Neuroanatomical correlates of individual differences in self-awareness of highly practiced visuomotor skills

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Abstract

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Preamble

Neuroanatomical correlates of individual differences in self-awareness of highly practiced visuomotor skills

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Abstract

Metacognition refers to the ability to introspectively evaluate our cognitive capacities, which plays an essential role in guiding and optimizing our activities. However, little is known about metacognitive capacity for highly practiced motor behaviors and their neural correlates. Using structural and functional magnetic resonance imaging (MRI), the present study examined the brain substrates underlying individual differences in self-awareness of handwriting in adults, a highly practiced visuomotor skill. Results showed that adult writers generally overestimate their handwriting skill, with this overestimation being more pronounced in males relative to females. The extent of overestimation of handwriting quality was positively correlated with grey matter volume in the left fusiform gyrus, right middle frontal gyrus, and right precuneus. Moreover, activation of these regions during a handwriting task was not correlated with self-awareness of handwriting, confirming that the identified relationship between brain structures and handwriting self-awareness is independent of task performance. The left fusiform gyrus and right middle frontal gyrus are thought to represent domain-specific brain mechanisms for handwriting self-awareness,

while the right precuneus likely constitutes a domain-general brain mechanism, suggesting that the ability to introspect practiced visuomotor skills relies on both domain-general and domain-specific brain systems. Together, this study is the first to reveal the neuroanatomical correlates of a highly practiced motor behavior, extending our understanding of the neural basis of human metacognition.

Key words: self-awareness, handwriting, individual differences, brain structure

Introduction

The capacity to introspectively evaluate the success of cognitive processing is conceptualized as metacognition (Nelson, 1990), which is key to guiding and optimizing everyday activities (Pouget, Drugowitsch, & Kepecs, 2016; Rosen et al., 2010). Previous studies have demonstrated that metacognitive accuracy varies substantially across individuals (Chen et al., 2011; Stephen M. Fleming, Weil, Nagy, Dolan, & Rees, 2010). Lesion studies (Stephen M. Fleming et al., 2014; O & Shany-Ur, 2014) and neuroimaging studies (Bang & Fleming, 2018; Stephen M. Fleming, Huijgen, & Dolan, 2012; Stephen M. Fleming et al., 2010; Molenberghs, Trautwein, Böckler, Singer, & Kanske, 2016; Morales, Lau, & Fleming, 2018) have extensively investigated the neural correlates of metacognition for perception and memory, revealing that distinct brain systems support metacognition in humans, primarily including the anterior prefrontal cortex (Allen et al., 2017; Baird, Smallwood, Gorgolewski, & Margulies, 2013; Fandakova et al., 2017; Stephen M. Fleming et al., 2010; Molenberghs et al., 2016) and precuneus (Allen et al., 2017; Morales et al., 2018; Ye, Zou, Lau, Hu, & Kwok, 2018). However, although the anterior prefrontal gyrus has been found to be commonly engaged in metacognition across perception and memory domains (Fandakova et al., 2017; Stephen M. Fleming & Dolan, 2012; Vaccaro & Fleming, 2018), convergent evidence from lesion studies (Stephen M. Fleming, Jihye, Golfinos, & Blackmon, 2014) and neuroimaging studies (Baird et al., 2013; McCurdy et al., 2013; Valk, Bernhardt, Böckler, Kanske, & Singer, 2016; Ye et al., 2018) suggests that different types of metacognition rely on dissociable brain systems. It is plausible that both domain-general and domain-specific mechanisms coexist in the coupling between brain systems and metacognition (Morales et al., 2018; Vaccaro & Fleming, 2018).

Although the aforementioned studies have substantially revealed the neural substrates of metacognition for perception and memory, our knowledge about the capacity to introspect motor skills remains relatively scarce. Metacognition is also an essential factor in motor learning efficiency (Simon & Bjork, 2001) and has been found to contribute to sport expertise (Berti et al., 2005). Some studies, however, have shown that individuals have poor insight into their motor capacities (Bègue et al., 2018; Fourneret & Jeannerod, 1998; West & Stanovich, 1997). Neurologically, one fMRI study demonstrated that confidence judgment of visuomotor performance activated the left precuneus and posterior middle temporal gyrus (Bègue et al., 2018). Another structural MRI study found that metacognitive sensitivity for visuomotor processing involves a distributed brain network, including the right prefrontal cortex, right anterior insula, and right fusiform gyrus (Sinanaj, Cojan, & Vuilleumier, 2015). These studies primarily show that self-awareness of motor skills is associated with prefrontal cortex, sensorimotor, and visual networks. However, the motor tasks used previously were completely novel for participants, and thus it remains unknown whether people can accurately introspect motor skills that have been highly practiced. Although infant studies show that metacognition is a genetically inherited capacity in humans (Goupil, Romand-Monnier, & Kouider, 2016), learning or experience has been postulated as a vital origin of metacognition (Heyes, Bang, Shea, Frith, & Fleming, 2020). For example, task experience has been found to support the evaluation of sensory evidence during confidence judgments of task performance (Shadlen & Shohamy, 2016).

Handwriting is a visuomotor skill, and individuals must undergo a long-term period of practice under naturalistic contexts before becoming skilled writers (Palmis, Danna, Velay, & Longcamp, 2017), thus offering a unique opportunity to examine the neural correlates associated with metacognition for practiced motor skills. Handwriting requires the retrieval of appropriate visual forms and the execution of specific motor programs. Previous lesion studies (Alexander, Friedman, Loverso, & Fischer, 1992; Anderson, Damasio, & Damasio, 1990; Rapcsak & Beeson, 2004) and neuroimaging studies (Longcamp et al., 2014; Planton, Jucla, Roux, & Démonet, 2013; Purcell, Turkeltaub, Eden, & Rapp, 2011; Rapp & Dufor, 2011) have illustrated that the left superior frontal sulcus, premotor cortex, inferior/superior parietal sulcus, fusiform gyrus, and cerebellum are implemented in different processing components of handwriting (Planton et al., 2013; Purcell et al., 2011). However, no prior study has examined the neural correlates of handwriting self-awareness in skilled writers.

The present study sought to identify brain structures associated with individual differences in metacognitive judgment of handwriting in adults with sufficient handwriting experience. Using voxel-based morphometry (VBM) analysis, we explored brain structures related to self-awareness of handwriting quality and speed, which were quantified by the discrepancy between self-report and objective measures. First, given that the coupling between brain anatomy and metacognition occurs in a domain-specific fashion (Morales et al., 2018; Ye et al., 2018), we expected to detect unique brain regions linked to individual differences in handwriting self-awareness. For example, based on findings that motor self-awareness relies on brain regions supporting the function being monitored (Berti et al., 2005), we hypothesized that visual and motor regions necessary for handwriting would be involved. Second, the anterior and dorsal prefrontal cortex have been implicated as a domain-general brain mechanism of metacognition (Stephen M. Fleming & Dolan, 2012; Stephen M. Fleming et al., 2010), and therefore they would also covary with variations in handwriting awareness. Finally, task performance is a critical confounding factor in the relationship between metacognition and brain substrates (Stephen M. Fleming et al., 2010; McCurdy et al., 2013). Thus, we conducted a complementary analysis to examine whether intersubject variations in handwriting self-awareness impact brain activation during actual handwriting. The rationale was that if the regions identified by brain structure-behavior correlation analysis are specific to metacognition, activation in these regions during the handwriting task would not be correlated with self-awareness scores.

Methods

Participants

Fifty-one adults participated in this study (26 males, mean age = 22.29 years). All participants were right-handed as evaluated by a handedness inventory (Snyder & Harris, 1993). Participants were physically healthy and reported no history of neurological disease or psychiatric disorder. The study was approved by the ethics committee of the Institute of Psychology, Chinese Academy of Sciences, and all methods were carried out in accordance with the approved guidelines. Prior to the experiment, free and informed consent was obtained from each participant.

Behavioral Measures of Handwriting

Following previous studies (Lahav, Maeir, & Weintraub, 2014), we examined both handwriting quality and speed. The material for evaluating handwriting quality came from a pen-and-paper copying task in which participants were required to copy 40 Chinese characters at the speed they typically use in daily life. Evaluation was based on six dimensions using a 7-point scale (1 = very bad, 7 = very good): stroke form, slant, organization of radicals, neatness, average size, and overall appearance (Yang et al., 2020b). The final score was the sum across all dimensions. Both participants and 31 external raters evaluated handwriting quality, yielding subjective and objective scores, respectively. The raters had similar handwriting experience (14 males, mean age = 24.61 years) as the participants and were thus capable of providing reliable evaluations of handwriting quality. Raters evaluated the handwriting twice with a 6-month interval, and the final objective score was the average of the two evaluations. Test-retest reliability was high (Cronbach' s Alpha = 0.978).

For handwriting speed, the subjective measure was also based on a 7-point scale (1 = very slow, 7 = very fast), and objective performance was derived from the average speed (characters/second) in the pen-and-paper copying task.

Handwriting Task During fMRI Scan

To examine whether individual differences in self-awareness of handwriting influence brain activation during actual handwriting, participants performed a copying task during scanning. Stimuli included thirty characters and fifteen nonsense symbols. Half of the characters were familiar "high frequency" characters (1500 times per million), and the other half were unfamiliar "low frequency" characters (< 5 times per million). A block design was employed, consisting of six blocks of copying characters (three blocks each for high- and low-frequency characters) and three blocks of drawing symbols in pseudo-random order. In each trial, a '+' symbol was first presented visually and centrally for 0.3 s, followed by presentation of a character stimulus for 1 s and then a response period of 4.7 s. Three blocks of central fixation, each with 12 s duration, were also interspersed among task and control blocks as a "rest" baseline. Detailed information about the experimental design has been reported previously (Yang et al., 2020a; Yang et al., 2018).

We used a tablet system specially developed for fMRI experiments to record behavioral data. The tablet system includes a touch-sensitive surface, a force-sensitive stylus, and an adjustable support frame, and is MRI-safe without significantly degrading fMRI data quality (Karimpoor et al., 2018; Tam, Churchill, Strother, & Graham, 2011).

Imaging Acquisition

Imaging was performed using a 3T MRI system (MAGNETOM Prismafit, Siemens, Erlangen, Germany) at the Beijing MRI Center for Brain Research of the Chinese Academy of Sciences. Functional MRI time series data with blood oxygenation level-dependent (BOLD) contrast were acquired using a two-dimensional, T2*-weighted, gradient-echo echo planar imaging (EPI) sequence (Moeller et al., 2010) (repetition time TR = 1000 ms, echo time TE = 30 ms, slice thickness = 2.2 mm, in-plane resolution = 2.2 mm × 2.2 mm, flip angle = 45°, 64 axial slices).

High spatial resolution anatomical images were acquired using a three-dimensional T1-weighted, magnetization-prepared rapid acquisition gradient echo (MPRAGE) sequence (TR = 2200 ms, TE = 2.08 ms, slice thickness = 1 mm, TI = 1000 ms, in-plane resolution = 1.0 mm × 1.0 mm, = 8°).

Data Analysis

Quantification of Self-Awareness of Handwriting First, we performed multiple linear regression analysis to examine the correlation between self-report scores and objective performance for handwriting quality and speed, respectively. For handwriting quality, raw scores were transformed into corrected self-awareness scores using the formula: corrected self-awareness = (self - others) / ((self + others)/2), to account for differences in rating or task performance between participants and raters (Clare, Whitaker, & Nelis, 2010). For handwriting speed, the raw scores of subjective and objective measures were heterogeneous, with the former being rank data and the latter continuous data. To make the two types of data comparable, raw scores were first normalized to a scale from 0 to 1 using min-max normalization: x_{normalized} = (x - x_{minimum}) / (x_{maximum} - x_{minimum}).

Finally, self-awareness of handwriting quality and speed was determined by the discrepancy between self-report and others'ratings or task performance. Positive scores indicate overestimation, while negative scores indicate underestimation of handwriting skill.

In-Scanner Performance During fMRI Scan For behavioral performance during fMRI scanning, only handwriting speed was analyzed. Handwritten outputs were produced using an atypical gesture in the scanner, which was not appropriate for quality evaluation. Following previous studies (S. Roux, Mckeeff, Grosjacques, Afonso, & Kandel, 2013), we analyzed both handwriting latency and duration. Latency was defined as the interval from the onset of the response stimulus to the beginning of writing/drawing, and duration was defined as the interval from the start of the response (first contact with the tablet) to the end of the last written or drawn stroke. Additionally, we computed the correlation between self-awareness scores and handwriting latency/duration.

VBM Analysis **Preprocessing.** VBM analysis of anatomical data was performed using the VBM8 toolbox (VBM8; http://dbm.neuro.uni-jena.de/vbm/) implemented in SPM8 (http://www.fil.ion.ucl.ac.uk/spm/, Wellcome Department of Cognitive Neurology, University College London, London). Using the high-dimensional Diffeomorphic Anatomical Registration (DARTEL) approach, raw T1 images were segmented into grey matter (GM), white matter (WM), and cerebrospinal fluid (CSF), which were then normalized to standardized Montreal Neurological Institute (MNI) space with 1.5 $\times$ 1.5 $\times$ 1.5 mm resolution. The segmented images were modulated by the Jacobian determinants of the warp field to preserve original differences in shape before normalization. Finally, the modulated GM images were spatially smoothed with a 6-mm FWHM isotropic Gaussian kernel.

Whole-Brain Multivariate Regression Analysis. The preprocessed GM images were entered into a multiple regression model in SPM8 to examine which brain regions correlated with variations in handwriting self-awareness. Scores of handwriting self-awareness (both quality and speed), total intracranial volume, age, and sex were entered as regressors. An absolute threshold of 0.2 was applied to circumvent possible edge effects among tissue types. The statistical threshold was set at voxelwise $p < 0.001$ and $p < 0.05$ family-wise error (FWE) corrected at the cluster level. For illustration, GM density in each region related to handwriting self-awareness was extracted using the MarsBar toolbox (http://marsbar.sourceforge.net/) and correlated with self-awareness scores.

Region of Interest Analysis. Region of interest (ROI) analysis was also employed. Four regions commonly related to metacognition in previous studies were selected as ROIs, including the left anterior prefrontal cortex (x = -20, y = 53, z = 12), (x = -12, y = 54, z = 16) and right anterior prefrontal cortex (x = 24, y = 65, z = 18), (x = 33, y = 50, z = 9), right dorsolateral prefrontal cortex (x = 36, y = 39, z = 21), and precuneus (x = 6, y = -57, z = 18), (x = 8, y = -64, z = 24) (Stephen M. Fleming et al., 2010; McCurdy et al., 2013). Spherical

ROIs were created with 6-mm radius. GM density was extracted from each ROI and correlated with self-awareness scores after controlling for age and sex. The threshold was set at $p < 0.0125$, corresponding to $p < 0.05$ after Bonferroni correction for multiple comparisons.

Brain Activation Analysis Preprocessing. Image preprocessing and statistical analyses were conducted using SPM8 (http://www.fil.ion.ucl.ac.uk/spm/, Wellcome Department of Cognitive Neurology, University College London, London). The fMRI time series data were first corrected for head motion, and the corrected images were co-registered to the associated anatomical imaging data. The anatomical images were transformed into Montreal Neurological Institute (MNI) stereotactic space, and the resulting transformation parameters were then applied to the fMRI time series data. These images were then spatially smoothed using an isotropic Gaussian kernel with 6 mm full-width at half-maximum.

Whole-Brain Multivariate Regression Analysis. The general linear model (GLM) method was used to generate activation maps for high-frequency characters, low-frequency characters, and symbols for each participant. The GLM design matrix included the block design time series convolved with a canonical hemodynamic response function. To minimize residual motion artifacts, head movement parameters (estimated with six degrees of freedom during motion correction) were included as nuisance covariates. Data were high-pass filtered at 0.008 Hz. At the first level, handwriting activation maps reporting the contrast between copying characters and symbols were generated for each participant. Individual activation maps were then entered into a multiple regression model to examine brain activation associated with handwriting self-awareness. Participants' sex and age were included as covariates. The voxelwise threshold was set at $p < 0.001$, and $p < 0.05$ family-wise error (FWE) corrected at the cluster level.

ROI Analysis. Brain regions identified by VBM analysis were selected as ROIs. Mean contrast estimates for participants' copying characters > symbols contrast images were extracted from each ROI and correlated with handwriting self-awareness scores. The threshold was set at $p < 0.05$ with Bonferroni correction for multiple comparisons.

Results

Behavioral Results

The mean (standard deviation, SD) raw scores for self-report and others' rating of handwriting quality were 27.24 (6.10) and 23.96 (4.53), which were significantly correlated after controlling for sex and age ($t(47) = 4.44$, $p < 0.001$) (Figure 1A [Figure 1: see original paper]). The corrected self-awareness score for handwriting quality was 0.12 (0.24) (Figure 1B), indicating that participants generally overestimated their handwriting quality ($t(50) = 3.56$, $p < 0.001$). Self-awareness of handwriting quality was not normally distributed as evaluated by the Shapiro-Wilk test (W = 0.93, p = 0.005). Finally, males showed a higher level of overestimation of handwriting quality than females (t(49) = 2.298, p = 0.026).

The mean raw scores for self-report and task performance of handwriting speed (characters/second) were 4.39 (1.06) and 0.4 (0.07). However, self-report score was not significantly correlated with task performance after controlling for sex and age (t(47) = 1.41, p = 0.165) (Figure 1C). After normalization, self-awareness of handwriting speed was 0.17 (0.3) (Figure 1D), suggesting overall overestimation of handwriting speed (t(50) = 4.07, $p < 0.001$). The score for self-awareness of handwriting speed followed a normal distribution (W = 0.99, p = 0.993). No significant sex difference in handwriting speed was found (t(49) = 1.09, p = 0.281).

Moreover, we found that the correlation between self-awareness of quality and speed was not significant (t(47) = 1.90, p = 0.063) after controlling for sex and age, implying that these two factors are independent.

Figure 1. Behavioral performances of handwriting. Scatter plots for the correlation between self-report and others' rating of handwriting quality (A). Distribution of self-awareness of handwriting quality (B). Scatter plots for the correlation between self-report and task performance of handwriting speed (C). Distribution of self-awareness of handwriting speed (D).

VBM Results

Whole-brain regression analysis indicated that GM volume in the left fusiform gyrus (peak at x = -35, y = -57, z = -20, in MNI) extending to the left cerebellum (Figure 2 [Figure 2: see original paper] A), and the right middle frontal gyrus (peak at x = 33, y = 2, z = 57) (Figure 2 B) were positively correlated with self-awareness of handwriting quality, indicating that greater GM volume was associated with greater overestimation. However, no brain regions showed significant correlation with self-awareness of handwriting speed. As behavioral analysis revealed sex differences in handwriting self-awareness, we examined sex differences in GM volume in these two regions, but no significant differences were detected: left fusiform gyrus (t(49) = -1.14, p = 0.261) and right middle frontal gyrus (t(49) = 0.56, p = 0.577).

ROI analysis indicated that self-awareness of handwriting quality was significantly associated with the volume of the right precuneus (centered on x = 8, y = -64, z = 24: t(47) = 2.86, p = 0.006) after correction for multiple comparisons across all ROIs (Figure 2 C).

Multiple linear regression analysis indicated a significantly positive correlation of GM volume between the left fusiform gyrus and right middle frontal gyrus ($\beta = 0.41$, t(47) = 2.08, p = 0.043), between the left fusiform gyrus and right precuneus ($\beta = 0.26$, t(47) = 2.21, p = 0.032), as well as between the right middle frontal gyrus and right precuneus ($\beta = 0.32$, $t(47) = 4.50$, $p < 0.001$).

To further explore the relative contributions of each region to variations in self-awareness of handwriting quality, we conducted a stepwise multiple linear regression analysis. Self-awareness of handwriting quality was included as the dependent variable, and GM density in the left fusiform gyrus, right middle frontal gyrus, right precuneus, sex, age, and total intracranial volume were entered as predictors. Results indicated that GM volume of the left fusiform gyrus (regression coefficient $\beta = 1.20$, $t(47) = 4.63$, $p < 0.001$), GM volume of the right middle frontal gyrus ($\beta = 0.83$, $t(47) = 4.26$, $p < 0.001$), and sex ($\beta = -0.16$, $t(47) = -3.68$, $p < 0.001$) significantly contributed to variations in self-awareness of handwriting quality (adjusted $R^2 = 0.56$, $F(3,47) = 22.29$, $p < 0.001$). Furthermore, hierarchical linear regression revealed that GM volume of the left fusiform gyrus explained an additional 15% variance beyond other predictors (adjusted R^2 change = 0.15), and GM volume of the right middle frontal gyrus explained an additional 16% variance beyond other predictors (adjusted R^2 change = 0.16). However, GM volume of the right precuneus made no additional contribution.

Figure 2. VBM analysis results. Axial, sagittal, and coronal views of the left fusiform gyrus (A), right middle frontal gyrus (B), and right precuneus (C), and their corresponding scatter plots for the correlations between gray matter volume and self-awareness of handwriting quality. FuG = fusiform gyrus and MFG = middle frontal gyrus. L = left, R = right. GM = grey matter.

Brain Activation Results

Brain activation analysis showed that copying characters or symbols recruited a large-scale brain network involving the bilateral superior/middle/inferior frontal gyrus, superior/inferior parietal lobule, inferior/middle occipital gyrus, fusiform gyrus, and cerebellum (Figure 3A [Figure 3: see original paper]). Multiple linear regression analysis of behavioral performance indicated that self-awareness of handwriting speed was not significantly correlated with handwriting performance during fMRI scanning: latency (high-frequency characters: $t(47) = 0.26$, $p = 0.800$; low-frequency characters: $t(47) = -0.20$, $p = 0.839$) and duration (high-frequency characters: $t(47) = 1.04$, $p = 0.304$; low-frequency characters: $t(47) = 1.68$, $p = 0.099$).

Critically, self-awareness of handwriting quality was not significantly correlated with activation of the left fusiform gyrus (high-frequency characters: $t(47) = -0.20$, $p = 0.845$; low-frequency characters: $t(47) = 0.53$, $p = 0.598$), right middle frontal gyrus (high-frequency characters: $t(47) = 1.06$, $p = 0.294$; low-frequency characters: $t(47) = -0.19$, $p = 0.849$), or right precuneus (high-frequency characters: $t(47) = -0.31$, $p = 0.760$; low-frequency characters: $t(47) = -0.79$, $p = 0.434$).

Figure 3. The results of brain activation during handwriting. Lateral view of brain activation for high-frequency and low-frequency characters (A). Con-

trast estimates of the left fusiform gyrus, right middle frontal gyrus, and right precuneus during the handwriting task (B). Scatter plots for the correlation between brain activation and self-awareness scores of handwriting quality. HFC = high frequency characters and LFC = low frequency characters. FuG = fusiform gyrus and MFG = middle frontal gyrus. L = left and R = right. *$P < 0.05$,* ***$P < 0.01$,*** $P < 0.001$.

Discussion

The present study examined the association between brain substrates and individual differences in self-awareness of handwriting, a highly practiced visuomotor skill. Behaviorally, we observed a trend toward overestimation of handwriting quality and speed, suggesting that people lack sufficient insight into their highly practiced motor skills. At the neural level, GM volume in the left fusiform gyrus, right middle frontal gyrus, and right precuneus was positively associated with self-awareness of handwriting quality. Moreover, examination of brain activation confirmed that the correspondence between brain structures and handwriting self-awareness is independent of task performance. The fusiform gyrus and premotor regions are thought to reflect domain-specific brain substrates of metacognition for handwriting, while the precuneus represents a domain-general brain basis. Collectively, this study is the first to identify brain mechanisms of self-awareness for highly practiced motor skills, supporting the view that both domain-general and domain-specific brain systems are recruited to support metacognition (Morales et al., 2018; Vaccaro & Fleming, 2018).

Consistent with previous findings in motor (Bègue et al., 2018) and emotional recognition (Bègue et al., 2019a) domains, we found that participants tended to overestimate their handwriting quality and speed. This result suggests that even for highly practiced motor skills, people still lack the ability to accurately estimate their performance. Moreover, we found that males showed a higher level of overestimation of handwriting quality than females, consistent with the Dunning-Kruger effect, which posits that unskilled individuals are likely to overestimate their abilities (Kruger & Dunning, 1999). Abundant evidence has shown reduced handwriting ability in males relative to females (Reilly, Neumann, & Andrews, 2019; Reynolds, Scheiber, Hajovsky, Schwartz, & Kaufman, 2015; Yang et al., 2020b).

Nevertheless, we found that self-report of handwriting speed was not correlated with handwriting speed during the copying task. Furthermore, no brain regions were identified as being associated with self-awareness of handwriting speed. One possibility is that self-estimation of handwriting speed might not be reliable. Compared to handwriting quality, fewer cues are available for assessing handwriting speed because far less direct feedback about speed can be obtained in daily life.

The left fusiform gyrus and right middle frontal gyrus were uniquely associated with handwriting quality, which has not been detected in other domains, suggesting they might constitute domain-specific brain substrates of metacognition for handwriting. Both the fusiform gyrus and right middle frontal gyrus have been activated in various handwriting tasks (Planton et al., 2013; Sugihara, Diltz, Averbeck, & Romanski, 2006; Yang et al., 2019), leading us to propose that self-awareness of handwriting relies on shared brain networks supporting the primary function being monitored. This interpretation aligns with previous lesion study findings showing that damage to right premotor areas leads to impairment in self-awareness of motor acts (Berti et al., 2005).

A prior study showed that confidence judgment of visuomotor processing was related to GM volume of the right fusiform gyrus (Bègue et al., 2018). However, we found that the left fusiform gyrus was associated with self-awareness of handwriting quality. This discrepancy might be due to differences in stimulus type. Self-awareness of handwriting quality in the present study refers to visual real words, whereas nonsense visual-spatial stimuli were used in Bègue et al.' s study (2018). Specifically, the peak of the left fusiform gyrus (x = -35, y = -57, z = -20) corresponds to the well-known visual word form area (VWFA) (Cohen et al., 2002; Kronbichler et al., 2004), which is thought to specifically house abstract representations of written letters or words in long-term memory (Dehaene & Cohen, 2011). Functional specificity of the VWFA is tuned by increased visual word experience (Dehaene et al., 2010). Collectively, we conjecture that handwriting self-awareness relies on brain substrates for long-term visual representation of words or letters. This hypothesis accords with the notion that self-awareness might be associated with learning and experience (Stephen M. Fleming et al., 2010). In addition to visual representation, a recent study has pointed out that the VWFA connects with both language and attentional networks and might serve as a neural interface for multimodal cognitive functions (L. Chen et al., 2019). From the standpoint of functional connectivity, it is plausible that the left fusiform gyrus receives attentional information to perform high-level self-monitoring of visual word production.

The right middle frontal gyrus (peak at x = 33, y = 2, z = 57) was positively correlated with self-awareness of handwriting quality. Such right premotor regions have been reported to be activated during handwriting (F. E. Roux et al., 2009), particularly when writing with the left hand (F. E. Roux et al., 2009; Sugihara et al., 2006), but its specific role in handwriting remains unclear (Planton et al., 2013). Presumably, it serves the transformation between orthographic and graphomotor codes, as does its left counterpart (F. E. Roux et al., 2009). Our findings suggest that the right premotor area might encode high-level information for introspective evaluation of handwriting quality. This view is supported by previous findings indicating that premotor areas are involved in self-related evaluation of daily activities, cognition, emotion, and social function (O & Shany-Ur, 2014). In a similar vein, a transcranial direct current stimulation (tDCS) study showed that perturbation of the right premotor area impairs self-awareness of motor and cognitive skills (Convento, Romano, Maravita, & Bolognini, 2018). Specifically, aesthetic evaluation of the appearance of handwritten scripts might be an important aspect of self-awareness of handwriting. This hypothesis is supported by a prior fMRI study indicating that judgment of beauty for language scripts specifically activated motor areas (Zhang, Lai, He, Zhao, & Lai, 2016).

Finally, ROI analysis also indicated that self-awareness of handwriting quality covaries with GM volume of the right precuneus. The right precuneus has been consistently linked to metacognition for memory (Baird et al., 2013; McCurdy et al., 2013) and perception (Stephen M. Fleming et al., 2010), emotion recognition (Bègue et al., 2019b), and visuomotor processing (Sinanaj et al., 2015), likely representing domain-general neural substrates for metacognition (McCurdy et al., 2013). Thus, this result implies that domain-general brain systems are also necessary for developing metacognitive capacity for practiced visuomotor skills. Functionally, both lesion (Simons, Peers, Mazuz, Berryhill, & Olson, 2010) and fMRI studies (Richter, Cooper, Bays, & Simons, 2016) have demonstrated that the right precuneus serves episodic memory retrieval. In the present study, episodic memory for handwriting processing is necessarily triggered when participants are required to judge handwriting quality.

Limitations and Future Directions

A caveat of the present study is that brain-behavior correlation analysis only revealed covariation between brain structures and self-awareness of handwriting, rather than causal relationships. Future studies are needed to examine whether these brain regions play a causal role in introspecting handwriting skill. Another limitation is the lack of direct measurement of functional activation during evaluation of handwriting skill. Thus, it remains unknown whether these brain regions showing structural correlation with self-awareness would be activated during a handwriting evaluation task, since the relationship between VBM and functional activation is not a one-to-one correspondence (Kanai & Rees, 2011). Finally, participants were required to make an offline judgment of handwriting performance, which could be conceived as retrospective metacognition for handwriting. Thus, our findings might not generalize to prospective metacognition for visuomotor skills. Previous studies have demonstrated dissociation of brain networks between prospective and retrospective metacognition judgments of memory (Stephen M. Fleming & Dolan, 2012; Modirrousta & Fellows, 2008; Pannu & Kaszniak, 2005).

Conclusion

In the present study, we identified the neuroanatomical substrates of handwriting self-awareness, involving the left fusiform gyrus, right middle frontal gyrus, and right precuneus. The fusiform gyrus and right motor regions belong to the neural network of handwriting itself, consistent with the view that self-awareness of motor skills shares brain networks with the monitored function (Berti et al., 2005). The precuneus might reflect the requirement of domain-general brain substrates for introspecting handwriting skill. This is the first study to reveal the neuroanatomical correlates of individual differences in self-awareness of a highly practiced visuomotor skill, extending our understanding of the neural basis of metacognition.

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Conflict of Interest Statement

The authors declare no conflict of interest.

Note: Figure translations are in progress. See original paper for figures.