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Abstract

Learning how to write is a demanding process that starts as early as age 2, when the first graphic movements are produced, and ends in late adolescence. This review focuses on the acquisition of the motor aspects of writing in skilled adults, and in 5 to 12-year-old children without learning disabilities. We first describe the behavioral aspects of writing in skilled adults, and the dominant models based on the notion of motor programs encoded in memory. We outline the behavioral changes occurring with learning. We show that handwriting acquisition is characterized by the transition from reactive movements programmed stroke-by-stroke in younger children, to an automatic, fully feedforward control of the whole trajectory when the motor programs are memorized at about 10 years old. In the second part, we describe the neural correlates of writing in adults, and the changes that could occur in the children's brains when learning how to write. We highlight the similarity between the trajectory followed by children to become expert writers and processes that have been described in the field of development and of motor learning with the acquisition of an expertise. The acquisition of a new skill is characterized by the optimization of neural resources, as reflected by the involvement of a network more restricted in space and where neural specificity is increased in the key regions. The cerebellum and the left dorsal premotor cortex are of fundamental importance in motor learning, and could be at the core of the acquisition and subsequent performance of handwriting. Finally, handwriting acquisition could lead to structural changes in the brain.

Keywords: Handwriting, Motor Learning, Children, Cerebellum, Premotor cortex, Kinematics

Introduction

Efficient handwriting is a pre-requisite for successful academic achievement. Handwriting *quality* is also thought to predict the performance in related cognitive domains such as text composition (Connelly, Dockrell, Walter, & Critten, 2012; S. Graham, Berninger, Abbott, Abbot, & Whitaker, 1997; Jones & Christensen, 1999; Puranik & AlOtaiba, 2012), spelling and orthographic skills (Graham et al., 1997; Pontart et al., 2013), and reading (Guan, Perfetti, & Meng, 2015; Shatil, Share, & Levin, 2000). This review article will focus on the acquisition of the motor aspects of writing in children without learning disabilities. Learning how to write is a long and demanding process that starts as early as age 2, when the first graphic movements are produced, and ends in late adolescence. However, the most massive changes in the features of writing occur between ages 5 and 10.

In the first part of the article, we review the dominant models of skilled handwriting that are based on the notion of motor programs encoded in memory. We describe the behavioral characteristics of handwriting in skilled adults and we outline the main behavioral changes occurring with learning. In the second part, we focus on the neural correlates of writing. We describe the handwriting brain network in adults. In order to better understand how this network is constructed, it is useful to consider general developmental brain changes in middle childhood, and their possible relationships with handwriting acquisition. It is also relevant to highlight the similarity between the trajectory followed by children to become expert writers and data from the field of motor learning. The neural changes that have been described in relation to motor learning and the acquisition of a motor expertise can inform us on how the brain correlates of handwriting evolve in children. In the final part, we review the existing neuroimaging studies on handwriting and related skills in children.

I. Models of handwriting and behavioral data

1- Models of expert handwriting

Models of writing originate either from cognitive neuropsychology with the analysis of errors of normal subjects and brain-damaged patients (Ellis, 1988; Margolin & Binder, 1984), or from the field of motor control (van Galen, 1991). They agree upon the hierarchical modular organization of writing, and upon the dissociation between “high-level” syntactic, semantic and

orthographic processes that converge in an orthographic working memory, and "low-level" motor processes. This general architecture has remained relatively unchanged over the last 30 years. Prior to the onset of motor processes, letter identities are still represented in an abstract way (Rothlein and Rapp, 2014). Those abstract letter representations can be externalized in several possible output modalities (oral spelling, typing, etc… Ellis, 1988; Margolin & Binder, 1984). In terms of motor processes specific to handwriting, the model of van Galen (1991) is the most widely used because it relies on a large body of research on motor production in handwriting. At the core of this model lies the idea that letter-forms, that is the possible instances of each letter (allographs) that have been learned, are stored in long-term memory in the form of "motor programs". At the so-called allographic level of processing, the motor program would therefore be selected from a long-term motor memory store. Note that the early notion of motor programs (Keele, 1968; Schmidt, 1975) has more recently been redefined as internal models (Wolpert, Ghahramani, & Jordan, 1995). However, for sake of clarity, the term of motor programs will be used in the present review. In handwriting, motor programs are codes that specify the number of basic motor units (strokes, see below for an operational definition of a stroke) and their spatiotemporal relations in an abstract, effector-independent way. Neuropsychological models developed a similar notion of "graphic motor pattern" or "motor engram". It originates from the observation of patients with apraxic agraphia, a condition in which writing is impaired despite intact spelling ability and normal sensorimotor skills (Ellis, 1982; Margolin & Binder, 1984). Apraxic agraphia is interpreted as a deficit affecting the graphic motor patterns caused by the brain lesion. In neuropsychological models, the selection of allographs is considered distinct from the selection of the motor program itself. Finally, the idea that motor programs are specified at the level of a letter has been debated. It is supported by the results of experiments showing for instance, that adding a letter to a sequence of letters increases the preparation time, whereas the number of strokes per letter does not affect this variable (Hulstijn & van Galen, 1983).

After the motor program is retrieved, at the lower level, information about movement parametrization and muscular adjustments would be encoded and stored in a motor working memory to produce the trajectories, with the desired size and slant. Several models of handwriting have described this last level. They seek to explain how the central motor representations are actually implemented in the neuromuscular system, in a real-time biophysical context (Hollerbach, 1981; Plamondon, 1995a, 1995b; Viviani & Flash, 1995). At this late stage of execution (Plamondon, 1995a, 1995b; van Galen, 1991), the stroke is usually

considered the basic motor unit of handwriting. A stroke is typically defined as the portion of the trajectory between two absolute velocity minima (Meulenbroek & van Galen, 1988), or between two points of zero "vertical" (in the y-axis) velocity (Hollerbach, 1981). Among those models, the kinematic model of Plamondon (1995a, 1995b) is currently the most accurate for skilled handwriting production. In this model, each stroke would result from a coordinated activity of the muscular system and would be defined by a velocity vector. Interestingly, only the orientation and amplitude of each velocity vector would be coded in the central nervous system.

The levels of representation in handwriting are summarized in figure 1.

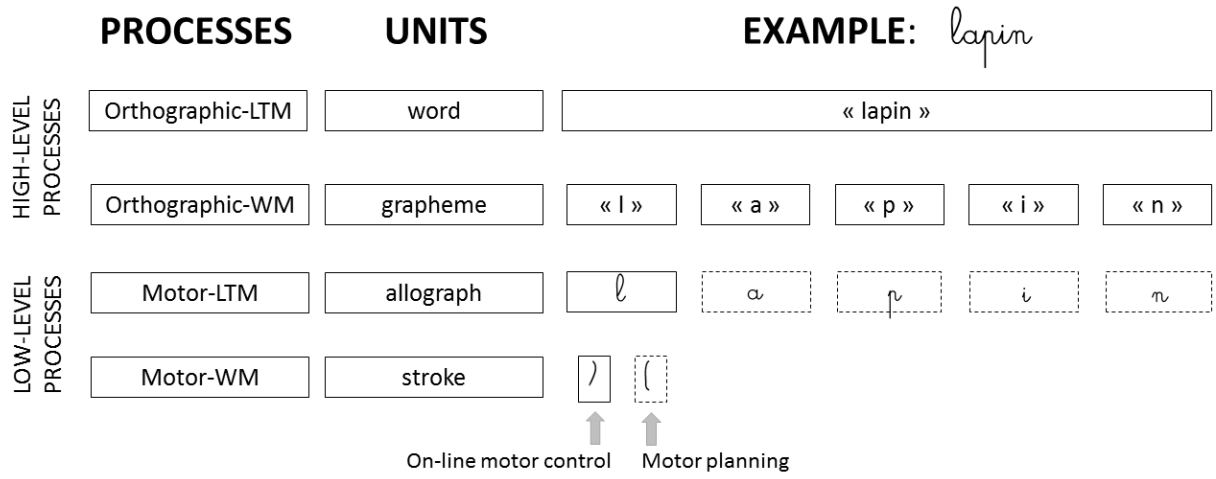

Figure 1. Schematic illustration of the different key processes and units activated during the production of the first stroke of the French word "lapin" (rabbit) in cursive handwriting. LTM = long-term memory; WM = working memory. At the high-level, the orthographic-LTM is responsible for the long term storage and retrieval of learned word spelling. The orthographic-WM is responsible for the on-line temporary storage and serial selection of graphemes for production. At the low-level, the motor-LTM is responsible for the long term storage and retrieval of the motor program corresponding to the selected allographic representation of each letter that constitutes the word. Note that neuropsychological models postulate an extra step for selecting the allograph before the motor program. Finally, the motor-WM is responsible for the on-line control of the current stroke production and for motor planning of the following stroke that constitutes the allograph.

2- Main characteristics of skilled handwriting in adults

Handwriting production is usually characterized through the handwriting product, i.e. the spatial accuracy of the written trace (shaping, size, legibility etc.) and through the handwriting process, i.e. the movement that generates this trace (Rosenblum, Weiss, & Parush, 2003; Tucha, & Lange, 2008). Such coupled analysis of handwriting product and process is possible when writing is recorded on graphic tablets from which several kinematic variables can be computed, such as the mean velocity, the number of lifts and stops (Paz-Villagrán, Danna, & Velay, 2014), or the movement fluency (e.g., Danna, Paz-Villagrán, & Velay, 2013). Note that when a graphic tablet is not available, the writing speed (that has been also called frequency of production) can be roughly approximated by counting the number of letters produced per minute (Graham, Berninger, Weintraub, & Schafer, 1998). A fluent movement is characterized by a smooth velocity profile, and broad velocity fluctuations (see the velocity profile of adult writing in Figure 2). Conversely, the more numerous the velocity peaks, the greater the number of abnormal accelerations and decelerations and therefore, the less fluent the movement. Finally, a possibly interesting index of the stability of the motor programs is the intra-individual variability of the performance. However, indexes of variability are investigated more rarely (Mojet, 1991; Rueckriegel et al., 2008; Zesiger, 1992).

Skilled handwriting is characterized by an optimal control of spatial and temporal constraints in order to produce a legible trace as quickly as possible. Handwriting is considered a fast motor activity. Surprisingly, handwriting speed does not result from the pen velocity, which generally reaches about 10 cm/s (a velocity 100 times lower than that of a tennis racket), but from the very rapid succession of short movements with many fast changes in direction. Handwriting is a rhythmic activity that can reach a frequency of about 5 Hz when accounting for the successive ascending and descending strokes produced by the pen (see figure 2, adult handwriting). Note that in studies comparing different styles of handwriting (e.g., cursive versus printing), the authors reported that cursive handwriting was slower than printing despite the numerous pen lifts in the latter case (Bara & Morin, 2013). Independently of the writing style, the high frequency limits the possibility of online control based on sensory information and imposes a mode of control so-called proactive, based on the execution of motor programs. The movement of a skilled writer can thus be considered as fully automated. Automation refers to the fact that writing is produced with minimal conscious “effort”, that is with minimal attentional involvement (Hasher & Zacks, 1979; Tucha et al., 2008). Automation is crucial in handwriting as it allows the allocation of cognitive resources to other processes (Berninger & Swanson, 1994; Jones & Christensen, 1999). An illustrated example of the effect of disruption

of the automatic movement control in adults can be found in Marquardt, Gentz, & Mai (1996). The participants were instructed to write while allocating attention to visually tracking the position of the tip of the pen. The timing and kinematics of the movement were dramatically deteriorated by this attentional instruction: the writing of the same word took a much longer time and the velocity profile indicated a disruption of the fluency, with several accelerations and decelerations within the same stroke. For some authors, fluency is the most accurate index of automation. An automated movement can be characterized by a minimal number of changes in velocity during execution (Tucha et al., 2008).

In spite of its high degree of automation, skilled handwriting requires visual and proprioceptive (tactile and kinesthetic) feedback. These two sensory systems play different and complementary roles in the integration and the processing of common features of handwriting, as for instance the trajectory orientation (Lajoie et al., 1992), or the curvature of the trace and velocity of the movement (see Danna & Velay, 2015 for review; Viviani & Stucchi, 1989). Smyth & Silvers (1987) evaluated adult handwriting in "blind" conditions, when vision was not allowed. They observed that the global spatial layout and the orientation of the words were impacted by the absence of visual feedback. However, the words shape and letters legibility were little deteriorated, except for letters with repetitive strokes ('n' and 'm'; 'u' and 'w') where some strokes could be added or omitted. A possible explanation is that vision is used to update a motor buffer containing the strokes of each letter (see figure 1). The role of proprioceptive feedback was evaluated by comparing the handwriting movements of deafferented subjects, who cannot perceive any tactile or kinesthetic information about their movement or the position of their own body, to that of controls adults (Hepp-Reymond, Chakarov, Schulte-Mönting, Huethe, & Kristeva, 2009; Teasdale et al., 1993). Without proprioceptive feedback, the handwriting kinematics was deteriorated because the subjects slow their pen down in order to control it visually. However, the words shape and letters legibility were not dramatically affected.

Visual and proprioceptive information can be used to adjust the parametrization phase (the last step in figure 1, where strokes are the units of processing), but have a negligible effect on the shape of the letters. This spatial invariance that is maintained despite variations in the context of execution is a typical and remarkable feature of handwriting. It can be highlighted when observing the invariance in the written product when varying the size or speed (Kadmon Harpaz, Flash, & Dinstein, 2014; Viviani & Terzuolo, 1980), or the effector (left hand, toe,

elbow,... Bernstein, 1947). This confirms that invariance results from the abstract nature of the information represented in the motor programs (Teulings & Schomaker, 1993).

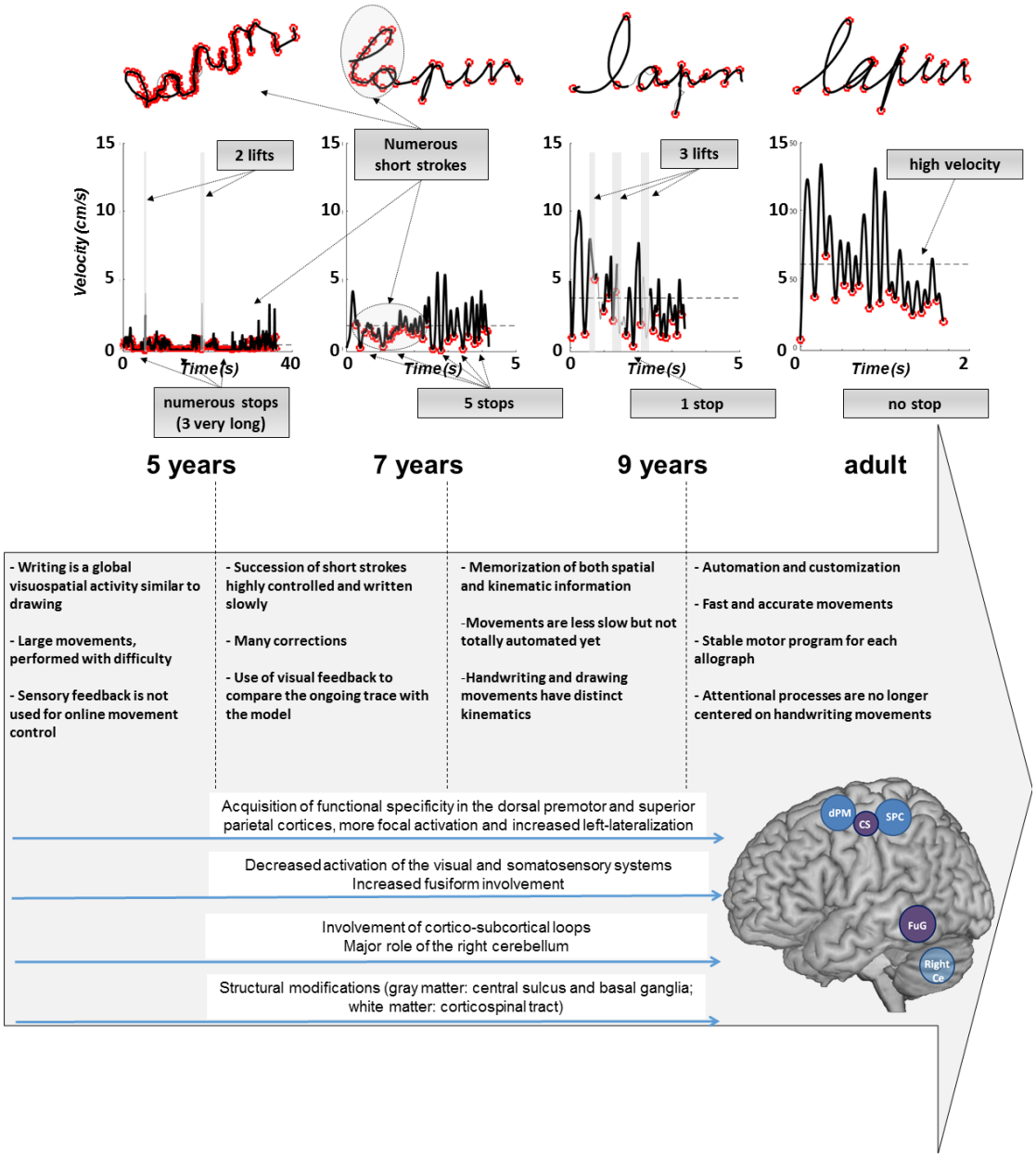

Figure 2. Time-frame showing the evolution of handwriting with learning and development. Top: typical exemplars of handwriting at age 5, 7 and 9, and from an adult, and corresponding velocity profiles. The red dots indicate the absolute velocity minima and their position in the trace. The time scale is different for the youngest child (40 s) and for the adult (2 s). Pen lifts and stops are indicated, and the dramatic evolution of movement fluency, mean velocity, total duration, and number of stops is clearly visible. Bottom: description of the main behavioral and brain changes, and view of the left-hemisphere showing the position of the main regions involved in handwriting and discussed in the text. The core of the handwriting network (dPM: dorsal premotor cortex; SPC: superior parietal cortex; Right Ce: right cerebellum, viewed in transparency) is in blue and the associated regions (CS: central sulcus, position of the hand motor cortex; FuG: fusiform gyrus) are in purple.

3- Characteristics of writing evolution in childhood

Several years and thousands of hours of practice pass between the first time a child holds a pen to write their name and the time they write series of words fluently. The construction and consolidation of motor programs in long term memory is therefore a long and extremely demanding process. Many studies (Meulenbroek & van Galen, 1988; Mojet, 1991; Zesiger, 1992) have tried to characterize the evolution of handwriting in childhood. Those studies display very variable methodologies both in the materials used (single letters, loops, bigrams, trigrams, words, sentences...) and in the variables considered (product and/or process). Figure 2 (top) presents the same word written by children aged 5, 7 or 9, and by an adult, as an illustration of the dramatic evolution of both the trace and the underlying process. The mean velocity increases (and therefore the duration of the whole word decreases). The number of absolute velocity minima (marked by red circles) decreases to reach an optimal value in the fluent adult handwriting. The trace becomes more legible. The low-skilled handwriting of 5-year-old children corresponds to a discrete succession of inaccurate strokes, produced with very variable velocity profiles, many stops and pen lifts. The children have learned the writing primitives through the practice of graphomotor exercises (e.g., production of loops and zigzag) but they fail the transition from one stroke to the next in the context of writing. The early evolution, between ages 5 and 7, has been interpreted as a transition from a ballistic strategy characterized by an inability to use sensory feedback (about the age of 5) to a control based mainly on visual feedback (at about 7). The youngest children perform rapid short gestures followed by error evaluation, while older children are characterized by a progressive on-line integration of visual and proprioceptive information. Around 7-8 years, despite two years of practice, the writing is still not automated. The size decreases but the movement velocity is still low. Children still pay attention to the distal movements of their hand. The correct motor pattern is not yet memorized and handwriting movement is mainly under the control of the on-line visual inspection of the trace. Finally, around 9-10 years, the children master and personalize their writing. Therefore, learning to write could be explained by a shift from a product-oriented (the written trace) to a process-oriented (the motor patterns generating the trace) control. Indeed, all authors agree upon the idea that children switch from a mainly retroactive mode of control at age 7, essentially based on visual feedback, to a proactive mode of control, based on stable motor representations at age 10. The motor programs for producing letters are acquired gradually over long time-periods, and the performance becomes automatic, allowing the children to devote less attention to the task.

The monotonic vs. non-monotonic nature of the evolution of motor control of handwriting with age has been a matter of debate. When the product is analyzed, there is general agreement on data showing that the evolution of legibility is non-monotonic (Graham et al., 1998; Mojet, 1991). In a systematic cross-sectional study of both the product and the process of handwriting in a representative sample of children (respectively 300 and 219) who were writing simple pseudowords, (Mojet, 1991), reported a marked increase of legibility at age 8-10 followed by a temporary decrease. This supports the idea of a phase of the acquisition where the children focus their handwriting on the respect of the calligraphic style, followed by a phase where they depart from standard letter shapes (Ajuriaguerra, 1971). For kinematic indexes, the evolution is less clear. On the one hand, early studies have identified periods of temporary regression of performance. Between the ages of 7 and 9, (Meulenbroek & van Galen, 1988) reported a decrease of movement velocity and fluency in a letter production task. Rueckriegel et al. (2008) also observed a decrease in fluency in their group of 8-9 year-olds compared to the group of 6-7 year-olds in the same type of task. One interpretation of the non-monotonic variations of kinematic indexes with age is that the evolution of handwriting depends on the developmental course of the child, as has been shown for other motor skills. In reaching movements for instance, Hay (1979) showed that 7-8 years old display velocity profiles that are more jerky than that of younger or older children. This loss of movement fluency is thought to occur because the maturation of the motor system in this age-group allows the use sensory information during movement execution. On the other hand, some authors have reported a fully monotonic improvement in the performance for most of the indexes analyzed (Mojet, 1991; Zesiger, 1992). Mojet (1991) for instance reported no discontinuity in any of the kinematic variables derived from the graphic tablet. The most important changes were nonetheless observed within a limited age range (between 7 and 9 years old). After age 10, the performance did not greatly evolve (see also Rueckriegel et al., 2008; Zesiger, 1992). However, significant differences between 12 year-olds and adults indicate that handwriting continues to progress slightly during adolescence (Zesiger, 1992). A monotonic profile of evolution would be more compatible with the idea that writing performance is mainly determined by the increase of the size of the motor programs the child is able to implement, not by an abrupt change in sensorimotor strategies due to development. This idea is at the core of The AVITEWRITE model (Grossberg & Paine, 2000; Paine, Grossberg, & Van Gemmert, 2004). This model accounts for the changes occurring during handwriting practice from the stroke to the letter production. It simulates an early, error-prone, learning stage consisting of visually guided short curves generated sequentially. The error between the actual and the desired position of the pen

is visually estimated and the motor command allowing error correction is computed. This process stops when the correct motor program is memorized and then used for automatic movement generation. In addition, the increasing ability of the child to anticipate the following strokes and letters could also be a determinant of the observed progressive improvements in the performance (Kandel & Perret, 2015).

This overview shows that, among the ages tested, a period of transition seems to occur between ages 7-8 and 10. Depending on the studies and variables, this age-range is characterized either by a temporary deterioration of the performance followed by an improvement, or by a massive improvement. Although the performance is not fully stabilized afterwards, kinematic indexes evolve slowly after age 10 and at this age writing starts to become automated. The motor programs for the allographs are likely to be acquired after this age, and writing can then be performed in an automatic way (Kandel & Perret, 2015).

II- Handwriting and the brain

1- Skilled handwriting brain network

How is motor control of handwriting implemented in the brain of skilled adults? The possible existence of a brain center containing the "motor images" of writing has been debated since the 19th century (Roux, Draper, Köpke, & Démonet, 2010). Following the first observations by Exner (1881) of apraxic agraphia (Ellis, 1982; Margolin & Binder, 1984) after a brain lesion, it is assumed that a part of the left dorsal premotor cortex, located at the junction between the middle frontal gyrus and the precentral gyrus, codes for the implementation of graphic motor patterns (Anderson, Damasio, & Damasio, 1990). This region is referred to as Exner's area. Its specificity for writing is confirmed by neuroimaging studies showing that it is only minimally activated during linguistic tasks that do not involve writing movements (Planton, Jucla, Roux, & Démonet, 2013; Planton, Longcamp, Péran, Démonet, & Jucla, 2017; Purcell, Napoliello, & Eden, 2011; Rapcsak & Beeson, 2004; Sugihara, Kaminaga, & Sugishita, 2006). It also responds preferentially to writing than to matched control manual movements (e.g., loops, zigzags, circles; Planton et al., 2013; Purcell et al., 2011) and even preferentially to writing letters than digits (Longcamp et al., 2014). It is possible that this dorsal premotor region displays functional specificity to letters because the corresponding motor programs are practiced more often and therefore coded in a more stable fashion. In addition, Roux et al. (2009) have suggested that this region, which they termed the Graphemic Motor Frontal area,

serves as an interface between linguistic processes and motor programs specific to handwriting. In neuroimaging studies however, the position of Exner's area along the precentral gyrus appears more dorsal than initially defined based on neurological observations. Neuroimaging studies indicate that Exner's area is located at the junction between the precentral gyrus and the superior frontal sulcus (Roux et al., 2009; Sugihara et al., 2006). The left dorsal premotor cortex is not the only part of the brain wherein lesions can cause motor deficits predominantly affecting writing. The left superior parietal cortex is also thought to play a key role in motor control of writing, as attested to by the number of cases of apraxic agraphia following a lesion in this region (Alexander, Fischer, & Friedman, 1992; Auerbach & Alexander, 1981; Basso, Taborelli, & Vignolo, 1978; Beeson, Rising, & Volk, 2003; Kinsbourne & Rosenfield, 1974; Magrassi, Bongetta, Bianchini, Berardesca, & Arienta, 2010; Roeltgen & Heilman, 1983; Sakurai et al., 2007; Takayama, Bergman, & Connell, 1994) and by neuroimaging studies focused on motor control of writing trajectory (Kadmon Harpaz et al., 2014; Menon & Desmond, 2001; Seitz et al., 1997). The left superior parietal involvement is consistent, irrespective of the type of linguistic task performed (Brownsett & Wise, 2010). Some authors have hypothesized that the motor programs for writing are actually stored in the dominant superior parietal lobe (Beeson et al., 2003). Indeed, in an experiment where participants had to write letters at different sizes, the left parietal cortex was found to code for scale-invariant representations, meaning that the pattern of activation varied as a function of the letter written, but remained similar for a given letter despite changes in size and therefore of muscular motor commands (Kadmon Harpaz et al., 2014). Interestingly, subcortical lesions (Ohno, Bando, Nagura, Ishii, & Yamanouchi, 2000; Vandenborre, van Dun, Engelborghs, & Mariën, 2015), and lesions of the right cerebellum (Mariën, De Smet, Paquier, & Verhoeven, 2010) have also been reported to cause apraxic agraphia. Writing impairments possibly occur through a reorganization of subcortico-cortical or cortico-cerebellar loops exerting a remote effect on premotor and parietal regions after the appearance of the lesion (Mariën et al., 2010; Ohno et al., 2000). Neuroimaging studies also demonstrated of a very consistent involvement of the right posterior cerebellar hemisphere in studies where the control tasks are otherwise well matched in terms of their motor complexity (Planton et al., 2013). This portion of the cerebellum, ipsilateral to the writing hand, is therefore considered a writing-specific motor region. Haggard, Jenner, & Wing (1994) proposed that in cases of cerebellar lesions, impaired proactive control might induce important deficits in the timing, smoothness and accuracy of writing movements due to over-dependence on cortical feedback loops for correcting errors. Although the exact function of the cerebellum in motor control remains debated, researchers agree upon its predominant involvement in motor learning

and in the retention of motor skills. Consistent right cerebellar involvement in writing could stem from an initial implication in early stages of acquisition (Doyon & Benali, 2005), followed by a role in the retention of the acquired graphomotor skills. Among the theories of cerebellar function, some non-exclusive views attribute to the cerebellum the implementation of inverse models allowing error correction in the course of acquisition, and storage of internal models allowing an automatic proactive movement (Manto et al., 2012).

The left parietal, dorsal premotor cortices and the right cerebellum may therefore constitute a network that codes for the effector-independent writing motor programs. Consistent with this idea, two studies demonstrated that when right-handed participants have to write with their dominant hand or with another effector (non-dominant hand or even toe), those 3 regions are consistently activated, among otherwise distinctly distributed sensorimotor activations (Rijntjes et al., 1999; Sugihara et al., 2006). The authors suggested that the motor representations of writing tend to cluster in brain regions initially devoted to controlling the movements of the dominant hand. The activation of the dorsal premotor and parietal cortices during writing is indeed right-lateralized in left-handers (Longcamp, Anton, Roth, & Velay, 2005; Siebner et al., 2002). In a single-case study, a left-handed agraphic patient with callosal disconnection produced well-formed letters but meaningless writing with the left hand and apraxic agraphia with the right hand (Varley, Cowell, Gibson, & Romanowski, 2005). The authors also concluded that the motor programs were stored in the right hemisphere in left-handers. In converted left-handers, who were forced to switch their writing hand in early childhood, the activation is more bilateral (Klöppel et al., 2007; Siebner et al., 2002). This confirms that the distribution of the writing network is determined by both the initial organization of the motor system and by training with a certain effector.

Finally, although the left fusiform cortex is not considered a part of the motor network, its role in writing processes should be acknowledged. First, the left fusiform gyrus is very consistently activated in spelling tasks (Planton et al., 2013; Purcell, Turkeltaub, Eden, & Rapp, 2011) as well as in reading tasks (Cohen et al., 2002; Flowers et al., 2004). Some researchers have proposed that it plays a key role in orthographic long-term memory because it is consistently found to be damaged in patients who produce more spelling errors on orthographically difficult (low frequency or irregular) words (Rapp, Purcell, Hillis, Capasso, & Miceli, 2016). In this fusiform region, the identity of the letters is represented in an abstract form: the similarity of the patterns of activation is not determined by the physical, phonological or motor similarity of the letters, but by their actual identity (for instance, visually presented

‘E’ and ‘e’ produce very similar patterns of activation in this region despite a different shape, whereas ‘b’ and ‘p’ do not despite similar physical and phonological features; Rothlein & Rapp, 2014).

How does this organization emerge to reach this expert state? Despite the scarcity of studies of handwriting in children with brain imaging tools, some elements can be found in the field of brain development, and of motor learning and expertise.

2- *Brain changes in development and in motor learning, and relationships with handwriting acquisition.*

Learning how to write probably relies on very similar organizing principles to learning other types of motor tasks. The main feature of handwriting is that the acquisition of a highly complex new motor skill spans over several years, while the brain is developing (Dick, Leech, Moses, & Saccuman, 2006). In that sense, learning handwriting is similar to learning how to play a musical instrument.

General brain changes during middle childhood

By the time most of the writing skill has been acquired, between ages 6 and 10, children are in a phase of neuronal development characterized by significant changes in gray and white matter densities (up to 6-10 years), and then by an increase of total gray matter during middle childhood and a decrease during adolescence (Gogtay et al., 2004; Wilke, Krägeloh-Mann, & Holland, 2007). The cortico-spinal white matter system grows denser continuously (Barnea-Goraly et al., 2005; Giedd et al., 2009; Giedd et al., 1999; Mills et al., 2016; Paus, 1999; Wilke et al., 2007). This neuronal maturation co-occurs with the development of motor abilities, with a decrease of latency, and an increase in accuracy (Adi-Japha, Badir, Dorfberger, & Karni, 2014; Gogtay et al., 2004; Savion-Lemieux, Bailey, & Penhune, 2009). The basic sensorimotor brain network is already well-segregated in young children when they start formal writing instruction, and its topography, extent and connectivity vary little between ages 6 and 10 (Grayson & Fair, 2017; Zielinski, Gennatas, Zhou, & Seeley, 2010). Functionally, children between ages 6 and 12 display a relatively similar distribution of cortical activation during a visuomotor tracing task. However, older children display more accurate performance and less

cortical motor activation than young children. This suggests a more efficient mobilization of the neural resources with age (Pangelinan, Hatfield, & Clark, 2013). In addition, as stated above, handwriting production is thought to rely on brain regions which display functional specificity for letters compared to other graphic shapes. Studies of the development, between ages 7 and 11, of the functional specificity to certain stimulus categories in the cortex, such as faces, show that the position of category-selective regions is determined early in childhood. However, the extent of category-specific tissue and the amplitude of the difference in activation between preferred- and non-preferred categories increase with age (Golarai, Liberman, & Grill-Spector, 2015). This co-occurs with improved performance (better discrimination of faces; (Natu et al., 2016). In summary, the development of a given skill relies on both the focalization and increase of activity in regions crucial for the task and on the decrease in regions uncorrelated with the task (Durston et al., 2006). It is accompanied by changes from local and diffuse connectivity to longer-range functional connectivity (Grayson & Fair, 2017; Kelly et al., 2009): brain regions relevant to the task become more specialized, and better organized in long-range networks, in the course of development (Johnson, 2011).

Neural correlates of motor learning

Because learning how to write co-occurs with brain development, it is likely that motor learning in children isn't fully comparable to motor learning in adults. For example, in children, stabilization in motor memory occurs faster, and is less susceptible to interference than in adults (Adi-Japha et al., 2014; Ashtamker & Karni, 2013). However, despite those differences, existing studies suggest that generally, the evolution of the performance of children during learning, and the underlying processes, are similar to that of adults (Adi-Japha et al., 2014; Julius & Adi-Japha, 2015). At the brain level, motor learning may also rely on similar mechanisms. For instance, cortico-cerebellar networks, which crucially participate in motor learning in adults, also display dynamic changes of activation between the early phase of training and the retention of a new motor skill, in children aged 8-12 (Zwicker, Missiuna, Harris, & Boyd, 2011). Motor learning research could therefore constitute an interesting framework leading to better understand the brain correlates of learning how to write.

Short- and long-term motor learning. In adults, motor learning occurs in two stages, an early stage with fast improvements and a late stage with slower improvements. Both stages depend on two neural circuits: the cortico-cerebellar loop that is composed of cortical motor areas (mainly the primary motor, somatosensory, dorsal premotor and parietal cortices), the thalamus, and the cerebellum, while the cortico-striatal loop is composed of the same motor cortical areas, the thalamus and basal ganglia (Doyon, Penhune, & Ungerleider, 2003; Hardwick, Rottschy, Miall, & Eickhoff, 2013). Prefrontal regions and the hippocampus interact with both circuits (Doyon & Benali, 2005; Floyer-Lea & Matthews, 2005; Schendan, Searl, Melrose, & Stern, 2003). The early motor stage is primarily driven by the cortico-cerebellar loop. It is characterized by slow and inaccurate movements, relying strongly on feedback, but the extent and rapidity of improvement are substantial. It has been shown that in the course of short-term training to new graphomotor sequences in adults, the pattern of activations is similar to that which is observed in other motor learning tasks (Swett, Contreras-Vidal, Birn, & Braun, 2010). Interestingly, when the activation in the very first trials of learning was contrasted to activation in the later trials, the authors observed an initially stronger activation of the visual system indicating visual coding of the sequences, followed by a shift towards a stronger subcortical (cerebellum and basal ganglia) activation indicating motor recoding. Long-term learning was not assessed in this study (Swett et al., 2010).

The late stage of motor learning corresponds to a slow phase during which the motor skill has been consolidated. Improvements still can be observed until the performance reaches an asymptotic level and motor execution becomes fully automatic (Doyon, Owen, Petrides, Sziklas, & Evans, 1996; Grafton, Woods, & Tyszka, 1994). Movements become faster, more accurate, less dependent on feedback (Halsband & Lange, 2006) and less variable (Krakauer & Mazzoni, 2011). This indicates a long term memorization of the motor skill which can be elicited efficiently even after a long delay without practice. The kinematic changes are accompanied by a shift from anterior to more posterior brain areas (Floyer-Lea & Matthews, 2005), highlighting the decrease of executive control, working memory and attention towards a more automatic performance (Kelly & Garavan, 2005). Important plastic changes have also been shown to occur in the primary motor cortex during slow learning, with a higher activation when performing the task and a decrease of excitability thresholds at the late stage, reflecting a more efficient recruitment of motor units with learning (Galea, Vazquez, Pasricha, de Xivry, & Celnik, 2011; Hardwick et al., 2013; Pascualleone et al., 1995). This suggests a role in the retention of learned movements through their repeated performance (Galea et al., 2011).

Interestingly, although the left primary motor cortex is not considered part of the core network for representing handwriting movements, meta-analyses show that it is often more activated in handwriting tasks than in control tasks (Planton et al., 2013; Purcell, Turkeltaub, et al., 2011). It could therefore also play a role in the retention of handwriting movements (Kadmon Harpaz et al., 2014).

Left dorsal premotor cortex and motor learning. In a meta-analysis including a large number of fMRI studies of manual motor learning, Hardwick et al. (2013) found that motor learning was strongly and systematically associated with left dorsal premotor activation at a location close to the position of Exner's area, regardless of the type of task and of the time-scale. According to Hardwick and colleagues (2013), the left dorsal premotor cortex constitutes "the core of motor learning". This central role could stem from a pivotal function in the visuomotor control of movement, through the selection and updating of motor responses according to visual cues. The left dorsal premotor cortex holds multiple connections with primary motor, parietal and prefrontal cortices, and is a potential node of convergence between sensorimotor information, decision making and other cognitive functions (Hardwick et al., 2015). It is therefore possible that the motor representations in Exner's area cluster at a subpart or in the close vicinity of the premotor region supporting motor learning. This fits well with the early idea that Exner's area is "especially trained from childhood through the formation of engrams to function as a writing center" (Nielsen, 1946).

Expertise. Importantly, the relative duration of fast and slow learning is highly task specific. Learning how to write is comparable to learning how to play a musical instrument, with the fast and slow stages and associated behavioral improvements extending over the course of months or even years (Dayan & Cohen, 2011). By the end of learning, expertise is achieved. Functionally, expert performance is associated with less strong, and more focused overall brain activation whereas novice performance is associated with more widespread activation (Lotze, Scheler, Tan, Braun, & Birbaumer, 2003; Milton, Solodkin, Hluštík, & Small, 2007). In addition, the regions primarily activated by task performance in motor experts are located in the cortical motor networks and in the cerebellum, and are more strongly activated than in novices (Lotze et al., 2003; Milton et al., 2007). This pattern of activation is associated with better behavioral performance (Lotze et al., 2003). It indicates that with expertise, the memory

trace is coded in regions that directly participate in the task performance. In the field of writing, the effects of expertise on functional brain activations have never been investigated. However, some insights can be found in the comparison of writing overlearned letter patterns to drawing pictures or unknown symbols. Drawing requires the implementation of similar graphomotor strokes, but non-automated and not-coded as a single motor program in memory. At about 5-6, reliably distinct action sequences can be observed for writing and drawing (Brenneman, Massey, Machado, & Gelman, 1996) and around age 7 the movement kinematics (velocity, fluency, pause-time…) for writing letters and drawing geometric symbols otherwise similar in their shape diverge (Adi-Japha & Freeman, 2001). This indicates that the brain networks underpinning the two activities are different in experts. At the brain level, neuroimaging data on adults show that in fact, writing and drawing rely on overlapping frontoparietal regions. Strikingly however, drawing recruits a much more extended amount of neural tissue (Harrington, Farias, Davis, & Buonocore, 2007; Planton et al., 2017; Yuan & Brown, 2015). In a recent study where they compared writing and drawing in a design controlled for minimizing possible kinematic differences between tasks, Planton et al. (2017) found that compared to writing, drawing overactivates the previously defined "handwriting network", including the left fusiform gyrus. Interestingly however, the lateralization of the premotor activation was strikingly different for the two tasks: it was completely bilateral for drawing whereas it was strongly left-lateralized for writing (participants were right-handers). And indeed, as stated above, the lateralization of the premotor and parietal activations in handwriting seems to be determined by handedness (Klöppel et al., 2007; Longcamp, Anton, et al., 2005; Siebner et al., 2002). It is therefore possible that, in the brain, the specificity of writing stems from learning and developmental processes leading to expertise and allowing both its spatial focalization and its lateralization at the cortical level.

Expertise also induces structural reorganizations at the level of the gray matter, as shown in experts such as musicians (Gaser & Schlaug, 2003; Han et al., 2009) and athletes (Park et al., 2009), or after long term training to juggling (Draganski et al., 2004). For instance, musicians present higher gray matter volumes in sensorimotor and premotor cortices and in the cerebellum compared to non-experts (Gaser & Schlaug, 2003; Hutchinson, Lee, Gaab, & Schlaug, 2003). Could the same type of modifications occur in relation to the acquisition of writing? Interestingly, in converted left-handers, an early forced switch in the hand used to write leads to structural modifications in the asymmetry of the central sulcus and in the volume of the middle part of the putamen, a part of the striatum dealing with executive and associative

functions (Kloppel, Mangin, Vongerichten, Frackowiak, & Siebner, 2010). In addition, structural modifications in the parietal cortex have been reported in expert typists (Cannonieri, Bonilha, Fernandes, Cendes, & Li, 2007). It is a good indication that, similar to experience with a musical instrument, writing experience shapes brain structure. Microstructural properties of the white matter, for instance in the corticospinal tract, are also modified after motor learning (Bengtsson et al., 2005; McKenzie et al., 2014; Schmithorst & Wilke, 2002). Although no direct evidence of such modifications exist in the field of handwriting, it is can be hypothesized that writing acquisition also modifies white matter tracts.

3- Neural correlates of writing acquisition in children

Few elements directly shed light on the neural mechanisms by which the key network for handwriting develops in children. Up to now, only two neuroimaging studies have directly assessed handwriting production in children (Richards et al., 2011; Richards et al., 2015). The lack of neuroimaging data in children is probably related to the sensitivity of the method to head movements induced by the mobilization of the hand and forearm, and by the difficulty to write in a supine position when the skill is not fully mastered. No study has yet compared children to adults.

The writing network described in adults seems to be active in children.

In an fMRI study involving participants aged between 10 and 12, Richards et al. (2015) compared the brain activation resulting from the writing of an unfamiliar letter shape (pseudoletter), to a highly practiced letter of comparable shape. It should be noted that, in this age-range, the children are likely to have automated their writing, as outlined in the first, behavioral, section. However, the degree of automation could be variable among children. Within this study, good writers were defined by an above-average rating on a legibility measure of handwriting. They were likely to display a fully automatized writing as they were more efficient in writing highly practiced letters than the poor writers. On the contrary, the poor writers were less likely to have reached automation of the movements. Similar to that which is observed in studies comparing writing to drawing in adults (see above), the premotor and parietal cortices, the right cerebellum and the fusiform gyrus were engaged more strongly when the children were writing a new letter (pseudoletter). However, this was only true in the case of the good writers, because the activation of those regions did not differ between newly taught

and highly practiced letters in the poor writers. Another important result was that efficient writing was linked to the involvement of a more restricted and focused brain network. The good writers engaged fewer neural regions to write a newly taught letter than did the poor writers. The poor writers displayed over-activation of the visual system, and extra parietal and cerebellar regions. Consistent with this finding, (Richards et al., 2015) reported that efficient handwriting is associated with less functional connectivity than poor handwriting. In summary, the development of a more focal activation of the premotor, and cerebellar regions while learning new letter shapes is associated with good writing skills whereas more widespread activation, and greater involvement of the visual system, of the left parietal cortex and of extra cerebellar regions is associated with poor writing skills. A possible interpretation of those findings is that, at least in children, good writers are better able to mobilize the brain systems for motor learning when learning a new symbol whereas poor writers display patterns of activation that resemble those of novice subjects in early learning phases.

Finally, the good and poor writers differed significantly in activation in left fusiform cortex when writing highly practiced letters compared to newly taught pseudo letter (Richards et al., 2011). Good writers showed significantly stronger activation in this region than poor writers." This individual fusiform activation correlated with behavioral measures of writing legibility. This suggests that there are critical interactions between the visual and motor systems in the acquisition of writing, since the efficiency depends both on the pattern of activation on motor-related brain regions when practicing new shapes and on the activation of the fusiform gyrus when writing highly practiced shapes. In addition, the fusiform involvement significantly predicted other language skills. The results of this study should nonetheless be replicated in a larger sample of children, if possible also including younger children who have not yet automatized their writing.

Handwriting acquisition leads to modulations in other functions.

It is likely that because of the thousands of hours of practice and of the corresponding functional and probably structural modifications, writing acquisition can impact other functions. For instance, writing acquisition can also affect the functioning of the visual system when processing written language. James and her collaborators studied the consequences of writing practice on functional brain activations during visual recognition of newly learned letters in preschoolers. The study of James (2010) revealed that writing training, but not visual-

only training, induces increased activation in bilateral anterior fusiform gyri, the portion of the fusiform gyrus sensitive to the visual configuration of single letters (Flowers et al., 2004), when pre-training and post-training fMRI measures of letter recognition were compared. The stability of the visual representations of letters is therefore strengthened when letters are trained by writing them repeatedly. A subsequent study with the same age-group confirmed this finding by observing a greater effect of freely producing letters by hand compared to tracing or typing them on the fusiform activation during letter perception (James & Engelhardt, 2012). When examining the whole-brain consequences of the training mode, James & Engelhard (2012) found that compared to the control conditions, active handwriting training led to subsequent greater activation of the bilateral precentral gyri, at the level of the primary motor cortex. This interesting finding shows that the motor representations built in the course of learning can be reactivated by the mere visual processing of letters. This is in agreement with previous observations in the course of single letter perception in adults (James & Atwood, 2009; Longcamp et al., 2008; Longcamp, Anton, Roth, & Velay, 2003; Longcamp, Zerbato-Poudou, & Velay, 2005). However, contrary to what has been found to occur in adults, the motor activation was more caudal (corresponding to the primary motor cortex and not the premotor cortex), and was bilateral. This bilateral activation has been interpreted as relating to the immaturity of the motor system in preschoolers. In another study, Richards et al (2009) have measured brain activity in groups of good and poor writers (again classified as being above or below the average level on a standardized measure of legibility of their writing) aged 10 to 12, who were engaged in a motor task involving a memorized finger sequence. They showed that the poor writers underactivated a broad frontoparietal network including the dorsal premotor cortex, the inferior occipito-temporal regions and the cerebellum. Their conclusion was that efficient handwriting is related to optimal activation of the neural circuits supporting the planning of sequential movements.

Conclusion

Handwriting acquisition is characterized by massive changes in a series of kinematic parameters between ages 7 and 10. This is thought to correspond to the progressive integration in long term motor memory of the various motor programs that are required to produce words fluently. This allows the motor system to be freed from attention and cognitive control. Handwriting can be produced in an automatic way. At the brain level, this is likely to induce a massive reorganization, both at the functional and at the structural levels. This reorganization

is of the same type as that which has previously been demonstrated in other kinds of motor expertise. It leads to the focalization of activations in a restricted network mainly constituted of the left dorsal premotor cortex at the junction between the superior frontal sulcus and the precentral gyrus, of the left superior parietal lobule and of the right cerebellum. The primary motor cortex is also a site of plasticity. The laterality of this network is probably inverted in left-handers.

The understanding of how motor control of writing emerges and stabilizes in the course of typical brain development will set the ground for the study of the neural bases of developmental dysgraphia. It will also contribute to the evaluation of potential interactions between cognitive and motor stages of processing in the acquisition of literacy.

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