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Research report

The "handwriting brain": A meta-analysis of neuroimaging studies of motor versus orthographic processes

Samuel Planton ^{*a,b,c,**}, Mélanie Jucla ^{*c*}, Franck-Emmanuel Roux ^{*a,b*} and Jean-François Démonet ^{*d*}

^a INSERM, Imagerie Cérébrale et Handicaps Neurologiques UMRS 825, Toulouse, France

^b Université de Toulouse, UPS, Imagerie Cérébrale et Handicaps Neurologiques UMRS 825, CHU Purpan, Toulouse, France

^c URI Octogone (EA 4156), Université Toulouse II Le Mirail, Toulouse, France

^d Centre Leenaards de la Mémoire, CHUV & Université de Lausanne, Lausanne, Switzerland

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ABSTRACT

Introduction: Handwriting is a modality of language production whose cerebral substrates remain poorly known although the existence of specific regions is postulated. The description of brain damaged patients with agraphia and, more recently, several neuroimaging studies suggest the involvement of different brain regions. However, results vary with the methodological choices made and may not always discriminate between "writingspecific" and motor or linguistic processes shared with other abilities.

Methods: We used the "Activation Likelihood Estimate" (ALE) meta-analytical method to identify the cerebral network of areas commonly activated during handwriting in 18 neuroimaging studies published in the literature. Included contrasts were also classified according to the control tasks used, whether non-specific motor/output-control or linguistic/input-control. These data were included in two secondary meta-analyses in order to reveal the functional role of the different areas of this network.

Results: An extensive, mainly left-hemisphere network of 12 cortical and sub-cortical areas was obtained; three of which were considered as primarily writing-specific (left superior frontal sulcus/middle frontal gyrus area, left intraparietal sulcus/superior parietal area, right cerebellum) while others related rather to non-specific motor (primary motor and sensorimotor cortex, supplementary motor area, thalamus and putamen) or linguistic processes (ventral premotor cortex, posterior/inferior temporal cortex).

Conclusions: This meta-analysis provides a description of the cerebral network of handwriting as revealed by various types of neuroimaging experiments and confirms the crucial involvement of the left frontal and superior parietal regions. These findings provide new insights into cognitive processes involved in handwriting and their cerebral substrates.

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E-mail address: samuel.planton@inserm.fr (S. Planton). 0010-9452/\$ – see front matter © 2013 Elsevier Ltd. All rights reserved.

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^{*} Corresponding author. INSERM, Imagerie Cérébrale et Handicaps Neurologiques UMRS 825, CHU Purpan, Place du Dr Baylac, F-31059 Toulouse Cedex 9, France.

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1. Introduction

1.1. The "handwriting brain"

Writing is a major cultural invention and an everyday communication tool for mankind, the earliest forms of which date from approximately 6 thousand years ago. Writing to communicate has since played a central role in the dissemination of culture and concepts. Handwriting is the most common way of learning and using written language even though typing has now taken on a central role in western societies. Whatever the orthographic system, the process of writing implies the contribution of several cognitive and motor functions. A complex set of neural underpinnings support this highly specific skill.

Most of our knowledge of the neuroanatomy of writing comes from neuropsychological studies of dysgraphias or agraphias seen after some brain lesions or diseases. A variety of writing disabilities have been described, from dysorthographias, affecting lexical or phonological components - i.e., central processes - with relative preservation of letter formation, to apraxic agraphias, affecting grapheme tracing i.e., peripheral processes (Roeltgen, 2003). Neuropsychological studies have suggested that lexical processes of writing relate to the angular gyrus (AG) (Roeltgen and Heilman, 1984) or the precentral gyrus (preCG) (Rapcsak et al., 1988) and phonological processes to the left perisylvian regions (Alexander et al., 1992b; Rapcsak et al., 2009). The motor components are believed to be linked to the left superior parietal or premotor regions (Alexander et al., 1992a; Anderson et al., 1990; Auerbach and Alexander, 1981). However, these results suffer from the usual limitations of lesion-based studies: spontaneous lesions are variable, difficult to delineate and the lesion-symptom relationship may be strongly influenced by neural plasticity and functional recovery.

Compared to other language skills, writing has long been neglected in functional brain imaging studies of healthy subjects. It is therefore difficult to establish a neurofunctional model of typical writing skills that might match the results reported in the literature on agraphia. More recently, several imaging studies have aimed to localize brain areas implicated in spelling or handwriting. The aim of the present paper is to present a meta-analysis of functional imaging studies reporting brain areas related specifically to handwriting and to isolate brain territories that characterize the written modality of language from those that also support other (motor or linguistic) abilities. Beyond the description of the network of brain areas involved, the importance of methodological aspects of these imaging experiments will be addressed.

A first meta-analysis has been recently provided by Purcell et al. (2011b), who aimed to distinguish central and peripheral processes of spelling. Central writing processes refer to the retrieval of abstract orthographic word-forms, via orthographic lexicon or phoneme-to-grapheme conversion mechanisms, and their temporary storage in working memory (in the "graphemic buffer", see Hillis and Caramazza, 1989). Peripheral processes involve letter production (selection of allographs or letter-shape conversion processes), planning and ordering of the sequence of letters and execution of specific motor programs (Ellis, 1982). Purcell et al. (2011b) limited their data exploration to alphabetic writing systems, and the studies considered did not necessarily involve tasks requiring the actual production of script. They focused on tasks eliciting the activation of an orthographic representation of a word, for example deciding if a particular letter was present or not in a heard word or if different words were spelled the same. While rhyme spelling tasks or spelling judgement have been used to study central spelling processes, one may consider that such tasks stray too far from the processes involved in everyday handwriting and their brain substrates. Here, we rather aimed at identifying handwriting-specific processes allowing actual written production (with the exception of "mental writing" tasks). We included various writing conditions (writing from dictation, written naming, generative writing), and different writing codes, both alphabetic and ideographic (Japanese Kanji). We also considered results from experiments that were not necessarily designed to study the neural substrates of writing per se (e.g., word retrieval, handedness, creativity, comparison of different types of writing).

Word writing involves many processes such as analysis of the input sensory information (visual or auditory), access to the orthographic representation of the word to be written (either directly or via a sublexical processing; see Rapp et al. (2002) for an example of such a 'dual-route' model) and its temporary storage into the graphemic buffer. These central stage processes are followed by allographic processes, i.e., the specification of the format in which letter series will be produced, including the idiosyncratic way each individual actually produces graphic scripts, and this involves the programming and neuromuscular execution of appropriate motor sequences (van Galen, 1991). As mentioned earlier, several of these processes are not specific to writing and can also be involved in other tasks, whether linguistic (e.g., reading) or motor (e.g., drawing). Neuroimaging studies should be able to disentangle writing/spelling processes (i.e., conceived as the preparation of a message and its conversion into a graphic form) from unrelated input or linguistic processing, and from or non-specific motor movements. The interpretation of their results thus relies strongly on the understanding of the experimental and control tasks involved.

1.2. Controlling for motor response

A first objective in experiments involving handwriting gestures is to tease apart the respective influences on brain activation of finger/hand motor activity (holding pen, moving joints) and visuospatial control of these movements. The most relevant control task consists of drawing non-linguistic stimuli such as circles (e.g., Roux et al., 2009), abstract symbols (e.g., Omura et al., 2004) or pseudo-letters (e.g., Longcamp et al., 2003). Yet another strategy is to attenuate the influence of the sensorimotor and visuospatial components in the experimental handwriting task itself. It is generally assumed that writing skills are independent of the tool or the effector since performance in agraphic patients is impaired regardless of the effector used. Some authors (especially in studies of the Japanese writing system) asked subjects to write with the finger on a board or in the air, with a limited amount of

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