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ARTICLES–STUDIES

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PRAXIS IN LEFT-HANDERS

ABSTRACT

Neuropsychological and neuroimaging evidence convincingly implicates the left cerebral hemisphere in the representation of skilled movements (praxis) in right-handers. Compelling and consistent data on the organization of praxis in left-handed individuals has only recently started to emerge. This new evidence, again both from neuropsychology and neuroimaging, supports the notion that in left-handers the neural substrate of praxis skills is less asymmetric, i.e., it is more bilaterally organized. Up until recently, though, the neuropsychological literature on brain-damaged left-handers was often dominated by descriptions of more or less atypical cases and dissociations of functions observed in such individuals. Associations of deficits, linked to anatomic proximity rather than to a common cerebral specialization, were rarely found worth publishing and/or in-depth discussions. This paper first reviews some of the most relevant and/or well-known reports on representations of different categories of skilled manual gestures in right- and left-handers, with a view to support the idea that these skills are mediated by a common system. Then, based on neuroimaging evidence from healthy subjects, a few individuals with unusual organization of praxis are discussed. These disparate cases quite likely represent natural variation in functional asymmetries. It is yet to be determined whether the effect of a more bilateral organization of cognitive skills in this population is just due to a much higher incidence of atypical representations of functions or rather a general tendency for all left-handers to have their brains less asymmetrically organized.

Key words:
communicative gestures, gesture planning, neural representations, asymmetries, dissociations

1. Introduction

It has been long argued that performance of skilled movements depends not only on the integrity of brain circuits involved in the low level, direct control of action execution, but also on regions engaged in higher-order movement (praxis) representations, e.g., the areas encoding internal models of skilled motor acts. Put differently, although the contribution of the contralateral primary sensory-motor systems in the actual performance of simple manual tasks is no doubt essential[1], more cognitive aspects of complex movements, such as sequencing and timing of finger/hand/arm configurations, and their functionally appropriate orientation or position, are controlled by the dominant left hemisphere[2]. Such left-lateralized cerebral specialization for praxis is evident in nearly all right-handers, irrespective of the hands that they use in the tasks. Therefore, although implemented primarily in the left inferior parietal, premotor, prefrontal, and caudal temporal areas, this specialization underlies hand-independent mechanisms selective to disparate cognitive requirements for different manual actions[3].

[1] H. Liepmann, *Apraxia*, "Ergebn. Ges. Med." 1920, No. 1, pp. 516–543; J. Brinkman, H.G. Kuypers, *Splitbrain Monkeys: Cerebral Control of Ipsilateral and Contralateral Arm, Hand, and Finger Movements*, "Science" 1972, No. 176(34), pp. 536–539; J. Brinkman, H.G. Kuypers, *Cerebral Control of Contralateral and Ipsilateral Arm, Hand and Finger Movements in the Split-brain Rhesus Monkey*, "Brain" 1973, No. 96(4), pp. 653–674.

[2] E.g. H. Liepmann, *Apraxia*, op.cit.; H. Goodglass, E. Kaplan, *Disturbance of Gesture and Pantomime in Aphasia*, "Brain" 1963, No. 86, pp. 703–720; D. Kimura, Y. Archibald, *Motor Functions of the Left Hemisphere*, "Brain" 1974, No. 97(2), pp. 337–350. For reviews, see K. Haaland, D.L. Harrington, *Hemispheric Asymmetry of Movement*, "Curr Opin Neurobiol" 1996, No. 6(6), pp. 796–800; R. Leiguarda, *Apraxias as Traditionally Defined* [in:] *Higher-Order Motor Disorders: From Neuroanatomy and Neurobiology to Clinical Neurology*, H.-J. Freund, M. Jeannerod, M. Hallett, R. Leiguarda (eds.), Oxford 2005, pp. 303–338; a Polish reader is also referred to a review on praxis by G. Króliczak, *Reprezentacja praksji u osób prawo- i leworęcznych* [Representation of Praxis in Right- and Left-Handed Individuals] [in:] *Na ścieżkach neuronauki* [On Paths of Neuroscience], P. Francuz (ed.), Lublin 2010, pp. 173–189; cf. G. Króliczak, C. Cavina-Pratesi, D.A. Goodman, J.C. Culham, *What Does the Brain Do when You Fake It? An FMRI Study of Pantomimed and Real Grasping*, "Journal of Neurophysiology" 2007, No. 97(3), pp. 2410–2422; see also G. Króliczak, C. Cavina Pratesi, M.E. Large, *Object Perception versus Target-Directed Manual Actions* [in:] *Neuroadaptive Systems: Theory and Applications*, M. Fafrowicz, T. Marek, W. Karwowski, D. Schmorrow (eds.), Bosa Roca 2012, pp. 69–95.

[3] K. Haaland, D.L. Harrington, *Hemispheric Asymmetry of Movement*, "Curr Opin Neurobiol" 1996, No. 6(6), pp. 796–800; R. Leiguarda, *Limb Apraxia: Cortical or Subcortical*, "Neuroimage" 2001, No. 14(1), pp. 137–141; S. Johnson-Frey, *The Neural Bases of Complex Tool Use in Humans*, "Trends Cogn Sci" 2004, No. 8(2), pp. 71–78; S. Frey, M.G. Funnell, V.E. Gerry, M.S. Gazzaniga, *A Dissociation between the*

The actual neural underpinning of praxic skills, such as deft control of the hand for simulated use of tools and utensils (transitive actions; e.g. cutting, stirring, painting), and for conventionalized manual signals and signs that do not require objects (intransitive actions; e.g. beckoning, waving, scolding) – has been extensively studied in patients with brain injuries since the turn of the 20th century[4]. Right from the start, different kinds of *apraxia* – i.e., an inability to perform skilled movements in the absence of primary sensory, lower-level motor, and linguistic deficits – have been distinguished and related to disparate lesion locations. Thus, the most basic praxic disorder, such as an inability to make precise movements of individual fingers – referred to as *limb-kinetic apraxia* – has been linked primarily[5], but not always[6] to contralateral lesions of the primary sensory-motor system, and sometimes[7] to lesions of the premotor cortices (PMC). In sharp contrast, an inability to properly time and spatially organize more complex gestural movements – called *ideomotor apraxia* – observed despite seemingly intact movement representations[8] occurs primarily following lesions to the left posterior parietal cortex

Representation of Tool-Use Skills and Hand Dominance: Insights from Left- and Right-Handed Callosotomy Patients, "J Cogn Neurosci" 2005, No. 17(2), pp. 262–272; S. Frey, *What Puts the how in where? Tool Use and the Divided Visual Streams Hypothesis*, "Cortex" 2007, No. 43(3), pp. 368–375; G. Króliczak, S.H. Frey, *A Common Network in the Left Cerebral Hemisphere Represents Planning of Tool Use Pantomimes and Familiar Intransitive Gestures at the Hand-Independent Level*, "Cereb Cortex" 2009, No. 19(10), pp. 2396–2410; see also G. Króliczak, D.A. Westwood, M.A. Goodale, *Differential Effects of Advance Semantic Cues on Grasping, Naming, and Manual Estimation*, "Experimental Brain Research" 2006, No. 175(1), pp. 139–152; G. Króliczak, C. Cavina Pratesi, M.E. Large, op.cit.

4 E. g. H. Liepmann, *Das Krankheitshild der Apraxie (Motorischen/Asymbolie)*, " Monatschrift fur Psychiatrie und Neurologie" 1900, No. 8, pp. 15–44, 102–132, 182–197; H. Liepmann, *Apraxia*, op.cit.; N. Geschwind, E. Kaplan, *A Human Cerebral Deconnection Syndrome. A Preliminary Report*, "Neurology" 1962, No. 12, pp. 675–685; H. Goodglass, E. Kaplan, op.cit.; E. Roy, P. Square-Storer, S. Hogg, S. Adams, *Analysis of Task Demands in Apraxia*, "Int J Neurosci" 1991, No. 56(1–4), pp. 177–186; K. Heilman, R.T. Watson, L.G. Rothi, *Limb Apraxias: Disorders of Skilled Movements* [in:] *Behavioural Neurology and Neuropsychology*, T.E. Feinberg, M.J. Farah (eds.), New York 1997; B. Hanna-Pladdy, S.K. Daniels, M.A. Fieselman, K. Thompson, J.J. Vasterling, K.M. Heilman, A.L. Foundas, *Praxis Lateralization: Errors in Right and Left Hemisphere Stroke*, "Cortex" 2001, No. 37(2), pp. 219–230; K. Heilman, L.J. Rothi, *Apraxia* [in:] *Clinical Neuropsychology*, K.M. Heilman, E. Valenstein (eds.), New York 2003, pp. 215–135; R. Leiguarda, *Apraxias as Traditionally…*, op.cit.; for one of the most recent attempts to look for cases of their dissociations see also V. Stamenova, E.A. Roy, S.E. Black, *Associations and Dissociations of Transitive and Intransitive Gestures in Left and Right Hemisphere Stroke Patients*, "Brain & Cognition" 2010, No. 72(3), pp. 483–490.

5 H. Liepmann, *Apraxia*, op.cit.

6 K. Heilman, K.J. Meador, D.W. Loring, *Hemispheric Asymmetries of Limb-Kinetic Apraxia: A Loss of Deftness*, "Neurology" 2000, No. 55(4), pp. 523–526.

7 H. Freund, H. Hummelsheim, *Lesions of Premotor Cortex in Man*, "Brain" 1985, No. 108, pp. 697–733.

8 E. g. H. Liepmann, *Apraxia*, op.cit.; L. Rothi, C. Ochipa, K.M. Heilman, *A Cognitive Neuropsychological Model of Limb Praxis*, "Cognitive Neuropsychology" 1991, No. 8(6), pp. 443–458.

(PPC), less frequently PMC, supplementary motor area (SMA), and lateral prefrontal cortex[9]. Finally, an inability to conceptualize proper movements for simulated (i.e., gestured) use of an imagined object – referred to as *ideational apraxia* – typically follows left parieto-occipital and parieto-temporal lesions[10]. Yet, similar movement disturbances have been also observed after left frontal and fronto-temporal lesions[11].

These and other subtypes of apraxia have been described and debated in the neuropsychological literature, both in the context of tool use pantomimes and intransitive gestures[12]. The overall patterns of findings have, of course, differed depending on the task employed, e.g., whether the tested gestures were performed on verbal command, imitated, or were triggered by the object or a related picture, and have, no doubt, been contingent upon how praxis and language were represented in the patient's brain[13]. It should be added, though, that some of the most intriguing patterns of deficits in limb praxis come from studies of patients with callosal infarction and/or surgical sectioning of the corpus callosum, which are referred to as the callosal disconnection syndrome. These cases indicate that – at least in right-handers – the laterality of praxis representation to the dominant left hemisphere is not always complete[14] and, unlike pantomiming to verbal command, imitation and actual object use can be also mediated by the right hemisphere. Some up to date support for these observations comes from reports of gradual changes in the hemispheric control of praxic skills over the time of recovery, in which the

[9] It is worth mentioning that ideomotor apraxia is often accompanied by damage to the intrahemispheric white matter connecting these areas; R. Leiguarda, C.D. Marsden, *Limb Apraxias: Higher-Order Disorders of Sensorimotor Integration*, "Brain" 2000, No. 123, pp. 860–879; R. Leiguarda, *Apraxias as Traditionally…*, op.cit.

[10] E.g. H. Liepmann, *Apraxia*, op.cit.; H. Freund, *The Apraxias* [in:] *Diseases of the Nervous System. Clinical Neurobiology*, A.K. Asbury, G.M. McKhann, W.J. McDonald (eds.), Philadelphia 1992, pp. 751–767.

[11] E.g. E. De Renzi, F. Lucchelli, *Ideational Apraxia*, "Brain" 1988, No. 111, pp. 1173–1185; K. Heilman, L.M. Maher, M.L. Greenwald, L.J. Rothi, *Conceptual Apraxia from Lateralized Lesions*, "Neurology" 1997, No. 49(2), pp. 457–464.

[12] For a review, see R. Leiguarda, *Apraxias as Traditionally…*, op.cit.

[13] E.g. H. Liepmann, O. Mass, *Fall von linksseitiger Agraphie und Apraxie bei rechsseitiger Lahmung*, "Zeitschrift fur Psychologie und Neurologie" 1907, No. 10, pp. 214–227; N. Geschwind, E. Kaplan, op.cit.; K. Heilman, L.J. Rothi, E. Valenstein, *Two Forms of Ideomotor Apraxia*, "Neurology" 1982, No. 32(4), pp. 342–346; R. Watson, K.M. Heilman, *Callosal Apraxia*, "Brain" 1983, No. 106, pp. 391–403; L. Rothi, K.M. Heilman, R.T. Watson, *Pantomime Comprehension and Ideomotor Apraxia*, "J Neurol Neurosurg Psychiatry" 1985, No. 48(3), pp. 207–210; V. Stamenova, E.A. Roy, S.E. Black, op.cit.

[14] N. Geschwind, E. Kaplan, op.cit.; M. Gazzaniga, J.E. Bogen, R.W. Sperry, *Dyspraxia following Division of the Cerebral Commissures*, "Arch Neurol" 1967, No. 16(6), pp. 606–612.

acute stage of deficits still suggests the initial lateralization of praxis to the left hemisphere[15].

More recent patient data strengthen the idea of left cerebral asymmetry in praxis representation. For example, Haaland and collaborators[16] showed that the areas of maximal lesion overlap in patients who were impaired in gesture imitation – most severely for the imitation of tool use gestures- are located primarily within and around the left intraparietal sulcus (IPS), and in the left middle frontal gyrus (MFG). In contrast, Goldenberg and collaborators[17] indicated that the areas of maximum difference between lesions in patients with impaired and normal pantomiming of tool use are located in the left inferior frontal gyrus (IFG), with the lesions extending both to the precentral gyrus (i.e., the ventral premotor cortex) and medially to the insular cortex. These results nicely converge with the outcomes of fMRI research showing that preparation and/or execution of tool use pantomimes leads to increased neural activity within and along IPS (often extending both to the inferior and superior parietal lobes; IPL and SPL), as well as in the left premotor and/or prefrontal cortex, including MFG[18]. Importantly, most of

15 R. Watson, K.M. Heilman, *Callosal Apraxia*, op.cit.

16 K. Haaland, D.L. Harrington, R.T. Knight, *Neural Representations of Skilled Movement*, "Brain" 2000, No. 123, pp. 2306–2313.

17 G. Goldenberg, J. Hermsdorfer, R. Glindemann, C. Rorden, H.O. Karnath, *Pantomime of Tool Use Depends on Integrity of Left Inferior Frontal Cortex*, "Cereb Cortex" 2007, No. 17(12), pp. 2769–2776.

18 J. Moll, R. de Oliveira-Souza, L.J. Passman, F.C. Cunha, F. Souza-Lima, P.A. Andreiuolo, *Functional MRI Correlates of Real and Imagined Tool-Use Pantomimes*, "Neurology" 2000, No. 54(6), pp. 1331–1336; S. Choi, D.L. Na, E. Kang, K.M. Lee, S.W. Lee, D.G. Na, *Functional Magnetic Resonance Imaging during Pantomiming Tool-Use Gestures*, "Exp Brain Res" 2001, No. 139(3), pp. 311–317; Y. Ohgami, K. Matsuo, N. Uchida, T. Nakai, *An fMRI Study of Tool-Use Gestures: Body Part as Object and Pantomime*, "Neuroreport" 2004, No. 15(12), pp. 1903–1906; R. Rumiati, P.H. Weiss, T. Shallice, G. Ottoboni, J. Noth, K. Zilles, G.R. Fink, *Neural Basis of Pantomiming the Use of Visually Presented Objects*, "Neuroimage" 2004, No. 21(4), pp. 1224–1231; S. Johnson-Frey, R. Newman-Norlund, S.T. Grafton, *A Distributed Left Hemisphere Network Active during Planning of Everyday Tool Use Skills*, "Cereb Cortex" 2005, No. 15(6), pp. 681–695; E. Fridman, I. Immisch, T. Hanakawa, S. Bohlhalter, D. Waldvogel, K. Kansaku, L. Wheaton, T. Wu, M. Hallett, *The Role of the Dorsal Stream for Gesture Production*, "Neuroimage" 2006, No. 29(2), pp. 417–428; G. Vingerhoets, *Knowing about Tools: Neural Correlates of Tool Familiarity and Experience*, "Neuroimage" 2008, No. 40(3), pp. 1380–1391; G. Króliczak, S.H. Frey, *A Common Network…*, op.cit.; S. Bohlhalter, N. Hattori, L. Wheaton, E. Fridman, E.A. Shamim, G. Garraux, M. Hallett, *Gesture Subtype-Dependent Left Lateralization of Praxis Planning: An Event-Related fMRI Study*, "Cereb Cortex" 2009, No. 19(6), pp. 1256–1262; G. Vingerhoets, F. Acke, P. Vandemaele, E. Achten, *Tool Responsive Regions in the Posterior Parietal Cortex: Effect of Differences in Motor Goal and Target Object During Imagined Transitive Movements*, "Neuroimage" 2009, No. 47(4), pp. 1832–1843; G. Vingerhoets, E. Vandekerckhove, P. Honore, P. Vandemaele, E. Achten, *Neural Correlates of Pantomiming Familiar and Unfamiliar Tools: Action Semantics versus Mechanical Problem Solving?*, "Human Brain Mapping" 2011, No. 32(6), pp. 905–918.

these neuroimaging studies also demonstrate that the observed increases of activation in the left parieto-frontal network are hand independent.

A much more contentious issue is whether or not the neural underpinning of intransitive gestures (including manual emblems, as compared to transitive skills) is also the same, or rather depends on dissociable, or at least partially different neural networks[19]. After all, since the time of Morlass (1928) it has been argued that the ability to perform and/or understand conventionalized intransitive gestures, while relying on basic praxis representations, may also call for mechanisms related to social skills and, therefore, be implemented in different brain areas (e.g., in the right hemisphere). Supported by at least two more contemporary, and in fact very famous, cases of left-hemisphere damages leading to no obvious impairments in intransitive gestures but very profound inability to pantomime the use of tools[20], this idea has prominently figured in modern theories of praxis[21]. Yet, some reports indicate that performance of intransitive gestures can be equally disrupted by damage to either cerebral hemisphere[22], suggesting that there might be either higher degree of individual variability in the lateralization of intransitive skills or that the mechanisms involved in activating manual emblems may be distributed across both hemispheres. In sharp contrast, a very similar argument – that some aspects of programming limb configurations and their timing may depend on bilateral representations – has been also put forward in the context of tool use pantomimes[23]. The gist of the discussion on cerebral lateralization (the laterality of neural representations) of transitive and intransitive skills is shown in a schematic form in Figure 1.

[19] See V. Stamenova, E.A. Roy, S.E. Black, op.cit. for one of the most recent neuropsychological reports on this topic; cf. F. Binkofski, L.J. Buxbaum, *Two Action Systems in the Human Brain*, "Brain and Language" 2012.

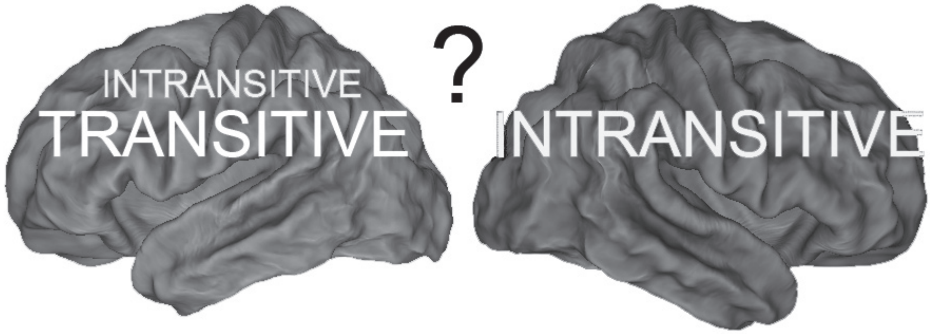
[20] S. Rapcsak, C. Ochipa, P.M. Beeson, A.B. Rubens, *Praxis and the Right Hemisphere*, "Brain Cogn" 1993, No. 23(2), pp. 181–202; C. Dumont, B. Ska, A. Schiavetto, *Selective Impairment of Transitive Gestures: An Unusual Case of Apraxia*, "Neurocase" 1999, No. 5, pp. 447–458.

[21] L. Rothi, C. Ochipa, K.M. Heilman, *A Cognitive…*, op.cit.; R. Cubelli, C. Marchetti, G. Boscolo, S. Della Sala, *Cognition in Action: Testing a Model of Limb Apraxia*, "Brain Cogn" 2000, No. 44(2), pp. 144–165; L. Buxbaum, *Ideomotor Apraxia: A Call to Action*, "Neurocase" 2001, No. 7(6), pp. 445–458.

[22] M. Heath, E.A. Roy, S.E. Black, D.A. Westwood, *Intransitive Limb Gestures and Apraxia Following Unilateral Stroke*, "J Clin Exp Neuropsychol" 2001, No. 23(5), pp. 628–642; see also V. Stamenova, E.A. Roy, S.E. Black, op.cit.

[23] B. Hanna-Pladdy, S.K. Daniels, M.A. Fieselman, K. Thompson, J.J. Vasterling, K.M. Heilman, A.L. Foundas, op.cit.

Figure 1.



Gesture laterality at a glance. There is a general agreement in the neuropsychological and neuroimaging literature that transitive gestures (tool use pantomimes) are represented in the left hemisphere, independent of the hand used. The topic of an ongoing discussion is whether or not intransitive gestures are mediated by the same or dissociable system. There is some evidence that these conventionalized gestures (that can be also used instead of speech) may rely more on the right hemisphere. However, left-hemisphere damages can also affect their performance. Population, landmark and surface-based atlas (PALs) of Van Essen[24] has been used in the background to represent the left and right hemispheres in their slightly inflated form (shown on the left and right side, respectively).

In one of the most recent reports on this topic[25], a few cases representing selective dissociations between intransitive and transitive skills have been shown either for imitation and/or pantomime of these gestures. Interestingly, deficient imitation of intransitive gestures (without deficits in their pantomimes, and no deficits whatsoever for transitive skills) was as likely to occur following damages to the right hemisphere (2 cases) or the left hemisphere (2 cases). Quite surprisingly, deficient pantomimes – i.e., verbally cued performance – of intransitive gestures (without problems with their imitation and no deficits in tests of transitive skills) have been linked only to right-hemisphere damages (another 2 cases). As can be seen, then, these very intriguing cases represent configurations of spared and/or lost abilities that would be very difficult to interpret within a general model, as the one presented above. A full appreciation of the observed patterns of acquired deficits will therefore depend on our understanding of the underlying causes for such striking

[24] D. Van Essen, *A Population-Average, Landmark- and Surface-Based (PALS) Atlas of Human Cerebral Cortex*, "Neuroimage" 2005, No. 28(3), pp. 635–662.

[25] V. Stamenova, E.A. Roy, S.E. Black, op.cit.

individual differences. As put elsewhere, "…in addition to detailed knowledge on lesion location, one would need to know whether the observed patterns result from visual recognition versus visuo-spatial deficits. Moreover, it should be explained why representations underlying these disparate (i.e., perceptual vs. spatial) skills would be selectively lateralized to one of the two hemispheres just for one gesture category"[26]. Nonetheless, it is worth emphasizing that the group data from the paper by Stamenova and collaborators[27] are quite coherent with earlier neuropsychological reports on apraxia of tool use and intransitive gestures.

Consistent with reports that apraxic patients with left-hemisphere lesions are often less impaired when they perform familiar intransitive gestures[28], Króliczak and Frey have recently demonstrated using fMRI that a common network located in the left cerebral hemisphere is taxed less by intransitive gestures. Yet, this left-lateralized network really represents both planning of transitive (tool use) and intransitive gestures at the hand-independent level. They presented at least three pieces of evidence to make their case. A direct contrast of activity related to planning tool use pantomimes (vs. intransitive gestures) was indeed associated with greater activation within and around left IPS, primary sensory-motor, and dorsal premotor (PMd) cortices. But this was the case only when the dominant right hand was involved. The inverse contrast (for intransitive vs. transitive gesture planning) yielded no significant results. Similarly, no significant difference between activation for planning of tool use pantomimes and intransitive gestures was observed when participants used their non-dominant left hands. Thus, also consistent with behavioral outcomes from healthy individuals, who under time pressure commit more errors during performance of transitive gestures[29], these results strongly suggest that the difficulties many apraxic patients have during pantomiming the use of tools (but little or no problems with intransitive skills) can be accounted for by an assumption that transitive gestures are simply harder to plan and/or execute than intransitive gestures. Yet, even such unidirectional differences in verbally cued planning of these skills are still consistent with the idea that both gesture categories

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26 G. Króliczak, *Representations of Transitive and Intransitive Gestures: Perception and Imitation*, "Journal of Neuroscience and Neuroengineering" 2013, No. 2(3), pp. 195–210.

27 V. Stamenova, E.A. Roy, S.E. Black, op.cit.

28 E. g. E. Roy, P. Square-Storer, S. Hogg, S. Adams, op.cit.; A. Foundas, B.L. Macauley, A.M. Raymer, L.M. Maher, L.J. Rothi, K.M. Heilman, *Ideomotor Apraxia in Alzheimer Disease and Left Hemisphere Stroke: Limb Transitive and Intransitive Movements*, "Neuropsychiatry Neuropsychol Behav Neurol" 1999, No. 12(3), pp. 161–166; K. Haaland, D.L. Harrington, R.T. Knight, op.cit.

29 J. Carmo, R.I. Rumiati, *Imitation of Transitive and Intransitive Actions in Healthy Individuals*, "Brain Cogn" 2009, No. 69(3), pp. 460–64.

capitalize on common neural mechanisms and processes forming the so-called *praxis representation network* or PRN[30].

The outcomes from fMRI studies on the recognition[31] and imitation[32] of these two gesture categories are also consistent with the idea of a common system, i.e., the *praxis representation network*, involved in processing and guidance of these skills. The study by Króliczak extends this notion to perceptual processing of the two gesture categories (or at least to watching them with the intention to imitate), and also to their subsequent, shortly delayed imitation. Consistent with Króliczak and Frey, this report nicely showed that transitive gestures, as having more complex movement kinematics, less often seen in real life, and clearly less often used (as compared to intransitive skills), are more difficult to retrieve and, subsequently, to imitate. In fact, this effect can be observed well before the retrieval of the to-be-performed (gesture) kinematics because even simple visual processing of these actions, in addition to visuomotor regions, strongly engages several lower-level and higher-order visual areas. Moreover, the need for deeper processing of transitive gestures also extends beyond the stage of their retrieval because, similarly to verbally cued pantomimes[33], the actual imitation of simulated tool use movements also leads to greater engagement of premotor and motor cortices on the left. Nevertheless, a case for dissociation has been also made because the actual imitation of intransitive gestures was accompanied by modulations of higher-order (parietal, and medial frontal) areas located outside of the left-lateralized praxis representation network[34]. It should be emphasized, though, that virtually none of these regions was involved when gesture-related activity (either watching or imitation) was measured versus resting baseline. Thus, the revealed clusters most likely reflect some differences in the suppression of brain activity (or perhaps even deactivation) and, therefore, their actual role or contribution is hard to interpret.

In summary, damage to the dominant left hemisphere in right-handers can lead to impairments in some but not all tests of apraxia. Apraxic patients can have no difficulty handling real objects and may find common, conventionalized gestures easier, especially on imitation[35]. This may in turn suggest the existence of some

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30 G. Króliczak, S.H. Frey, *A Common Network…*, op.cit.

31 M. Villarreal, E.A. Fridman, A. Amengual, G. Falasco, E.R. Gerscovich, E.R. Ulloa, R.C. Leiguarda, *The Neural Substrate of Gesture Recognition*, "Neuropsychologia" 2008, No. 46(9), pp. 2371–2382; G. Króliczak, *Representations of Transitive…*, op.cit.

32 G. Króliczak, *Representations of…*, op.cit.

33 G. Króliczak, S.H. Frey, *A Common Network…*, op.cit.

34 G. Króliczak, *Representations of Transitive…*, op.cit.

35 E. g. H. Goodglass, E. Kaplan, op.cit.

praxic mechanisms within the non-dominant hemisphere. Indeed, right-hand dominant individuals can experience apraxia as a result of damage to their right hemispheres, too[36]. Thus, despite the consensus that the vast majority of apraxic deficits in right-handers are associated with damage to the left hemisphere, praxis lateralization does not seem to be fully determined by hand preference, or vice versa, and may depend on multiple factors. This hypothesis gains further support from reports of apraxia in left-handed patients.

2. Praxis representation in left-handed individuals

It has been often assumed that hand preference might be one of the most reliable behavioral indicators of hemispheric specialization for praxis in humans[37]. If this were the case and, hypothetically speaking, the cerebral representation of praxis was always contralateral to the dominant hand then the pattern of lesions and the related praxis deficits in left- and right-handers should be mirror images of each other. Although such a case has indeed been reported[38], this is not what has been typically observed in the apraxia literature. In fact, there is much less agreement on the lateralization of the control of more complex movements required for praxic skills in left-handed individuals, in part because extensive and systematic studies have been scarce until recently[39].

[36] E.g. S. Rapcsak, L.J. Gonzalez Rothi, K.M. Heilman, *Apraxia in a Patient with Atypical Cerebral Dominance*, "Brain Cogn" 1987, No. 6(4), pp. 450–463; B. Hanna-Pladdy, S.K. Daniels, M.A. Fieselman, K. Thompson, J.J. Vasterling, K.M. Heilman, A.L. Foundas, op.cit.; V. Stamenova, E.A. Roy, S.E. Black, op.cit.; cf. A. Falchook, D.B. Burtis, L.M. Acosta, L. Salazar, V.S. Hedna, A.Y. Khanna, K.M. Heilman, *Praxis and Writing in a Right-Hander with Crossed Aphasia*, "Neurocase" 2013, where right-hemisphere lesion in a right-hander resulted only in deficient selection of the praxis programs, and a perseverative agraphia, but the praxic system seemed largely intact.

[37] Cf. K. Haaland, D.L. Harrington, op.cit.; see also J. Volkmann, A. Schnitzler, O.W. Witte, H. Freund, *Handedness and Asymmetry of Hand Representation in Human Motor Cortex*, "J Neurophysiol" 1998, No. 79(4), pp. 2149–2154.

[38] E.g. D. Delis, R.T. Knight, G. Simpson, *Reversed Hemispheric Organization in a Left-Hander*, "Neuropsychologia" 1983, No. 21(1), pp. 13–24; but cf. R. Fischer, M.P. Alexander, C. Gabriel, E. Gould, J. Milione, *Reversed Lateralization of Cognitive Functions in Right Handers. Exceptions to Classical Aphasiology*, "Brain" 1991, No. 114, pp. 245–261.

[39] M. Rocca, A. Falini, G. Comi, G. Scotti, M. Filippi, *The Mirror-Neuron System and Handedness: A „Right" World?*, "Human Brain Mapping" 2008, No. 29(11), pp. 1243–1254; G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization of Language Predicts Cerebral Asymmetries in Parietal Gesture Representations*, "Neuropsychologia" 2011, No. 49(7), pp. 1698–1702; G. Vingerhoets, A.S. Alderweireldt, P. Vandemaele, Q. Cai, L. Van der Haegen, M. Brysbaert, E. Achten, *Praxis and Language Are Linked: Evidence from Co-lateralization in Individuals with Atypical Language Dominance*, "Cortex" 2013, No. 49, pp. 172–183; G. Goldenberg, *Apraxia in Left-Handers*, "Brain" 2013, No. 136(8), pp. 2592–2601.

Even if the relative incidence of apraxia among left-handers is comparable to that of right-handers[40], the probability of finding such patients is several times smaller because their population is much smaller. Moreover, most of the so-called left-handed individuals also exhibit some degree of ambidexterity. Even furthermore, in the past many *sinistrals* had their writing switched to their right hands, either by their parents or teachers. This fact alone may still considerably affect the outcomes of tests from the population of left-handed patients studied today. Indeed, the last two factors could contribute to a lower probability of finding a left-hander who – in terms of hemispheric specialization – would be a mirror image of a typical right-hander. Put another way, being somewhat ambidextrous, or having ones writing successfully switched could depend on, or be accompanied by, a different, more balanced representation of praxic skills.

Two further hypotheses are also worth considering here. The control of praxis could be strongly left lateralized only in people with very consistent hand preference, whether such individuals are right-, or left-handed. Alternatively, or in addition, the lateralization of praxis may on top follow the neuronal mechanisms devoted to the lateralization of language[41]. The consequences of such relationships would be clear cut, then, because in the majority of left-handed individuals language is still lateralized to the left hemisphere[42]. Any atypical case should then have both language and praxis atypically lateralized.

Early evidence that praxis representation in left-handers could follow the lateralization of language skills was mixed. One of the first, but relatively little known modern case of a left-handed patient described by Poeck and Kerschensteiner had the right-hemispheric lesion which resulted in left hemiplegia and right-hand apraxia. Because the two impairments were also accompanied by aphasia, in this particular case the right hemisphere mediated both praxis and language. This is somewhat different from what was reported a few years later in two quite famous

[40] D. Kimura, *Speech Representation in an Unbiased Sample of Left-Handers*, “Hum Neurobiol” 1983, No. 2(3), pp. 147–154.

[41] Cf. K. Meador, D.W. Loring, K. Lee, M. Hughes, G. Lee, M. Nichols, K.M. Heilman, *Cerebral Lateralization: Relationship of Language and Ideomotor Praxis*, “Neurology” 1999, No. 53(9), pp. 2028–2031.

[42] Indeed, Kimura’s findings seem to indicate that the right hemisphere almost never participates in language functions in left-handers unless there is an incidence of some kind of early left-hemisphere damage. D. Kimura, op.cit.; see also S. Knecht, B. Drager, M. Deppe, L. Bobe, H. Lohmann, A. Floel, E.B. Ringelstein, H. Henningsen, *Handedness and Hemispheric Language Dominance in Healthy Humans*, “Brain” 2000, No. 123, pp. 2512–2518.

studies that revealed rather clear dissociations. Heilman and collaborators[43] described two left-handed patients who, as a result of right hemisphere lesions, became apraxic and even showed apraxic agraphia but nonetheless did not have aphasia. Thus, it was inferred that in these two cases language skills were indeed lateralized to their left hemispheres but higher-order movement representations must have been stored in their right hemispheres. Notably, Heilman and colleagues[44] have also revived a description of an interesting left-handed case, a woman described earlier by Dejerine and André-Thomas. Their patient had a massive infarction of almost the whole right hemisphere and, therefore, developed severe left hemiplegia. Yet, she was also diagnosed with aphasia, but, notably, with comprehension deficits limited merely to written language. In other words, the processing of spoken language was basically intact in her. Interestingly, during the course of her recovery from the acute phase, the impaired language functions started to return. Although this process must have been mediated by the intact, left hemisphere, she still showed agraphia while using her right hand (which was controlled primarily by this same, intact hemisphere). This suggests that the representation of praxis in this particular patient was localized to the right hemisphere but her language skills must have had a more balanced representation.

Yet another atypical left-handed patient, following a right-hemisphere infarction, lost his knowledge of tool functions (i.e., was diagnosed with ideational apraxia), but these difficulties were not accompanied by agnosia and language comprehension deficits[45]. His problems with using tools, both in the experimental and natural settings, and a Broca's type aphasia (i.e., non-fluent speech), suggest that at least some critical aspects of his knowledge of tools, as well as his language skills, must have been mediated by the right hemisphere. However, his ability to name tools or point to tools in response to their names (as opposed to their functional descriptions), must have depended on his intact left hemisphere[46]. In sum, this case is yet another example of a partial dissociation where a general language competence mediated by the left-hemisphere is accompanied by the specialization for manual praxis and speech represented in the right-hemisphere.

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43 K. Heilman, J.M. Coyle, E.F. Gonyea, N. Geschwind, *Apraxia and Agraphia in a Left-Hander*, "Brain" 1973, No. 96(1), pp. 21–28; E. Valenstein, K.M. Heilman, *Apraxic Agraphia with Neglect-Induced Paragraphia*, "Arch Neurol" 1979, No. 36(8), pp. 506–508.

44 K. Heilman, J.M. Coyle, E.F. Gonyea, N. Geschwind, op.cit.

45 C. Ochipa, L.J. Rothi, K.M. Heilman, *Ideational Apraxia: A Deficit in Tool Selection and Use*, "Ann Neurol" 1989, No. 25(2), pp. 190–193.

46 Cf. a complementary case described by D. Roeltgen, K.M. Heilman, *Apractic Agraphia in a Patient with Normal Praxis*, "Brain Lang" 1983, No. 18(1), pp. 35–46.

Two more recent reports are in some opposition to all of the above-mentioned cases because their left-handed patients seemed to have both praxis and language lateralized similarly to typical right-handed individuals. A patient described by Lausberg and collaborators[47] had an ischemic infarction that caused selective damage nearly along the entire corpus callosum but did not affect much of the neighboring tissue and gray matter. What we have here is a rather unusual case of an almost complete *callosal disconnection syndrome* in which a left-handed individual shows a pattern of deficits similar to the ones observed in right-handed callosotomy patients. Apraxia was evident when he used his left, but not right, hand and both on verbal command and on imitation. His problems were not apparent, though, when routine motor tasks when performed spontaneously. Moreover, this patient was not able either to read words or name visual stimuli when they were presented to his left hemifield. Finally, the tests also revealed left hand agraphia. A very similar pattern of deficits and spared abilities was also described in a callosotomy patient studied by Frey and colleagues[48]. His patient (V.J.) also revealed a profound left hemispheric dominance for tool-use skills despite the fact that she acquired them and then continued to perform these skills with her dominant left hand. Both her pre-surgical Wada testing (i.e., the intracarotid sodium amobarbital procedure or ISAP introduced by Wada) and post-surgical tests indicated that she was also left-hemisphere dominant for language. As the report shows, however, the observed praxis deficits were not caused by simple verbal-motor disconnection because they were evident also when tool use pantomimes were cued with nonverbal stimuli. All in all, based on symptoms observed in both of these patients it becomes clear that, despite left-handedness – i.e., right hemisphere dominance for simple motor skills – the left hemisphere can still dominate in representing praxis and language. In other words, hand dominance can be dissociated from praxis representation, which in turn seems to be related more to language representation.

This potentially close relationship of praxis and language warrants more attention. As it turns out, atypical language dominance can be often linked to more bilaterally organized praxic skills. There is also strong evidence indicating that handedness is irrelevant in such cases. That is, right-handers with atypical language dominance seem to show patterns of praxis deficits similar to those of left-handers with atypical language dominance. Not surprisingly, then, left-handed individuals

[47] H. Lausberg, R. Gottert, U. Munssinger, F. Boegner, P. Marx, *Callosal Disconnection Syndrome in a Left-Handed Patient due to Infarction of the Total Length of the Corpus Callosum*, "Neuropsychologia" 1999, No. 37(3), pp. 253–265.

[48] S. Frey, M.G. Funnell, V.E. Gerry, M.S. Gazzaniga, op.cit.

with language lateralized to the left hemisphere often show praxis deficits comparable to those observed in typical right-handers who have language strongly left lateralized[49]. In view of that, one of the remaining questions is what pattern of language-praxic dominance is typical in lefthanders? After all, studying a few cases, although quite informative, may not reflect what really happens at the population level. Moreover, patients, whether with prior medical problems (e.g., intractable seizures from early childhood) or not, may show higher incidence of *anomalous* hemispheric specialization due to the ongoing functional reorganization. Finally, the rather rare right hemispheric dominance for language in left-handers that often seemed to be related to an early incidence of left-hemisphere damage[50] may in fact reflect one of the default patterns of hemispheric specialization that is expected to appear in the population[51].

The most extensive and up to date report on relationships between praxis, language, and handedness, based on studies in a rather large population of left-handed patients (N = 50, who were subsequently compared to a similar sample of right-handed patients) has been recently published by Goldenberg. For the sake of argument, substantial emphasis was put in this report on a few cases of clear dissociations and the relevant associations. In three patients, associations of aphasia with apraxia were observed as a result of left-sided lesions, which in left-handed individuals constitute clear dissociations of apraxia from handedness (which should be predominantly controlled by the right hemisphere). In another three patients, apraxia was closely associated with defective hand dominance mechanisms, i.e., resulted from right-hemisphere lesions, and clearly dissociated from the control of language (i.e., these are cases of dissociation of apraxia from aphasia). Interestingly, apraxia of simulated tool use, as well as defective tool use was rarely observed without aphasia (following different patterns of lesions). In sharp contrast, deficient imitation of hand postures was more common following right-hemisphere lesions, and was clearly associated with hemi-neglect. These particular problems with imitation may, therefore, have much less to do with deficient control of either handedness or praxis skills, and could be more closely related to impaired visuo-spatial processing, characteristic for the right hemisphere.

When directly contrasted with properly matched group of right-handed patients, no differences in the severity of imitation problems were observed. It was

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49 K. Meador, D.W. Loring, K. Lee, M. Hughes, G. Lee, M. Nichols, K.M. Heilman, op.cit.; S. Frey, M.G. Funnell, V.E. Gerry, M.S. Gazzaniga, op.cit.

50 D. Kimura, op.cit.

51 Cf. S. Knecht, A. Jansen, A. Frank, J. van Randenborgh, J. Sommer, M. Kanowski, H.J. Heinze, *How Atypical is Atypical Language Dominance?*, "Neuroimage" 2003, No. 18(4), pp. 917–927.

a weaker impairment on pantomime of tool use, and in fact milder aphasia (at least fewer cases of global aphasia) that was characteristic for left-handed apraxic patients. This in turn suggests that both praxis and language are more bilaterally represented in the majority of left-handed individuals[52]. Alternatively, the number of atypical cases of praxis and language laterality among left-handers is high enough to considerably bias the group data. In other words, a substantial number of left-handers could still be quite indistinguishable from right-handers in terms of their cerebral organization and praxis and language.

3. Dissociations of transitive and intransitive gesture representations in healthy left-handed individuals

Given the importance of dissociations in neuropsychology, and the fact that atypical organization of brain functions is most often seen in left-handers, this paper will be concluded with detailed, and yet unpublished, analyses of atypical cases reported earlier by Króliczak and collaborators[53]. Of course, the emphasis will be put on the most striking differences in the lateralization of brain activity, i.e., putative cases of dissociations between the two studied gesture categories at the individual subject level. Following a method described previously[54], the laterality of signal modulation during the planning of tool use pantomimes (transitive), and intransitive gestures was assessed. These methods will be briefly summarized here.

4. Methods

Upon collection and full processing of the fMRI data with FSL[55], the lateralization of activity related to planning tool use pantomimes or intransitive gestures in individual participants was assessed in Brodmann Area [BA] 40. This area – crucial for praxis skills – was delineated in standard neuroimaging space (Montreal Neurological Institute template) with two cytoarchitectonic maps marking the most

52 G. Goldenberg, *Apraxia in Left-handers*, "Brain" 2013, No. 136(8), pp. 2592–2601.

53 G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

54 Ibidem.

55 FMRIB Software Library, http://www.fmrib.ox.ac.uk/fsl/; see G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.; cf. G. Króliczak, S.H. Frey, *A Common Network…*, op.cit. if any further details are needed.

relevant divisions of the inferior parietal lobule: PF and PFm[56]. To avoid overlap with neighboring cytoarchitectonic areas, the original maps (taken from the Juelish histological atlas implemented in FSL) were first thresholded at the 50th percentile probability value[57]. The specific method of calculating lateralization indices (LIs) – also described by Króliczak and collaborators – was the following. The assessment of spatial extent of activation in the left and right hemisphere BA40 was performed by counting the number of voxels whose activity exceeded six prespecified percentage of maximum (POM) activation thresholds, namely 90, 80, 70, 60, 50 and 40% of maximum z-value[58]. By utilizing several thresholds to activity maps with all activated voxels (i.e., having positive z-values), we guard against the possibility of biasing the results by choosing just one, arbitrary threshold[59]. Indeed, an average of LIs from several thresholds gives more stable and reproducible outcomes[60]. For each participant, LIs were calculated using the formula: $[(L-R)/(L + R)]\times 100$; where L (left) and R (right) are then substituted by the number of suprathreshold voxels in the respective ROIs. Such LIs can range from +100 to −100, with 0 signifying an equal number of voxels exceeding the chosen activity threshold. As in our earlier work, the values of +100 through +33.3 are thought to reflect a strong to weak left-hemispheric dominance, and −33.3 through −100 are thought to indicate a weak to strong right-hemispheric dominance[61].

5. Results

In general, among the 15 healthy left-handed subjects tested in this study, and who showed significant correlations between the laterality of praxis and language[62], there were five participants who demonstrated clear but only partial – hand-de-

56 S. Caspers, S. Geyer, A. Schleicher, H. Mohlberg, K. Amunts, K. Zilles, *The Human Inferior Parietal Cortex: Cytoarchitectonic Parcellation and Interindividual Variability*, "Neuroimage" 2006, No. 33(2), pp. 430–448; G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

57 S.B. Eickhoff, T. Paus, S. Caspers, M.H. Grosbras, A.C. Evans, K. Zilles, K. Amunts, *Assignment of Functional Activations to Probabilistic Cytoarchitectonic Areas Revisited*, "Neuroimage" 2007, No. 36(3), pp. 511–521.

58 P. Chlebus, M. Mikl, M. Brazdil, M. Pazourkova, P. Krupa, I. Rektor, *fMRI Evaluation of Hemispheric Language Dominance Using Various Methods of Laterality Index Calculation*, "Exp Brain Res" 2007, No. 179(3), pp. 365–374.

59 G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

60 P. Chlebus, M. Mikl, M. Brazdil, M. Pazourkova, P. Krupa, I. Rektor, op.cit.; G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

61 G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

62 Ibidem.

pendent – dissociations of tool use pantomimes and intransitive gesture representations. Notably, only one of these individuals, i.e., case 1 (C1) shown in Figure 2, had atypical, i.e., right-hemispheric lateralization of language as assessed earlier in Brodmann Area 44/45 (typically associated with the Broca's area[63]). Three of the remaining participants (C3, C4, C5 in Fig. 2) had language strongly left lateralized, and in one case (C2) a weaker but still left-hemispheric representation of language was observed. In these latter four subjects, planning related activity was differently lateralized for transitive and intransitive gestures when their dominant left hands were used. Specifically, participants C4 and C5, and to some degree C2 (shown in Fig. 2A) showed effects consistent with patient data suggesting that representations of transitive actions are left lateralized, and intransitive actions have either right-hemispheric (C4) or bilateral (C5 and C2) representations. One participant (C3) showed an unexpected, reversed pattern. The lateralization indices for gesture planning with the dominant left hand, supplemented with the laterality indices for language, are shown for these participants in Fig. 2A.

Individual cases showing different, hand-dependent neural representations of transitive and intransitive gestures, as well as praxis representations (irrespective of gesture type). There were five participants who demonstrated hand-dependent dissociations of tool use pantomimes and intransitive gesture representations, but only one (C1) had atypical, right-hemispheric lateralization of language in BA 44/45. (A) Planning transitive and intransitive gestures with the left hand. Participants C4 and C5, and to some degree C2 had left-lateralized representations of transitive gestures and right-hemispheric (C4) or bilateral (C5 and C2) representations of intransitive gestures. Participant C3 showed an unexpected, reversed pattern. (B) Planning transitive and intransitive gestures with the right hand. Participant C4 had now bilateral representation of transitive gestures, and strongly left-hemispheric lateralization of intransitive gestures. Participant C1 have shown a similar effect. (C) Praxis planning irrespective of gesture type. Participants C1 showed the right-hemispheric control of the left hand, and left-hemisphere advantage in the control of the right hand. Participant C2 showed nearly the opposite effect, with the right hand being controlled predominantly by the right hemisphere and the left hand controlled predominantly by the left hemisphere.

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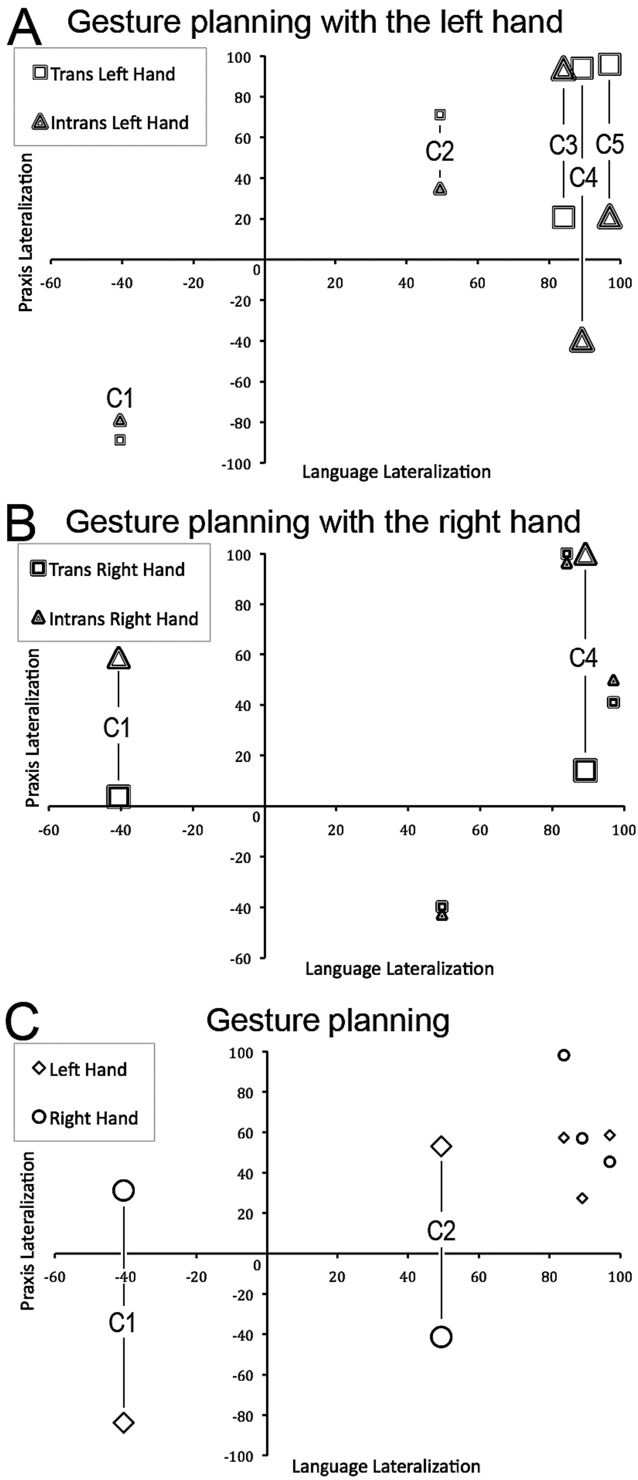
When the right hand was used for gesture planning, one of these four participants (C4) showed a very different pattern, i.e., the bilateral representation of tran-

63 Ibidem.

Figure 2.


A
Gesture planning with the left hand
Trans Left Hand
Intrans Left Hand
Praxis Lateralization
Language Lateralization
C1
C2
C3
C4
C5
B
Gesture planning with the right hand
Trans Right Hand
Intrans Right Hand
Praxis Lateralization
Language Lateralization
C1
C4
C
Gesture planning
Left Hand
Right Hand
Praxis Lateralization
Language Lateralization
C1
C2

sitive gestures, and strongly left-hemispheric lateralization of intransitive gestures. Moreover, case C1 who did not show evidence of dissociable neural substrate for the two gesture types when they were planned with the left hand has now shown a similar effect (bilaterally represented transitive and left lateralized intransitive gesture planning). These lateralization indices, for gesture preparation with the non-dominant right hand, together with the laterality indices for language, are shown in Fig. 2B.

Finally, it is worth emphasizing that cases C1 and C2 demonstrate quite different, hand-depended effects of the lateralization of praxis planning (irrespective of gesture type). C1 shows an effect consistent with a common intuition that, even for skilled gestures, the left hand is under the control of the right hemisphere, and the right hand is under the control of the left hemisphere. (In fact, in C1 there is only a small advantage of left-hemisphere control.) Participant C2 is nearly the opposite of what some might expect, with the right hand controlled predominantly by the right hemisphere and the left hand controlled predominantly by the left hemisphere. These cases are depicted in Fig. 2C.

6. Discussion

A higher incidence of atypical lateralization of functions in left-handers was a driving force behind this attempt to look for dissociations between the neural substrate of tool use (transitive) pantomimes and familiar intransitive gestures in this cohort of participants. Yet, because only a third of these individuals typically have somewhat unusual organization of higher-order cognitive skills[64], a conventional fMRI approach of presenting group averages is not an optimal strategy for tackling this issue. Moreover, given that relevant neuropsychological cases have been typically evaluated based on performance with ipsilesional hands, traditional patient-based views on the neural underpinnings of higher-order motor skills should be confronted with evidence from the control of either hand.

An assessment of the extent of fMRI activity in the left and right supramarginal gyrus indeed revealed a few cases with atypical organization of the two gesture categories. There were three participants with different lateralization of transitive and intransitive skills when these gestures were planned with the left hand. Two cases were in the predicted direction, showing left-hemisphere representa-

[64] S. Knecht, B. Drager, M. Deppe, L. Bobe, H. Lohmann, A. Floel, E.B. Ringelstein, H. Henningsen, op.cit.; G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

tions of transitive, and right-sided or bilateral representations of intransitive gestures[65]. Yet, one participant revealed a reversed pattern, difficult to reconcile with the classic neuropsychological findings and models[66]. Indeed, two individuals, including one with the expected dissociation for the left hand, and one with atypically represented language, demonstrated the reversed organization of these gesture categories when they used their right hands. These findings corroborate an earlier prediction that left hemisphere injuries could sometimes differentially affect the control of transitive vs. intransitive gestures, but this fact would become apparent only if it was possible to assess performance of the right hand[67]. Moreover, these and earlier results[68] strongly indicate that it should be much easier to find individuals with atypically lateralized praxis (gestures) than atypically represented language skills[69], although they also envisage different configurations of such impairments[70]. Interestingly, when collapsed across hands and gesture types, the laterality indices for praxis reveal a clear link with language lateralization[71], consistent with related outcomes from a report by Vingerhoets and collaborators[72] and neuropsychological findings of Goldenberg. However, the strength of this association clearly varies, and in some individuals is quite loose when analyzed for a particular hand or gesture type. Overall, these outcomes are consistent with case reports of partial dissociations between transitive and intransitive skills[73] but also call for cautiousness when drawing inferences based on testing a single hand.

A recent fMRI report indicates that representations of tool-use gestures in right- and left-handers are quite similarly organized, differing only in the strength

[65] E.g. S. Rapcsak, C. Ochipa, P.M. Beeson, A.B. Rubens, op.cit.; M. Heath, E.A. Roy, D. Westwood, S.E. Black, *Patterns of Apraxia Associated with the Production of Intransitive Limb Gestures Following Left and Right Hemisphere Stroke*, "Brain Cogn" 2001, No. 46(1–2), pp. 165–169.

[66] But see B. Hanna-Pladdy, S.K. Daniels, M.A. Fieselman, K. Thompson, J.J. Vasterling, K.M. Heilman, A.L. Foundas, op.cit.; V. Stamenova, E.A. Roy, S.E. Black, op.cit.

[67] G. Króliczak, S.H. Frey, *A Common Network…*, op.cit.

[68] G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

[69] K. Heilman, J.M. Coyle, E.F. Gonyea, N. Geschwind, op.cit.; D. Margolin, *Right Hemisphere Dominance for Praxis and Left Hemisphere Dominance for Speech in a Left-Hander*, "Neuropsychologia" 1980, No. 18(6), pp. 715–719.

[70] K. Poeck, M. Kerschensteiner, *Ideomotor Apraxia Following Right-Sided Cerebral Lesion in a Left-Handed Subject*, "Neuropsychologia" 1971, No. 9(3), pp. 359–361; E. Valenstein, K.M. Heilman, op.cit.; S. Frey, M.G. Funnell, V.E. Gerry, M.S. Gazzaniga, op.cit.

[71] G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

[72] G. Vingerhoets, A.S. Alderweireldt, P. Vandemaele, Q. Cai, L. Van der Haegen, M. Brysbaert, E. Achten, *Praxis and Language…*, op.cit.

[73] V. Stamenova, E.A. Roy, S.E. Black, op.cit.

of this lateralization[74]. While consistent with these outcomes, these and previous results[75] extend this notion to both gesture planning, and intransitive skills[76]. Moreover, these findings also point to important hand-dependent and hand-independent differences[77]. Such effects are worth further and systematic investigations given that no apparent differences in performance were noticed by Goldenberg (2013), even though some of his apraxic patients did use their right hands. Further tests could, for example, determine whether the greater involvement of the inferior parietal lobule of the right hemisphere reflects higher demands on attentional processes or rather demands on motor cognition in the hemisphere that happens to control the dominant, left hand[78].

7. Summary

The outcomes of a few recent studies[79] are consistent with the idea that a common network of areas mediates praxis skills (here: the planning of tool use pantomimes and intransitive gestures) regardless of the hand and, more importantly, handedness. The often observed, greater hand-dependent involvement of motor, or sensorymotor, and premotor cortices for transitive gestures indicates that these skills are more difficult to plan or execute (pantomime, imitate) than intransitive gestures. Notably, consistent with earlier reports in brain-damaged patients, this project shows that it is not difficult to find a healthy left-handed individual who demonstrates an unexpected organization of transitive and intransitive skills. Nevertheless, although the actual patterns of brain activity for gesture planning can vary quite dramatically in these subjects, at a population level their lateraliza-

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[74] G. Vingerhoets, F. Acke, A.S. Alderweireldt, J. Nys, P. Vandemaele, E. Achten, *Cerebral Lateralization of Praxis in Right- and Left-Handedness: Same Pattern, Different Strength*, "Human Brain Mapping" 2012, No. 33(4), pp. 763–777; for related neuropsychological evidence see also G. Goldenberg, *Apraxia in Left-Handers*, "Brain" 2013, No. 136(8), pp. 2592–2601.

[75] G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

[76] Not tested in G. Vingerhoets, F. Acke, A.S. Alderweireldt, J. Nys, P. Vandemaele, E. Achten, *Cerebral Lateralization…*, op.cit.; collapsed with tools use gestures in G. Goldenberg, *Apraxia in Left-Handers*, "Brain" 2013, No. 136(8), pp. 2592–2601.

[77] Cf. K. Martin, S. Jacobs, S.H. Frey, *Handedness-Dependent and-Independent Cerebral Asymmetries in the Anterior Intraparietal Sulcus and Ventral Premotor Cortex During Grasp Planning*, "Neuroimage" 2011, No. 57(2), pp. 502–512.

[78] Ibidem.

[79] Including G. Króliczak, S.H. Frey, *A Common Network…*, op.cit.; G. Króliczak, B.J. Piper, S.H. Frey, *Atypical Lateralization…*, op.cit.

tion typically follows the laterality of language[80]. It would be of great interest not only to know whether in some Chinese ethnic groups (e.g., the Han) the lower prevalence of aphasia in right-handers (dextrals) following left-hemisphere lesions[81] is also associated with a lower incidence of apraxia, but whether similar patterns can be observed in their left-handers (sinistrals). Indeed, would the Hans also show the close links between language and praxis regardless of handedness and the dominant hemisphere? Finally, although not directly contrasted with right-handed individuals in this project, this and earlier reports[82] indicate that during different gesture tasks sinistrals (no doubts the individuals with atypically represented functions, but also as a group) engage subdivisions of the right parietal cortex more than dextrals. This observation is consistent with the idea that praxis, as well as language skills in left-handers are more symmetrically represented[83]. The remaining question is whether or not this is also the case in groups using non-phonetic or "ideographical" languages?

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