps, including analysis types, were the same as described earlier in reports by Króliczak et al. (2011), Biduła et al. (2017), and Przybylski and Króliczak (2017). FSL (FMRIB’s Software Library v4.1.4, then v5.0.6, and later; <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/>; Jenkinson et al., 2012) was used to obtain maps of neural activity, and initial cytoarchitectonic maps for ROIs (which were thresholded separately at the 50<sup>th</sup>% of their maximum probability values using a function from “fslmaths” operations), and custom-made scripts, utilizing “fslmaths” and “fslstats” functions, for LI calculation. Most of the less known neuroanatomical labels used

throughout this report are taken from the “connectome workbench” atlas by Glasser and collaborators (Glasser et al., 2016). The descriptive statistics and correlational analyses of LIs were obtained and performed with IBM® SPSS® Statistics for Macintosh v.25.0, Armonk, NY: IBM Corp.

## RESULTS

Our participants were first divided into typical and atypical based exclusively on their engagement of BA44-45 in our language task. Namely, their LIs must have been at least +50 during silent word generation to be considered typical. The resulting neural activity from our praxis and language tasks is shown in Fig. 2A and 2B. Because language and praxis are linked, one can expect that most, if not all typical individuals will also have typically organized praxis skills. Yet, the assignment to the praxis group is based on (at least partly) an independent criterion – a different task.

### Praxis-related neural activity

In individuals with so-defined typical representations of language, performance of tool use pantomimes (transitive gestures) was associated with widespread bilateral neural activity, which was nevertheless greater and/or wider in the left hemisphere. Of particular interest, here, is the involvement of several areas often associated with the *praxis representation network* (PRN; e.g., Przybylski & Króliczak, 2017; see also Styrkowiec, Nowik & Króliczak, 2019; Potok, Maskiewicz, Króliczak & Marangon, 2019). For example, contributions from the anterior supramarginal gyrus (aSMG; area PFt), mid-to-posterior AIP, as well as a subdivision of the middle frontal gyrus (MFG; namely area 46; all as defined by Glasser et al., 2016) were observed exclusively on the left. Moreover, whereas in the vicinity of the temporo-parieto-occipital junction (TPOJ), the right-hemisphere activity was limited almost exclusively to TPOJ1-3, in the left hemisphere this activity extended both dorsally and posteriorly (to subdivisions PGs, PGi, and PGp), as well as to more ventral areas (LO3, MT, MST, FST, and PHT). Similarly, contributions from mid SMG (area PF) and the nearby parietal opercular, as well as frontal opercular and insular cortices were also greater on the left. So was the engagement of numerous areas belonging to the more superior, *dorso-dorsal* and *medio-dorsal* streams (which are of less theoretical importance, here). These effects are shown in Fig. 2A.

Most of the praxis-related neural activity common to fifteen atypical participants (also defined by the engagement of BA44-45 in our language task) was also common with the one observed for typical subjects. Yet, as can be seen in the right panel of Fig. 2A, in addition to the bilateral engagement of the inferior parietal area PF, and the more superior dorso-dorsal streams, this activity was mostly limited to the right hemisphere. Particularly striking were contributions from counterparts of the already-mentioned occipito-temporal areas (such as right PH and PHT).

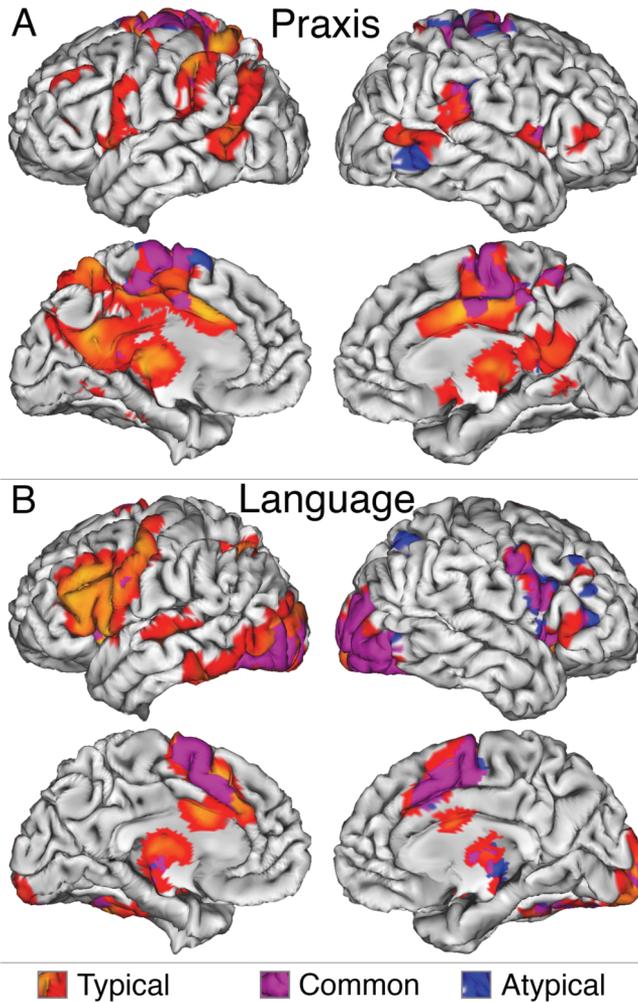


Figure 2. Main group results. (A) Brain areas showing significantly greater neural activity in our praxis task: tool use pantomimes vs. a control task. (B) Brain areas showing significantly greater neural activity in our language task: silent (subvocal) word generation vs. a control fixation task. Only volumetric surface renderings are displayed. All images shown here were thresholded using  $Z > 3.1$  and a corrected cluster significance threshold of  $P = 0.05$ . Warm colors (yellow-red) reflect neural activity in typical participants, cold (blue) colors reflect neural activity in atypical participants, and lavender or magenta their overlaps. Due to greater variability in the way praxis and language are represented in atypical participants at an individual level, the obtained group results are not mirror images of the typical, left-hemisphere dominant activation patterns

### Language-related neural activity

Neural activity from these same two cohorts of individuals was subsequently corroborated at a group level in our language task. The obtained effects are shown in Fig. 2B. As will become clear later on, using praxis laterality as an independent criterion for assigning participants to typical and atypical language groups would make less sense here.

Not surprisingly, the typical group had predominantly left-lateralized neural activity in the frontal and prefrontal regions usually associated with language production, starting from the dorsal and ventral premotor regions (e.g., 6a, 55b, 6r), through the middle and inferior frontal gyri (e.g., areas 8c, 46, a9-46v, and 44, 45, respectively), as well as the frontal opercular (e.g., FOP4-5) and insular cortices (AVI). Of note is the exclusive engagement of a superior temporal subdivision, dubbed STSdp, and extending to TPOJ1. Except for the left anterior cingulate cortex (e.g., a32pr, 33pr), the contributions from the supplementary and presupplementary motor cortices were more symmetrical. So were the inputs from the lateral, and ventral visual cortices, except for a few higher-order areas (e.g., FST, PH, FFC, and TE1p), again on the left. Interestingly, there was also exclusively left-sided involvement of several functional subdivisions located within the intraparietal sulcus (IPS).

In atypical participants, the neural activity observed in the frontal and prefrontal cortices largely overlapped with the one for typical individuals. Yet, as shown in the right panel of Fig. 2B, it was limited primarily to the right hemisphere. Moreover, this group did not seem to engage most of the anterior insula (i.e., AAIC, and AVI). Little differential neural activity was observed in early visual areas. Finally, the mirror-reversed contribution from the right IPS was present, but was now only of a limited extent (found mainly in AIP, IP2, and LIPd).

### **Praxis-language relationships**

As before, but now with a much larger sample of left-handed individuals, the analyses revealed significant (two-tailed, Pearson coefficients) correlations between individuals' praxis and language LIs, both for POM (the percentage of maximum)-derived LIs ( $r = 0.50$ ,  $p < 0.001$ ) and PSC (the % signal change)-derived LIs ( $r = 0.42$ ,  $p < 0.001$ ). This was the case even with the assumption that these relationships are not linear, as revealed by (two-tailed, Spearman rho) correlations for POM LIs ( $\rho = 0.37$ ,  $p < 0.01$ ), and PSC LIs (again,  $\rho = 0.37$ ,  $p < 0.01$ ). As shown in Figure 3, the vast majority of our left-handed participants revealed the typical left-hemisphere dominance for both praxis in BA40 (58.9%), and language in BA44-45 (73.2%), falling in the top corner of the upper right quadrant of Fig. 3A. Similar percentages can be found for PSC data – but only when the  $\geq +33$  criterion is used – for praxis in BA40 (53.6%), and language in BA44-45 (67.9%), as illustrated in the upper right quadrant of Fig. 3B. Yet, for simplicity, the latter approach will no longer be used for more detailed analyses presented below.

Somewhat surprisingly, out of the 41.1% (23) of individuals who showed either a more balanced (atypical bilateral) or right-lateralized (mirror-reversed) organization of praxis in BA40, only 23.2% (13) demonstrated bilateral or right lateralized language organization in BA44-45 (Fig. 3A). On the other hand, out of the 26.8% (15) of individuals who showed atypical bilateral organization or right-lateralized language, as many as 23.2% (13) also showed atypically organized praxis. In other words, the more common dissociation between praxis and language is the one observed in a direction involving atypical praxis vs. typical lan-

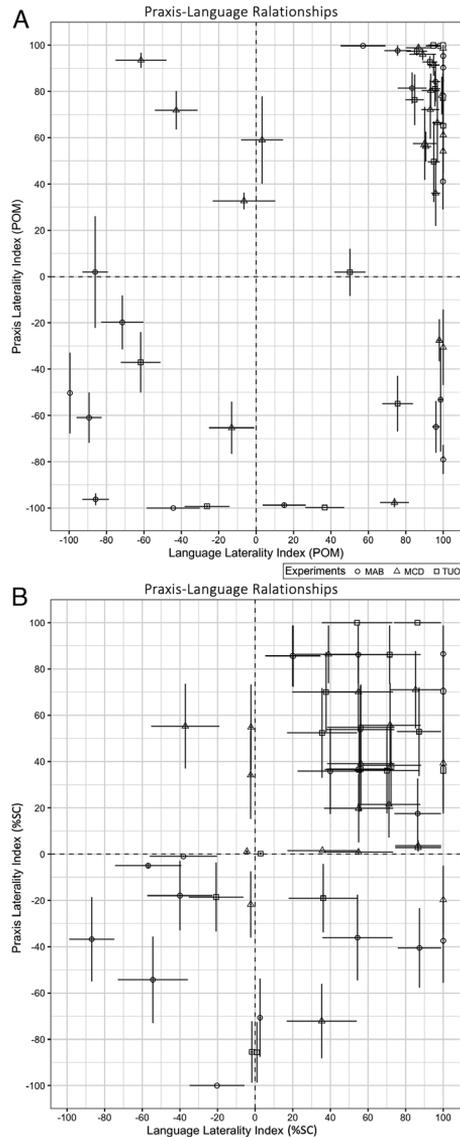


Figure 3. Laterality indices (LIs) of praxis and language. (A) LIs based on activation extent. Only voxels that first survived six pre-specified percentage of the maximum (POM) thresholds (90–40%, in decrements of 10) were used in the repeated calculations of LIs, before their averaging that resulted in one individual task LI. Z-maximum value was derived from the most highly activated voxel in the Z-stat (unthresholded) image within the paired ROIs. (B) Praxis and language LIs based on the magnitude of the fMRI percent signal change (%SC). The mean %SC values were derived from all activated voxels (having positive z-values within an ROI), that again survived the six pre-specified thresholds. All calculations were performed separately for each task (praxis, language) and each brain region (BA40, BA44-45). Each LI, regardless of its inputs (voxel count, mean % signal change), was calculated with the formula  $[(L-R)/(L + R)] \times 100$ . A value of +100 indicates complete left lateralization of the studied function, -100 its complete right lateralization, and 0 a balanced engagement of both ROIs. Error bars indicate within-subject standard errors of the mean LIs, based on the six contributing thresholds. MAB, MCD, and TUO are codes of the three projects from which the data were taken

guage. Yet, as revealed in the upper left quadrant of Fig. 3A, there are also two cases with atypically represented language (one showing weak, and one strong right-hemisphere dominance), who at the same time demonstrate quite typically represented, i.e., left-lateralized praxis.

## DISCUSSION

Based on a much larger sample of left-handed individuals, the observed strong correlations between the two functions studied here not only replicate but also provide further compelling evidence for a link between the cerebral representation of praxis and language in the healthy brain. Indeed, without any reference to causality, the current findings allow for an even more convincing statement that the parietal organization of tool use gestures is highly predictive of the frontal organization of productive language (Vingerhoets, 2014; cf. Goldenberg, 2013b; for a recent review, see Vingerhoets, 2019). As before, we still favor the interpretation that the relationships observed between these two fundamental behaviors are contingent on a common cerebral specialization (exploiting, for example, symbolic representations, computing complex motor sequences, or even orchestrating their hierarchies; Kimura & Archibald, 1974; Greenfield, 1991; see also Bradshaw & Nettleton, 1982), and therefore they tend to stick together even in the atypical form. In other words, as convincingly demonstrated here in a large cohort with considerable natural variation in praxis and language representations, we see little evidence for an accidental reshuffling of these two functions to one hemisphere or the other.

If such a reshuffling was one of the main principles organizing related (and perhaps even complementary) functions in the brain then, in neuropsychological patients, there should indeed be little evidence for any relations between apraxia and aphasia, or between apraxia and handedness (Goldenberg, 2013a; Goldenberg, 2013b). Yet, quite a substantial number (more than a third) of cases with right-lateralized or bilaterally organized praxis among our lefthanders indirectly points to potential neuropsychological deficiencies, or the lack of thereof, following a right-hemisphere stroke. More importantly, and somewhat consistent with the former speculation, we found numerous participants (nearly one fourth) revealing such atypical organization of praxis and quite standard, left-hemisphere language laterality. For a strong proponent of the idea of praxis-language links, such a segregation of these skills might be puzzling at first. However, more detailed analyses of mechanisms that might contribute to the development of relatively common cases of right versus left praxis-language dissociations (RH Praxis–LH Language), and even more surprising the very rare (here: 3.6%) incidence of reversed cases with right versus left language-praxis segregation (RH Language–LH Praxis) can shed some new light on this issue.

It could be argued that the elimination of redundant mechanisms, possibly associated with an enhancement of parallel processing, but also accompanied by segregation of unrelated functions, is one of the most critical organizational principles whereby the brain maximizes its efficiency (e.g., Vallortigara, Rogers &

Bisazza, 1999; Vingerhoets, 2019). If in a left-handed infant, acquisition of uni-manual manipulation preferences substantially precedes a development of hand preference (cf. Michel, 2018, who postulates a different order of development), then it is also quite likely that the much later acquired praxis skills will also be more dependent on lower-level mechanisms for hand manipulation. This could eventually lead to the bilateral organization of praxis. More importantly, if the mechanisms for hand preference are implemented in the brain substantially earlier than the development of speech production (a scenario quite likely in a left-hander; Johnston, Nicholls, Shah & Shields, 2009), the two factors combined could jointly exert sufficient pressure for the development of RH Praxis–LH Language pattern. After all, following a substantial expansion of a common hand-manipulation/praxis frame of reference, conflict prevention could also further support a segregation of language from hand dominance mechanisms.

Conversely, if speech development is simultaneous with or even precedes the acquisition of hand preference then praxis and language could be more tightly linked. One of its auxiliary consequences could be their segregation from lower-level mechanisms for hand/finger manipulation and therefore, in a left-hander, their typical implementation in the left hemisphere. In fact, this putative developmental order of skill acquisition would lead to the predominantly observed language-praxis organization and their (at least partial dissociation) from hand dominance mechanisms.

It is much harder to explain why the mechanisms underlying language production are occasionally and accidentally displaced to the right hemisphere, especially in left-handed individuals. What is particularly uncertain is the kind of redundancy elimination or processing enhancement that could be a factor here. One could postulate, though, that unless computations essential for other, possibly complementary (not to be mixed with related) functions, such as attention and visuospatial processing, are put into the equation, the RH Language–LH Praxis dissociation could constitute a canonical case of the accidental reshuffling postulated earlier by Goldenberg (Goldenberg, 2013a; Goldenberg, 2013b). Consistent with this notion, the most common historical arguments pointing to brain pathology, including early injuries, epilepsy, or deficiencies in blood flow affecting more the left hemisphere (e.g., Rasmussen & Milner, 1977; Lazar et al., 2000) and pushing language to the right hemisphere, seem to be less dependent on handedness, too. Of course, there is also some evidence that the factors contributing to the development of lefthandedness may also hinder the organization of the typical left-hemisphere dominance for language (Brown & Hecaen, 1976). While still somewhat dependent on early brain anomalies, the co-localization of more or most of the major language functions (i.e., production, prosody, intonation, stress and rhythm) into one hemisphere could be a result, as well. This effect could be referred to as pseudo crowding (cf. Badzakova-Trajkov, Corballis & Haberling, 2016; Vingerhoets, 2019), because all these functions are related. At the same time, such an argument also calls for an explanation of why praxis (despite initial putative brain pathology) would nevertheless remain to be repre-

sented in the left hemisphere. Yet in this case, presumably, it is still reasonable to assume that the timing of its development is also a key factor.

Finally, it should be emphasized that, whereas some of the arguments put forward here are based on findings from ROIs (regions of interest), complex cognitive brain functions are supported by much larger networks of regions (see also Pachalska et al. 2018). Based on the group-level results, the take home message from this study is that there are many common neural mechanisms underlying praxis and/or language skills represented in their typical and atypical forms. However, it should be immediately added that the – not so impressive – common denominator, i.e., overlap of their activity, would most likely be greater if there was less variability in the way praxis and language skills are bilaterally organized or lateralized in atypical participants at an individual level (see Biduła et al., 2017).

## **CONCLUSIONS**

Despite numerous cases of unidirectional dissociations between right-lateralized praxis and left-lateralized language, the main indices of neural underpinnings for tool use gestures and language production were nevertheless closely linked. The tendency for praxis to be represented in the right hemisphere can be credibly explained by the principle of redundancy elimination, and the associated attraction or immersion of praxis-related computations in hand dominance mechanisms. The inverse pattern of right-lateralized language and left-lateralized praxis is not only less likely to emerge but also more difficult to explain. We will, therefore, conclude with a statement that this very rare segregation or dissociation of the neural substrates for atypical language and typical praxis warrants a particularly careful examination in any future studies. The alternative is that, given it is so rare, it must be rather maladaptive, and there is no major underlying principle for its development.

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