MULTISENSORY INTEGRATION AS A PATHWAY TO NEURAL SPECIALIZATION FOR PRINT IN TYPICAL AND DYSLEXIC READERS ACROSS WRITING SYSTEMS

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MULTISENSORY INTEGRATION AS A PATHWAY TO NEURAL SPECIALIZATION FOR PRINT IN TYPICAL AND DYSLEXIC READERS ACROSS WRITING SYSTEMS

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Editorial: Multisensory integration as a pathway to neural specialization for print in typical and dyslexic readers across writing systems

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Editorial on the Research Topic
Multisensory integration as a pathway to neural specialization for print in typical and dyslexic readers across writing systems

Active participation as a citizen depends on fluent decoding and production of written language. Efficient processing of graphs[1] is the foundation of reading (Pelli et al., 2003), as graphs are the building blocks of written words from early on in reading acquisition to skillful reading (Grainger, 2018). How does the human brain become specialized and process graphs and written words in the context of the multimodal nature of the reading experience? This is the focus of this Research Topic. It includes a Research Topic of 13 articles that cover current issues in the cognition and neurobiology of reading development and variability. Groups with a wide range of reading skills took part in these studies, and various behavioral tests and neuroimaging techniques (EEG-ERPs, fMRI) were used to investigate how learning audio-visual and motor-visual associations relate to (in)efficient graph recognition and reading across alphabetic and logographic writing systems.

This Research Topic begins with two studies focusing on orthographic processing (i.e., encoding of information about letter identities and letter positions), a key interface between low-level visual processes and higher-level processing of words during reading (Grainger, 2018). Fernández-López et al. investigated the early precursors of precise letter position coding in pre-schoolers via the transposed-letter effect, i.e., failing to efficiently differentiate between CHOLOCATE and CHOCOLATE. Results highlighted

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[1] We adopt the term "graph" to refer to characters of a written script which code linguistic units as phonemes or syllables, such as letters or aksharas.

that learning to read is built also on a basic cognitive foundation, by showing that sequential memory and perception skills shape pre-readers' ability to encode letter position accurately (reflected in the size of the transposed-letter effect in a same-different task: TZ-ZT vs. TZ-TZ, previously reported in Perea et al., 2016). The importance of orthographic processing for reading development is also reflected in the longitudinal study by Eberhard-Moscicka et al. They investigated 1st-grade children with EEG and tested reading skills in the same children 3 years later. *N1 print tuning*, measured as an N1 increase in response to words compared to false-font strings, together with the mismatch negativity (MMN) improved the prediction of future reading skills compared to behavioral measures alone (RAN, vocabulary, and block design).

The second part of this Research Topic comprises six studies investigating letter-speech sound integration as an emergent property of learning to read. In a review article, Romanovska and Bonte offer a comprehensive picture of the brain basis of reading and a unifying framework with a developmental, dynamic skill learning perspective. They consider the shift from preliterate speech processing to the reading processes in the literate brain, and how dorsal spoken language and the ventral visual brain networks are gradually shaped, by the incremental development of phonological and orthographic knowledge, into an integrated audio-visual reading network. Karipidis et al. provided empirical longitudinal evidence of reading skill-dependent development, from pre-reading to the 1st and 2nd grades, in the functional activity of the superior temporal gyrus (STG), inferior frontal gyrus (IFG), and vOTC during audiovisual processing of single letter-speech sound correspondences.

In turn, four articles provided evidence regarding the audiovisual integration of single characters (in Latin alphabet and Chinese Calabrich et al.; Fraga-González et al.; Xia et al.) and of letter strings and spoken words (Varga et al.) by dyslexic readers. Specifically, Xia et al. provided evidence that the IFG and STG regions are also involved in the audiovisual processing of morpho-syllabic Chinese. While audiovisual integration effects in these regions did not differ between children with and without dyslexia for Chinese characters, a different correlational pattern of these effects with cognitive measures suggested that different neurocognitive networks shape the integration effects in children with and without dyslexia. Moreover, the same study also found a different audiovisual integration pattern for alphabetic pinyin compared to characters, which may reflect the specific role of pinyin as a scaffolding mechanism for learning Chinese characters. In an eye-tracking study, Calabrich et al. showed that adults with dyslexia recognized and recalled fewer newly learned letter-speech sound bindings than control readers. Dyslexics also showed an overreliance on (seemingly irrelevant) episodic cues during stimulus exposure to aid memory retrieval, specifically on the consistency of contextual stimulus properties, which "may be indicative of a more fragile memory representation" (p. 12). Fraga-González et al. adopted a graph theoretical approach for assessing EEG activity in dyslexic and typical readers during an artificial audiovisual learning task. Dyslexic were as able as control adults to accurately learn the novel bindings (i.e., no behavioral group difference), but showed lower theta connectivity during task performance and lower theta degree correlation over task and rest recordings, suggesting reduced (long distance) network integration and less communication between network nodes compared to typical readers. Finally, at the word level, using an implicit same-different perceptual-matching task, Varga et al. found that, whilst reading groups did not differ in ERP correlates of letter identity and letter position encoding in the visual modality, only typical adult readers but not those with dyslexia seemed to show automatic phonological processing and audiovisual integration when the visual letters and speech sounds were presented simultaneously (i.e., larger N1 responses to words than to pseudowords when orthographic stimuli were presented audiovisually).

The last part of this Research Topic focused on the other cross-modal binding promoted when learning to read, that is, between the visual representation of graphs and the corresponding writing gestures. It has been demonstrated that handwriting training during learning of visual graphs is more beneficial for subsequent visual graph recognition than are other learning experiences (e.g., viewing only, typewriting; for a recent meta-analysis, see Araújo et al., 2022). In an opinion article, Fernandes and Araújo reviewed and discussed the available evidence and the three theoretical proposals regarding the underlying mechanism(s) underpinning this handwriting benefit and proposed new directions to disentangle and investigate them. Seyll and Content provided empirical evidence in preschool children for the proposal that detailed visual analysis, which is inherent to handwriting, could be the key to the benefit of this learning experience in subsequent visual graph recognition rather than the graphic motor programs *per se*. Guan et al. showed that, relative to a view-only control training, the contribution of handwriting to visual word recognition also holds in a non-alphabetic script, both at behavioral and electrophysiological levels. Children with dyslexia did not benefit from such a multisensory graph integration. Note, however, that this conclusion might be premature, given that participants were engaged in handwriting for a few seconds and in a single exposure.

Vinci-Booher and James investigated the developmental trajectory of the neural system supporting handwriting, by contrasting fMRI, BOLD-signal change in children and adults during handwriting, and two sensorimotor control tasks. The results indicated that ventral-temporal involvement during handwriting may be adult-like by as early as 5–8 years of age, but a dorsal neural system including the more anterior parietal and frontal motor regions (related to the execution of the motor action) may still be developing in young children at the earliest stages of learning to read. A positive correlation further indicated that the response in these dorsal motor regions during handwriting may be related to children's emerging literacy skills (i.e., letter-word identification).

Finally, Fischer and Luxembourger addressed the challenge of mirror-image discrimination that beginners face when learning to read and write (e.g., b is different than d). These authors tested three candidate models for explaining the almost systematic reversal errors (e.g., b-d) found in writing by learners, using the data made publicly available by Torres et al. (2021). Given that none of these models convincingly accounted for this evidence, the authors suggest that reversal errors may result from a process of symmetrization, achieved through the homotopic interhemispheric exchange in the formation of memory circuits (Corballis, 2018) which may also be determined by the graphs themselves, specifically by the dynamics of writing letters.

This Research Topic provides an exciting overview of the importance of multi-systems interplay during reading development. This collection of papers illustrates the diversity of approaches in this research topic, from experimental psychology and cognitive and clinical neurosciences, adopting different paradigms, combining behavioral and neuroimaging tools, and testing different populations, such as beginning readers, typically-developing and dyslexic readers, alphabet and Chinese literate. It will also hopefully prompt and inspire new questions and directions in reading research in the context of the multimodal experience of reading which bridges visual, auditory, and motor brain systems.

Author contributions

SA, UM, and TF conceptualized together this Research Topic, critically revised the Editorial, and prepared the revised version. SA has the first authorship and wrote the first draft of the manuscript. All authors approved the final version submitted and the revised version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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BRIEF RESEARCH REPORT
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Which Factors Modulate Letter Position Coding in Pre-literate Children?

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One of the central landmarks of learning to read is the emergence of orthographic processing (i.e., the encoding of letter identity and letter order): it constitutes the necessary link between the low-level stages of visual processing and the higher-level processing of words. Regarding the processing of letter position, many experiments have shown worse performance in various tasks for the transposed-letter pair judge-JUDGE than for the orthographic control jupte-JUDGE. Importantly, 4-y.o. pre-literate children also show letter transposition effects in a same-different task: TZ-ZT is more error-prone than TZ-PH. Here, we examined whether this effect with pre-literate children is related to the cognitive and linguistic skills required to learn to read. Specifically, we examined the relation of the transposed-letter in a same-different task with the scores of these children in phonological, alphabetic and metalinguistic awareness, linguistic skills, and basic cognitive processes. To that end, we used a standardized battery to assess the abilities related with early reading acquisition. Results showed that the size of the transposed-letter effect in pre-literate children was strongly associated with the sub-test on basic cognitive processes (i.e., memory and perception) but not with the other sub-tests. Importantly, identifying children who may need a pre-literacy intervention is crucial to minimize eventual reading difficulties. We discuss how this marker can be used as a tool to anticipate reading difficulties in beginning readers.

Keywords: learning to read, orthographic processing, cognitive processing, pre-literate, transposed-letter effect

INTRODUCTION

Whereas language is a unique and sophisticated human ability that emerges naturally in children, reading is a learned skill that needs intensive practice. In fact, reading acquisition is a complex process that involves functional brain changes and requires the correct execution of numerous mental functions (see Maurer et al., 2005). For this reason, children must have adequate perceptual and cognitive skills before the initial steps of reading instruction. Once acquired, reading becomes the most important tool for knowledge acquisition in academic settings and beyond.

In alphabetic scripts, readers can quickly map the visual input into abstract letter representations and, subsequently, into word representations (see Dehaene et al., 2005; Grainger et al., 2008). The emergence of these abstract letter representations would occur during the first 2 years of reading acquisition (Jackson and Coltheart, 2001). Consistent with this view, using Forster and Davis (1984) masked priming technique, Gomez and Perea (2020) found that, for Grade 2 readers, the identification time of a word like EDGE is virtually the same when rapidly preceded by the physically identical prime EDGE and when preceded by the nominally (but not physically) identical prime edge.

Importantly, the process of visual word recognition requires not only the encoding of the abstract identity of the letters that compose each word but also the encoding of the serial order of the words' letters. If this process was absent, we would not be able to distinguish similarly spelled words like spot and stop. Notably, in a recent paper with adult readers, Schmitt and Lachmann (2020), demonstrated that when a target has to be identified in a string, processing occurs in serial order (i.e., from left to right) for letter stimuli, but not for strings composed of letters from an unknown alphabet (Cyrillic and Hebrew). At the same time, a considerable wealth of experiments with children and adults have shown that the encoding of letter order is only approximate: Readers often perceive jumbled words (e.g., JUGDE or CHOLOCATE) as the original words (see Perea and Lupker, 2003, 2004; Castles et al., 2007; Guerrera and Forster, 2008; Lupker et al., 2008). As serial order processing is a key component of a wide range of psychological processes, from perception to action (Logan, 2021), it is not surprising that the encoding of serial order is also an essential part of reading and literacy. The main goal of the present study is to shed some light on which cognitive factors are associated with pre-readers' ability to encode letter position accurately.

In the context of reading development, Castles et al. (2007) proposed a "lexical tuning" model in which children encode progressively more precisely the letter positions within words. For instance, in a series of masked priming experiments, they found that the prime dark was much more effective at activating DARK in Grade 3 than in Grade 6 children. The rationale of this model is that, as reading abilities develop, letter position coding becomes more accurate (see Perfetti's, 2017 lexical quality hypothesis, for a similar claim; but see Grainger and Ziegler, 2011, for a different view).[1] Evidence supporting the lexical tuning model has been obtained not only with children of different ages but also with children of the same age: Better readers encode letter position more accurately than the worse readers (see Gómez et al., 2021; Pagán et al., 2021, for evidence with children and see also Andrews and Lo, 2012; Perea et al., 2016, for parallel evidence with adult readers). Furthermore, a poor encoding of serial order may lead to reading difficulties. Friedmann and Gvion (2001) were the first to report that some individuals present problems at encoding letter position, making frequent errors of letter migration within words—reading broad for board. This deficit, which has been termed "letter position" dyslexia, has been found in many different languages, including English (Kohnen et al., 2012; see Güven and Friedmann, 2019, for a recent review).

Somewhat surprisingly, examining how the encoding of letter order emerges in young readers and whether some preexisting abilities may help encode serial order in pre-readers has been overlooked in the literature. One of the few exceptions is the longitudinal experiment conducted by Duñabeitia et al. (2015). They used a same-different task with two sequentially presented four-letter strings, and children had to decide whether the letter strings were the same or different. The "different" trials were composed of pairs with two transposed letters (transposed-letter pairs; e.g., rzsk-rszk) and pairs with two replaced letters (replacement-letter pairs; e.g., rzsk-rhck). If letter position coding is flexible, transposed-letter pairs would be perceptually more similar than replacement-letter pairs, thus producing worse performance (e.g., more false positives). The "transposed-letter" effect is the difference in performance between these two conditions. Duñabeitia et al. (2015) tested the children three times: (1) in their year before preschool (M = 4.24 years) (2) in their preschool year (M = 5.21 years), and (3) in the first year of primary school (M = 6.32 years). They only found a transposed-letter effect when the children had learned to read (first-grade children; more error responses for transposed [42.9%] vs. replaced-letter pairs [30.6%]). Duñabeitia et al. (2015) concluded that "position uncertainty emerges as a consequence of literacy training" (p. 549).

An interpretive issue in the Duñabeitia et al. (2015) experiment is that the pre-readers performed very poorly in the same-different task and the sensitivity index, d', was close to zero for both for replaced and transposed conditions (Perea et al., 2016). This pattern suggests that their version of the same-different task was too difficult for the pre-readers (i.e., the working memory load probably exceeded the children's capacity; see Riggs et al., 2006); thus, one cannot make any inferences on these data. To draw firm conclusions on the encoding of the serial position of letters in pre-readers, Perea et al. (2016) simplified some elements of Duñabeitia et al.'s (2015) same-different task: (1) they used two-letter string pairs instead of four-letter string pairs (2) the pairs were presented simultaneously instead of sequentially, and (3) the responses were done verbally (i.e., saying "same" vs. "different") instead of manually (pressing one of two buttons; see **Figure 1**). Along with "same" pairs (TZ-TZ), Perea et al. (2016) included the following "different" pairs: transposed-letter pairs (TZ-ZT), one-letter replacement pairs (TZ-PZ), and two-letter replacement pairs (TZ-PH). They found a sizeable transposed-letter effect in 4-years-old children (i.e., pre-readers). Specifically, the number of false positives (i.e., "same" responses) was greater to transposed-letter strings (TZ-ZT) than to 1 or 2 replacement-letter strings (TZ-PZ; TZ-PH). Perea et al. (2016) concluded that this pattern reflected a noisy perception of location order, common to all visual objects (see Gomez et al., 2008), rather than an effect that emerges with literacy. Notably, while not analyzed in their paper, shortly after conducting their experiment, Perea et al. (2016) collected the scores of these children in a battery of abilities related to early reading acquisition in Spanish (BIL battery; Sellés et al., 2008).

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[1] In fairness to Grainger and Ziegler (2011), their dual-route model of visual word recognition focuses on the initial steps of learning to read. The serial letter encoding, which involves precise letter position encoding, would emerge first in reading development (phonological route). Later in development, the parallel encoding of the word's letters (orthographic route) would make letter position coding coarser.

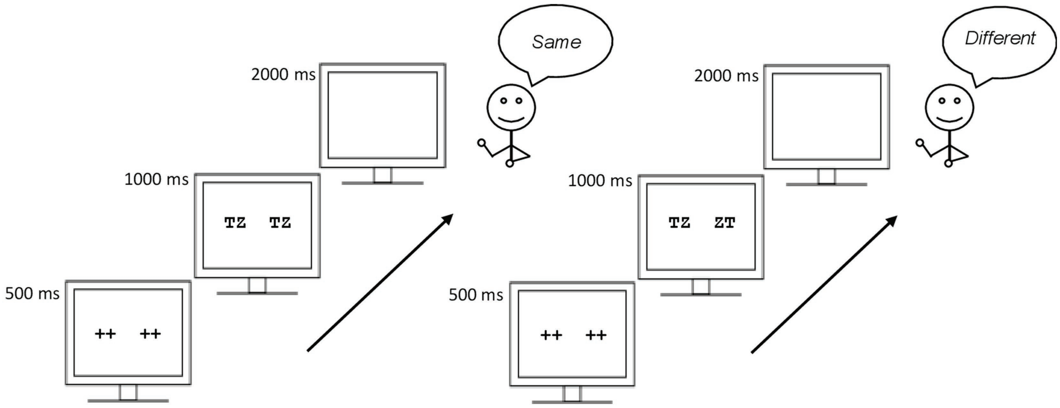

FIGURE 1 | Depiction of the same-different task used in the Perea et al. (2016) study.

In the present study, we aim to take a step forward by exploring the potential precursors of letter position coding in pre-readers. To that end, we examined the relationship between the ability of pre-literate children to encode accurately the order of letters—taken from the Perea et al. (2016) experiment—with the five sub-tests related to reading readiness and subsequent reading success from the BIL battery: phonological and alphabetic awareness, metalinguistic knowledge, linguistic skills, and basic cognitive processes. The examination of this issue is important not only at a theoretical level but also at a practical level. Before learning to read, children must have acquired some perceptual, cognitive, and linguistic skills. Defining the early precursors of precise coding of letter position will shed light on the roots of the processing of serial order when reading letters in words. These analyses would allow us to identify children who may present some deficit (e.g., some mild forms of letter position dyslexia) and start intervening as soon as possible, preventing future reading difficulties.

Thus, in the present study, we examined the relationship between the sensitivity of the readers to distinguish transposed-letter pairs from identity pairs (e.g., TZ-ZT vs. TZ-TZ) and the scores of pre-readers (*M* = 4.5 years old) in phonological and alphabetic awareness, metalinguistic knowledge, linguistic skills, and basic cognitive processes (visual perception and sequential auditory memory) in the BIL battery (Sellés et al., 2008). We focused on transposed-letter pairs, as the mechanisms employed to discriminate TZ-ZT from ZT-ZT are based exclusively on letter order. The predictions are clear. In adult readers, basic cognitive processes, such as spatial and visual attention, have been assumed to play a key role in encoding letter position (see McCann et al., 1992; Gomez et al., 2008). If this generalizes to pre-readers, we expect a positive relationship between the abilities at discriminating TZ-ZT and the scores in these basic cognitive processes. This outcome would imply that educators could use this simple same-different task with a transposed-letter pairs to predict reading readiness before starting with the reading instruction. Furthermore, it may also operate as an incentive to design other tasks for pre-readers on perceptive and executive skills to prevent—or at least minimize—potential difficulties at locating letters within words during learning to read. In addition, we expect no relation between linguistic factors (i.e., phonological and alphabetic awareness, metalinguistic knowledge, and linguistic skills) and the sensitivity at distinguishing TZ-ZT in pre-readers—at the time of the experiment, the children did not know the consonant names.

MATERIALS AND METHODS

Participants

They were the 20 preschoolers (*M* = 4.54 years; SD = 3.6; 7 girls) from a private school of Valencia (Spain). All of them were native speakers of Spanish with no learning developmental problems. An informed consent from their parents was obtained before running the experiment, and the study was approved by the Experimental Research Ethics Committee of the University of Valencia. At the time of testing, the preschoolers were starting to learn the vowels but they did not know the name or sound of the consonant letters (as confirmed by results of the BIL battery).

Procedure

The experiment took place individually in a quiet room within the school premises. DMDX software (Forster and Forster, 2003) was employed for stimulus presentation and recording of the responses. A depiction of the procedure in the same-different task can be found in **Figure 1**. Accuracy was stressed in the instructions. Ten practice trials preceded the 64 experimental trials. Moreover, the children were assessed with a battery of abilities related to early reading acquisition in Spanish (BIL battery; Sellés et al., 2008).

Materials

For the same-different task, the stimuli were 64 pairs of consonant strings made of two consonants. There were 16 trials in each of the conditions: (1) same pairs (TZ-TZ) (2) transposed-letter pairs (TZ-ZT) (3) one-letter replacement pairs (TZ-PZ), and (4) two-letter replacement pairs (TZ-PH). Four counterbalanced lists were created in a Latin square manner, so that each stimulus was rotated across the different conditions. The presentation of the items was randomized for each participant.

To assess the abilities related to early reading acquisition, we employed the BIL battery (Sellés et al., 2008). This battery comprises five sub-tests: phonological awareness, alphabetic awareness, metalinguistic knowledge, linguistic skills, and basic cognitive processes—we obtained a score from each sub-test. For the goals of the present study, we focused on the sub-test measuring basic cognitive processes. This sub-test explores a series of cognitive processes that take place when we face reading: (1) attention, which leads the mind to concentrate on specific stimuli; (2) sensation (i.e., detection and differentiation of sensory information); and (3) perception, which integrates sensory experiences and interprets them for recognition and identification (i.e., giving meaning to what has been selected and picked up at the attentional and sensory level), relying on the patterns stored in the (4) memory. To that end, the sub-test assesses the child's sequential auditory memory and the ability to visually discriminate between similar letters and symbols (the child had to circle the symbols that were the same as a target; see Sellés et al., 2008, for a depiction of the other sub-tests).

RESULTS

To test whether better pre-reading skills (as measured by the BIL battery) were associated with better performance at differentiating between same and transposed-letter pairs in the same-different task, we conducted frequentist and Bayesian correlation analyses with JASP (Faulkenberry et al., 2020). To compute the Bayes factors, we used the default Cauchy distribution (centered around 0 and with a width parameter $\delta = 0.707$; see Rouder et al., 2009; Wagenmakers et al., 2017, 2018, for discussion). Specifically, we examined the relation between *d*' (a measure of sensitivity obtained from the accuracy data of Perea et al., 2016) and the percentile scores in sub-tests of the BIL battery—of note, these findings were virtually the same if we had employed the raw scores from the sub-scales. For the computation of d', we used the hit rate for same trials and the false alarm rate for the transposed-letter trials (TZ-TZ vs. TZ-ZT)—in signal detection theory, chance-level performance [d' = 0 or no sensitivity] occurs when the hit rate for the identical items is the equal to the false alarm rate for the different items. Of note, mean accuracy for same trials in the Perea et al. (2016) was 0.83; for different trials, it was 0.33 for transposed-letter strings and 0.68 and 0.88 for one-letter and two-letter replacement strings, respectively.

Results of the correlational analyses in the present study showed that those children who better differ transposed letter from "same" pairs (TZ-ZT vs. TZ-TZ) had the higher scores in the sub-test on basic cognitive processes ($r = 0.634$, $p = 0.003$; see **Figure 2**). Indeed, the alternative hypothesis was 18.6 (BF_{10} = 18.559) times more likely than the null hypothesis with the present data (see Jeffreys, 1961, for interpretation of Bayes factors). In addition, there were no signs of a relationship between the children's performance differentiating between same and transposed-letter pairs and the other (linguistic) sub-tests (all $ps > 0.24$, BFs10 < 0.528).

For completeness, we explored the relationship between performance in the replacement-letter conditions and the BIL battery; to this end, we computed separately d's for same vs. one-letter replacement trials (TZ-TZ vs. TZ-PZ) and for same vs. two-letter replacement trials (TZ-TZ vs. TZ-PH), and then calculated the correlations between these two d's and the sub-test of the BIL battery. None of these correlations produced evidence in favor of a relationship (all *p*s > 0.147; all $BF_{10} < 0.478$).

DISCUSSION

Identifying the cognitive precursors of reading is vital to determine those children who are ready to start learning to read and those who still need some cognitive maturation or some early intervention. This would prevent later reading difficulties and disorders and the frustration and psychological discomfort that such problems usually entail. With this matter in mind, in the present study, we scrutinized the roots of the mechanisms underlying the encoding of letter position in strings (i.e., one of the critical factors of efficient reading; see Castles et al., 2007; Logan, 2021). Specifically, we examined the relationship between the capability of pre-literates to differentiate between transposed-letter pairs and identity pairs (e.g., TZ-ZT vs. TZ-TZ) and these children's scores in basic cognitive processes. Results showed that the pre-literate children who best differentiated between TZ-ZT and TZ-TZ in a same-different task were those with higher scores on basic cognitive processes (see **Figure 2**). Notably, the sub-test of basic cognitive processes was not generically associated with sensitivity in the same-different task (i.e., it

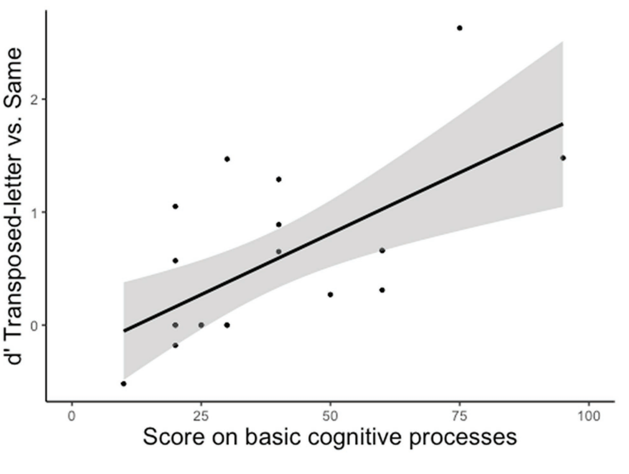

FIGURE 2 | Correlation between the d' when discriminating transposed-letter pairs from same pairs and the scores on the basic cognitive processes of BIL.

was not related to performance for replacement-letter trials); instead, it is uniquely associated with accuracy in letter position coding. Thus, at the theoretical level, this outcome reflects that basic cognitive skills shape the ability to encode serial order in letter strings (e.g., a smaller value of the parameter responsible for perceptual uncertainty in models of letter position coding; see Gomez et al., 2008; Davis, 2010). Furthermore, at an applied/educational level, our findings imply that a simple same-different task can be used to assess reading readiness: the better the performance in this task, the better the encoding of letter order, diminishing the chances of letter position dyslexia.

In addition, our findings suggest that the preparing-to-reading arises early in development with some non-specialized processes that would be recruited and adjusted to guide the subsequent functional reading progress (see Lachmann and van Leeuwen, 2014). Further support to this idea can be found in the study of Saygin et al. (2016). They found that the cortical location of the visual word form area (i.e., the brain region specialized for letter string; Dehaene and Cohen, 2011) at age 8 (when children read) can be predicted by the distinctive connectivity of the same region at age 5 (pre-literates). Taken together, these studies emphasize that early detection of deficiencies in the visual analysis of the input is crucial to prevent later reading difficulties (Friedmann and Gvion, 2001; Shetreet and Friedmann, 2011). This is consistent with the assumption that children with reading difficulties have a general impairment in domains other than linguistic (e.g., an impairment in multisensory integration; see Gori and Facoetti, 2014; Lachmann and van Leeuwen, 2014). Therefore, there are possibly many (complementary) ways to test whether pre-readers are prepared to starting reading learning (e.g., the same-different task or the "avatar task"; see Perea et al., 2014); this would be a valuable endeavor for the future studies.

We acknowledge that the present study comes with some limitations. Firstly, because of the correction criteria of the BIL test, it was not possible to obtain separate scores for the tasks that make up the basic cognitive processes sub-test (sequential auditory memory and visual discrimination). Furthermore, although the processes assessed in the basic cognitive sub-test were not linguistic in nature, the stimuli contained symbols, letters, and words, thus, making it difficult to clearly disentangle basic cognitive processes and verbal processes. Future tests should be more specific to characterize all possible aspects that shape the cognitive processes of pre-literates. In addition, it would have been desirable to have obtained further data from the same children once they started reading learning. These data would have allowed us to test whether the findings in the same-different task with transposed letters in pre-literate children were a good predictor of letter position coding once children acquired knowledge about letters. Furthermore, these longitudinal data would have also allowed us to examine the interplay between the emergence of orthographic processing during learning and the scores in cognitive and linguistic processes. Indeed, once the children start to read, other elements would begin playing a significant role, such as alphabetic knowledge or phonologic awareness (see Dehaene et al., 2015).

A complementary strategy for the future research would be to run parallel longitudinal same-different experiments on serial order using to-be-learned letters vs. unknown letters (e.g., letters from another alphabet). The data pattern should be similar for the pre-readers for both types of stimuli, but one would expect differences when the children learn to read. Critically, these differences could be considered as markers of the emergence of orthographic processing (see Grainger, 2018). While this approach is ideal on an *a priori* basis, it suffers from various methodological issues. One would need to design a feasible task for children of different tasks that minimizes both ground and ceiling effects. However, it is challenging to create a task achievable for pre-literates and complicated enough to draw differences among developing readers. For instance, deciding whether two four-letter strings are the same is extremely challenging for pre-literates, whereas deciding whether two-letter strings are the same may be too easy for developing readers (see Perea et al., 2016, for discussion). As a result, it is very difficult to experimentally study the emergence and development of orthographic processes in pre-readers. To further complicate matters, there are also other potential limitations, such as the lack of control for prior letter knowledge and other linguistic elements in pre-readers, or that the duration of experiments for pre-readers would need to be quite short to keep them attentive. An alternative is to design laboratory analogs of children's reading acquisition that consists of training adults to read a novel script (see Fernández-López et al., 2021; see also Chetail, 2017; Taylor et al., 2017). This approximation is not as ecological as one would desire (see Maurer et al., 2010; Taylor et al., 2017), but it definitively increases the control on the process of acquiring the novel orthography.

In sum, the early identification of potential problems that may slow down reading development is of fundamental importance for psychologists and educators. In the present study, we found that those pre-readers who performed better in basic cognitive processes tended to be those who would encode more accurately letter position in a simple same-different task. This finding highlights that learning to read should not be based solely on letter knowledge and phonological decoding. We also need to consider that learning to read is built on a basic cognitive foundation, probably related to multisensory integration based on visual attention.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found at: https://osf.io/hz7m2/?view_only=2073b5df420e4d5f95c627ec4eee6e81b.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Comité de Ética de Investigación en Humanos (CEIH).

Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

MP, PG and MF-L contributed to conception, design of the study, and performed the statistical analysis. PG organized the database. MF-L wrote the first draft of the manuscript. MF-L and MP wrote sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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A Test of Three Models of Character Reversal in Typically Developing Children's Writing

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Multisensory learning to read involves, to a large extent, learning to write. A major problem in the initial teaching of handwriting is preventing children from producing reversed letters, especially when the reversed letters are identical to other letters. Torres et al. (2021) offer an efficient method for remediating this problem. Here, we analyze the reversals in their writing data, obtained on Brazilian first-graders (M_{age} = 6.0 years). Surprisingly, this analysis led to the observation that the first graders almost systematically reverse both the letters b and d in the particular copying conditions (the students look at one letter at a time for 3 s, then immediately after they had to write it while blindfolded). We first describe succinctly and discuss three models susceptible to account for reversal writing, with the aim to question their capacity of account for the curious observation just mentioned. The three models respectively attribute a major role to 1) initial (perceptive) mirror equivalence, 2) intra-hemispheric transfer, 3) orientation of the letters. Because none of the three models examined accounts convincingly for the observation, we accommodated and specified Model 2, adding also a major idea of Model 3. The resulting model assumes that the mirror-letter reversed image representation (b for d and vice-versa) is strongly activated in the right cerebral hemisphere, and that the top-down processes originating from this hemisphere were exacerbated by the eyes closed condition. Of course, this post-hoc and speculative model should be tested in other conditions and with other children.

Keywords: mirror writing, letter reversal, interhemispheric transfer, mirror letter, first grade

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1 INTRODUCTION

Knowledge is often acquired through reading and transmitted through writing. Not surprisingly, much research then supports a unidirectional relationship from reading to writing (Ahmed et al., 2014; Kim et al., 2018). For example, Ahmed et al.'s modeling suggested that a unidirectional reading-to-writing model was better at the word and text levels of analysis. However, their modeling also revealed that a bidirectional model best fit the sentence-level data. Besides, the study of the relation between reading and writing necessarily excludes children who cannot sufficiently read. For example, the Kim et al.'s longitudinal data do not include students before third grade (in the United States). For learners who are beginning to read—typically preschoolers or first graders at the beginning of the school year—, and at the letter-level, the relationship between reading (or letter recognition) and writing might be somewhat different.

First, children in literate societies learn about some of the formal properties of writing long before they go to school (Treiman and Kessler, 2014). In modern societies, they develop some knowledge about the outer form of writing as early as 2 or 3 years of age (Treiman, 2017). Second, reading and writing are usually taught/learned at the same time. Perhaps this is why they have been found to be associated in the brain, at least at the letter-level (Longcamp et al., 2016). Third, teaching/learning, whether at school or at home, often begins with a copy/writing task (especially of the first name) that combines or even merges the two tasks. Fourth, reading is fundamentally addressed in the visual modality. Braille reading seems to be an exception, but it only concerns a limited population: blindness is rare, and not all blind people read Braille; furthermore, Braille reading declines with the today multiplication of audio-books and voice synthesis software that read aloud any document in digital version. In consequence, multisensory learning of reading should mainly be indirect, namely through multisensory learning to write. The research by Torres et al. (2021) seems an example of how multisensory learning to read can be improved by learning to write, even if multi-sensory learning is not a panacea (Madan and Singhal, 2021). Indeed, in their brief targeted intervention (30 min/day for 3 weeks), Torres et al. (2021) used a majority of learning to write activities, namely "air-writing" and "writing on a paper," in addition to a tactile perception of letter traces activity, "perceiving letters on hands." Finally, the contribution of learning to write to learning to read was empirically demonstrated in French preschoolers (Ouzoulias et al., 2000).

One of the main difficulties in reading beginners is the distinction of a letter from its reversal, which is fundamental for distinguish b and d, or p and q. Thus, it is important to know that writing and reading, at least its letter recognition sub-component, do not raise the same treatment of reversal in children (Fischer and Luxembourger, 2020; but see McIntosh et al., 2018b). Many researchers certainly consider the two tasks to be closely related, but given their relative importance, they investigate reading exclusively, following the example of Wechsler and Pignatelli (1937). By the way, research on adults or older children is forced to limit itself to reversal in reading, since such participants no longer make letter reversal in writing. Moreover, in reading, letter reversal can hardly be studied directly. Indirectly, it is often investigated with priming techniques, on typical adults (Duñabeitia et al., 2011; Borst et al., 2015; Ahr et al., 2017; Soares et al., 2019; Soares et al., 2021) or typically developing children beyond age six (Perea et al., 2011; Ahr et al., 2016; Brault-Foisy et al., 2017).

Yet, a particular reading dysfunction—dyslexia, or strephosymbolia, as it was first named by Orton (1925)—has been specifically studied in its relationship to reversal (Fernandes and Leite, 2017). Historically, Orton and Gillingham (1933) noted that the twist in reproduction, suggested by mirror writing, is "of considerable interest and probably of some prognostic value" (p. 268). As a support, they noted that most of the children they have seen who exhibited this initial tendency to twist also experienced considerable difficulty in reading later on. More recently, Lachmann (2008) noted that reversal errors have been diagnosed as one of the primary symptoms of developmental dyslexia. However, Cheng-Lai et al. (2013) report no reversal errors in their sample of 45 nine-years-old Chinese children with dyslexia, despite the inclusion of a 70-item left/right reversal subtest assessing ability to identify the correct orientation of orthographic units, such as simple Chinese characters and Arabic numbers. Indeed, the argument used by Orton and Gillingham sounds like a tautology since almost all children—and thus also future dyslexic children—exhibit this initial tendency to twist. For example, in Fischer and Tazouti (2012) Experiment 2, approximately 95% of the 356 typical children reversed at least one character (uppercase letter or digit) out of the 33 characters they were asked to write under dictation. Furthermore, Orton and Gillingham's argument does not imply a causal relationship. In order to refine then our understanding of the relationship between mirror writing and dyslexia, the selection of a relevant model of handwriting reversal by typical children is a first step. This first step, at least for letter reversal, was the main objective of the present paper.

Accordingly, we will successively describe three candidate models for explaining the initial mirror reversal in writing by typically developing children. An empirical test of these models was possible with the recent data made publically available by Torres et al. (2021). In addition, these data also allowed us to investigate the relationship between mirror writing and mirror image discrimination in a visual task. The result of the test led to a speculative accommodated model for the particular condition of copying/writing blindfolded used by Torres et al. (2021).

1.1 Model 1 of Initial Mirror-Equivalence and Mirror-Letter Confusion

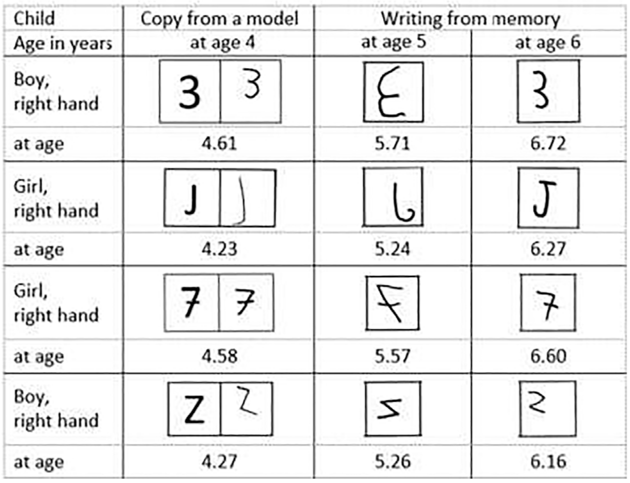
Model 1 is premised on brain blindness to letter orientation in children. In this model letter perception begins developmentally with visual processes that are orientation insensitive (Blackburne et al., 2014; Pegado et al., 2014; Torres et al., 2021). As Torres et al. point out, this creates then "confusion between mirror letters (e.g., b-d in the Latin alphabet)" (*p*. 1).

Here we will review studies showing that the basis of this model, that is initial brain blindness to character orientation in very young children, is inconsistent with the data, and that "memory-image generalization describes an effect of memory formation and not of perception" (Lachmann and Geyer, 2003). First, there are many old behavioral tests supporting this conclusion. Over and Over (1967) showed that 3–6 years-old children can discriminate between mirror-image oblique lines under detection conditions but not under recognition conditions. Over (1967) concludes that "the child perceives that mirror image obliques differ in orientation but seems unable to remember from trial to trial which is the "correct" oblique" (*p*. 1272). In the 1970s, some of Bryant (1969) and Bryant (1973) results were interpreted in a controversial way. Bryant has shown that two non mirror-image obliques are just as confused as two mirror-image obliques by 4–7 year-olds. However, we refer here simply to Bryant (1969) observation that 5 year-olds made very few errors in a simultaneous presentation but performed at chance level in a successive comparison of obliques. In accordance, Corballis and Zalik (1977) concluded that, what is clear about Bryant's findings, "is that the difficulty of discriminating mirror-image obliques is a problem of memory rather than of perception" (*p*. 516). Even babies (3–4 month-old) were able to discriminate differences in orientation, although they tended to view mirror images as equivalent stimuli (Bornstein et al., 1978).

Second, there are physiological evidence that orientation is detected very early in the primary visual cortex (also known as V1). Hubel et al. (1977) demonstrated the presence of a system of orientation columns in the macaque monkey visual cortex. Whereas afferent thalamic neurons are generally orientation insensitive (Priebe, 2016), a key emergent property of V1 is the orientation selectivity of its neurons (Dragoi et al., 2000; but see Antinucci and Hindges, 2018). Dragoi et al. showed that the development of orientation tuning does not require visual experience, although selective experience in early life can modify the orientation preference of neurons. Garg et al. (2019) found that a notable proportions of V1 neurons strongly preferred color stimuli and were also orientation selective. Thus, processing of orientation and color seems combined at the earliest stages of visual processing. Finally, Jia et al. (2021) trained adult participants in an orientation discrimination task while using functional magnetic resonance imaging (fMRI), thereby revealing orientation-specific neural patterns in V1 before training.

Third, mirror confusion could then occur because the perceived orientation information is lost in the memory code. Because this forgetting leads to non-discrimination of an image from its mirror, it appears as a generalization process, forgetting being a central mechanism of generalization (Vlach and Kalish, 2014). The credibility of this temporary forgetting is strengthened by sensitivity to mirror reversals in an earlier visual processing object-selective region, the lateral occipital sulcus, followed by tolerance to mirror reversals in one object-selective region, the posterior fusiform sulcus (Dilks et al., 2011). Rollenhagen and Olson (2000) discovered cells with mirror-symmetric tuning, and Freiwald and Tsao (2010) found, in the macaque face-processing system, that such cells were agglomerated within a single intermediate node, not in the most posterior face-selective region as one might have expected in case of non-distinction, initially in V1, between an image and its mirror. In humans, literate individuals diverge from illiterate in the ability to discriminate horizontal mirror images (*enantiomorphy*) at a later, postperceptual representational level. Therefore, the deficiency in enantiomorphy seems not a problem in input coding (Kolinsky et al., 2011).

Fourth, Fischer and coworkers compared the easiness, with respect to reversal errors, of a character copying task with a character writing from memory task. Indirect confirmation of this easiness was provided by two experiments by Fischer and Tazouti (2012). In their Experiment 1a, on 5–6 year-old children, 143 of them copied the eight asymmetrical digits and wrote eight asymmetrical capital letters from memory, and 156 others copied these letters and wrote the digits from memory. The result was very clear: The children reversed the characters much less frequently (and even very rarely) when they copied them (0.4% reversal) than when they wrote them from memory (20.4% reversal). In their Experiment 1b, 205 children (4–5 years-old) produced only 7.3% reversals in copying the digits, whereas 153 children (5–6 years-old, from Expt 1a) produced 21.8% reversals in writing the digits from memory. A more direct confirmation comes from the longitudinal study by Fischer and Koch (2016) who found that the 166 children in the middle section of the French *école maternelle* produced only 3.6% reversals in copying the characters, whereas the same children, when they had integrated the upper section, produced 25.4% mirror reversals in writing the characters from memory. As shown in **Figure 1**, many children copied correctly a character when aged 4 years, mirror wrote the same character at age 5 years, and wrote it correctly at 6 years.



Child	Copy from a model	Writing from memory	
Age in years	at age 4	at age 5	at age 6
Boy, right hand	3 3	Ɛ	3
at age	4.61	5.71	6.72
Girl, right hand	J J	ᒐ	J
at age	4.23	5.24	6.27
Girl, right hand	7 7	Ꞁ	7
at age	4.58	5.57	6.60
Boy, right hand	Z Z	Ƨ	Z
at age	4.27	5.26	6.16

FIGURE 1 | Characters correctly copied at age four, mirror written at age five, and correctly written at age six by the same children (data from Fischer and Koch, 2016).

1.2 Model 2 of Interhemispheric Reversal

Model 2 relies on different character representations in the two hemispheres due to interhemispheric mirror-image reversal during the transfer (Corballis and Beale, 1976). More specifically, Corballis et al. (2010) suggested that reversed exemplars of the letters may be laid down in the right cerebral hemisphere.

First, reinforcing our preceding conclusion, Corballis (2018) underlines that the mirror-image confusion "is almost certainly a matter of recognition rather than perception *per se*" (p. 3), and, further, that "early processing retains left-right information for perception, but this is lost at the later stage where recognition takes place" (p. 4). In Corballis' theory, the mirror-image storage is achieved through the process of interhemispheric mirror-image reversal as a result of homotopic connections between the hemispheres. By this process, each hemisphere perceives correctly, for example, the symbol b, but in the memory storage process, the representation of b is transferred and reversed between hemispheres.

Evidence for the implication of the anterior commissure in the transfer was obtained in great part on patients without functional corpus callosum. Notably, a callotomized patient, DDV, showed systematic left–right reversal of the letters in the left visual field (i.e., right hemisphere), with a bias to respond b in a b-d discrimination task in the left, but not right visual field (Corballis et al., 2010). Interestingly, the same research demonstrates that even in normal participants, discrimination

TABLE 1 | Reversal of the asymmetrical letters, in percentages, after Richmond (2012) for lowercase letters and Fischer and Luxembourger (2018a, **Table 2**) for capital letters.

Letter	Lowercase *N* = 126; Grade: 1–4	Uppercase[a] *N* = 679; Age: 5.72 years
A	0	—
B	0.8	6.49
C	0.8	10.95
D	1.6	6.09
E	0	7.84
F	0	8.09
G	0	6.29
H	0	—
I	0.8	—
J	9.5	47.86
K	0	4.62
L	1.6	11.14
M	0	—
N	0	2.46
O	0	—
P	1.6	7.70
Q	0.8	13.08
R	0	6.42
S	2.4	19.02
T	0.8	—
U	0	—
V	0	—
W	0	—
X	0	—
Y	0	—
Z	11.9	51.32

[a] *Dash are for symmetrical capital letters.*

of mirror-image letters depends on matching to an exemplar, for which the right-hemisphere is dominant.

Experimentations on non-human animals also support the implication of the hippocampal commissure in the transfer. It would be interesting to further investigate this implication as it may help to understand children's learning of character orientation. Indeed, as Fischer (1999) points out for the digit 3, learning to bind the oral name of a digit and its Arabic handwriting is fundamentally a declarative learning. And this type of learning is precisely a specificity of the hippocampus (Squire, 1992; Eichenbaum, 2004; Menon and Chang, 2021). Thus, the inhibition of interhemispheric transfer by way of the hippocampal commissure could support the behavioral observations of mirror-image inhibition, reported or suggested by many authors (Duñabeitia et al., 2011; Borst et al., 2015; Ahr et al., 2016; Brault-Foisy et al., 2017; Soares et al., 2019). This suggestion fits well with the description of the hippocampus as a "suppressor of inappropriate associations" (McNaughton and Wickens, 2003), less well albeit not in contradiction with its capacity to abstract and generalize[1] from a format to the other (Viganò et al., 2021).

In addition, Mather (2001) suggestion that dyslexia develops from learning the alphabet in the wrong hemisphere fits well with Corballis' theory. A literature review leads Mather to write that "dyslexics perform as if there were little interaction of their two cerebral hemispheres" (p. 287), and Mather et al. (2015) to the suggestion that "spontaneous mirror-writing may reflect right hemisphere representations laid down during the beginning stages of handwriting learning" (*pp.* 570–571). Moreover, Gordon (1980) hypothesized that dyslexics were "locked" into a right hemisphere mode of processing which governed all their cognitive activity. Therefore, Mather's suggestion—dyslexic children use the wrong hemisphere (usually the right depository of the reversed representations)—can seem compelling. However, because the suggestion implies a causal relationship between reversal and dyslexia, it seems at odds with our discussion of Orton and Gillingham's argument in the introduction, as well as many other arguments against causality. For example, that by Treiman et al. (2014) that reversal errors do not predict later reading ability, whereas other production errors do.

However, Model 2 does not explain why, in writing, the intrusion of reversal representations affects some letters (see the present **Tables 1**, **2**) and digits (Fischer and Luxembourger, 2018a, **Table 1**) much more than others. With Mather's wording, the question becomes: Why do children use the wrong hemisphere for some letters and not for others?

1.3 Model 3 of Character Right Orienting

Model 3 of letter orientation in the direction of writing (Fischer, 2017) starts with the observation that children have few problems copying the characters, but the process of memorization erases the character orientations (cf., Dehaene, 2009). Because of the resulting un-oriented representation of the characters, the children must choose an orientation when writing characters from memory. Then, the model adds a somewhat original idea (but see Simner, 1984; Simner, 2003; Treiman and Kessler, 2011): the characters themselves, rather than certain characteristics of the children (e.g., left-handedness), explain the reversal. This idea that characters, or more generally items, play a fundamental role in the participants' performance has long been overlooked in many areas of research, despite Clark (1973) seminal article in psycholinguistics. Generally, only participants' variability is taken into account in the widely practiced ANOVA and t-tests analysis of variance procedures (Judd et al., 2017). This is no longer the case since appropriate designs and analytic models that incorporate items' variation, known as mixed effects models, have been developed. Commenting on these new models, Brysbaert and Stevens (2018) strikingly note that "a revolution is taking place in the statistical analysis of psychological studies" (p. 1).

Fischer and colleagues then hypothesized that left-oriented characters—the digits 1, 2, 3, 7, and 9, and the capital letters J and Z—should be more reversed than the other asymmetrical characters because children typically adopt the rule of orienting characters in the direction of writing, which in our culture is to the right. Left-orientation cannot be defined mathematically because the dynamics of writing must be taken into account to categorize certain characters (e.g., 4), but the evaluation of orientation by adult students has confirmed this

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[1] The generalization referred to here is not mirror symmetrization, but, for example, the generalization from one correct graphic form to another (also correct), which is particularly important for solving the problem of spatial variability of handwritten letters.

TABLE 2 | Categorization of the letter-writings in the Baseline test.

Letter	Correct writing	Mirror writing	Vertical mirror	Double mirror	Other product.	Non-response	Number children	Percent mirror[a]
B	16	94	2	1	3	1	117	85%
C	101	1	0	0	5	10	117	1%
A	86	2	1	1	13	14	117	2%
F	83	3	0	0	6	25	117	3%
E	85	11	1	1	9	10	117	11%
D	15	99	1	1	1	0	117	87%
G	58	7	7	1	13	31	117	11%
H	76	24	0	0	12	5	117	24%
K	73	14	0	0	7	23	117	16%
S	33	78	0	0	1	5	117	70%
Z	13	100	0	0	4	0	117	88%
p	30	73	1	5	4	4	117	71%
j	24	4	0	0	3	5	36	14%
q	13	22	0	0	1	0	36	63%
r	22	0	0	0	13	1	36	0%
t	18	3	1	0	11	3	36	14%
y	24	2	0	0	8	2	36	8%

[a] *Calculated taking into account only writings relevant to the discussion (i.e., horizontal mirror and correct writings).*

categorization (Fischer, 2018). The hypothesis was subsequently widely supported, not only in the research by Fischer and colleagues (Fischer and Luxembourger, 2018a), but also by others (Treiman et al., 2014; McIntosh et al., 2018a; McIntosh et al., 2018b; Portex et al., 2018; see also **Table 1**).

Children who apply the right-orienting rule will reverse the left-oriented characters, whereas the children (rare in our culture) who apply a left-orienting rule would reverse the right-oriented characters. Therefore the within-children correlation between reversal of the left-oriented and right-oriented characters should be negative. This fine prediction was verified for the digits by Fischer (2013), and for the combined digits and capital letters by Fischer and Koch (2016). There are more left-oriented digits than right-oriented digits (five vs. three), and the right-orienting rule seems more usual than a left-orienting rule in our culture. Therefore, the within-child bi-serial correlation of reversal of any digit with the percentage of reversal in the subsample of other digits, should be greater for the left-oriented digits than for the right-oriented digits. If miswriting in 4–5 year-olds, as studied by Fischer and Thierry (2021), consists primarily in mirror writing, this other fine prediction was verified for the digits 1–5 by these authors.

2 AN EMPIRICAL TEST

Torres et al. (2021) used a complex letter writing task as one of the measure allowing to assess the efficiency of first graders' learning to distinguish a letter and its mirror-image, b and d for example. Their data, which are publically accessible on https://osf.io/643jh/, or, more specifically, the children's writings on https://osf.io/qc8bn/, offer the possibility to test our three models.

2.1 Method

2.1.1 Participants

The data on writing were collected by Torres et al. during three replicas including 32, 60, and 48 first-graders, respectively, with initial mean age 5.99 years (50.7% girls). The children were recruited in Natal (Brazil), and tested in September for the Baseline, in October just after the Intervention, and about 120 days after in February of the following academic year (which starts in February in Brazil). Participants were randomly assigned to one of the two training groups, Training (T) or Training + Sleep (T + S), or one of the two control groups, Control (C) and Active Control (AC). They received a rudimentary phonics lesson on the letters before the baseline tests. Training consisted of multisensory-motor activities aimed to distinguish asymmetrical letters from their mirror version. In the Active Control (AC) group participants received similar multisensory-motor activities as in the training groups but played only with the symmetrical letters (e.g., A–X).

2.1.2 Procedure

In the writing task, participants had to copy the asymmetrical letters b, c, a, f, e, d, g, h, k, s, z, p, and, in Replica three, five additional letters (j, q, r, t, y). The letters were displayed in Arial 90 points (see **Figure 2**). Each child was given a blank sheet of paper divided into squares (one for each copy of the letter). The researcher showed one letter at a time for 3 s, and immediately afterwards the participant had to write the letter blindfolded.

Torres et al. also included a visual discrimination task in which children had to decide if an image (a lowercase letter or an icon) is the same or different from another which was different, the same (though 25% larger) or its mirror, respectively.

2.1.3 Coding

Children's productions were coded and classified into six categories (see **Tables 2**, **3**, also **Figure 2**) by an experienced coder (one of the co-authors): 1) correct (readable); 2) horizontal mirror writing (left–right reversal); 3) vertical mirror writing (upside-down inversion); 4) double mirror writing (horizontal and vertical mirror); 5) other (other character, unreadable, intermediate writing); 6) No response (the corresponding case

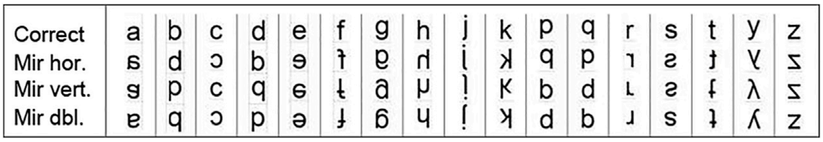

FIGURE 2 | The asymmetrical lower case letters, originally displayed in Arial 90 dots, and their different mirrors: horizontal, vertical, double (both horizontal and vertical).

TABLE 3 | Categorization of the letter-writings in the combined "Immediate after" and "After delay" writing test by the control participants (C + AC).

Letter	Correct writing	Mirror writing	Vertical mirror	Double mirror	Other product	Non-response	Number writings	Percent mirror[a]
b	11	102	0	0	0	0	113	90%
c	96	2	0	0	1	14	113	2%
a	70	2	1	0	11	29	113	3%
f	63	9	1	0	6	34	113	13%
e	79	2	2	2	9	19	113	2%
d	10	96	1	0	4	2	113	91%
g	59	8	7	1	5	33	113	12%
h	70	15	0	0	12	16	113	18%
k	51	11	0	0	16	35	113	18%
s	28	69	0	0	3	13	113	71%
z	11	94	0	0	1	7	113	90%
p	23	82	1	1	2	4	113	78%
j	7	13	0	0	4	10	34	65%
q	10	20	1	0	3	0	34	67%
r	20	1	0	0	8	5	34	5%
t	6	1	0	1	20	6	34	14%
y	24	0	0	0	8	2	34	0%

[a] *Calculated taking into account only writings relevant to the discussion (i.e., horizontal mirror and correct writings).*

was blank). Quality of the writings was not taken into account, as long as a letters' left-right orientation was identifiable. Though they are sometimes difficult to read, this coding of the scanned children's writings generally poses no problem with respect to our primarily concern—reversal of b-d (and p-q).

2.1.4 Hypotheses

With respect to the reversal of the two crucial mirror-letters b and d (the data for mirror-letter q are small), Model 1 predicts confusion or at least non-distinction between b and d. If the children who already know the writing of the letters are excluded, this confusion could then lead children to reverse each letter—b in d and d in b—in 50% of their writings. Consequently, by chance, only 25% of the children should both reverse b (in d) and d (in b). Model 2 does not predict systematic confusion, but b should have the same chance being reversed in d than d in b. Model 3 predicts the reversal of d in b, but not the reversal of b in d. Only the third model allows prediction for the reversal of other individual letters. That is, the left-oriented letters (a, g, z, j, y) should be more reversed than the right-oriented letters (c, f, e, h, k, s, r, t).[2]

Concerning the relationship between the results of the visual discrimination and writing tasks, a logical hypothesis was that visual discrimination of mirrored images correlates with, and even explains for letter-icons, reversal in writing.

2.2 Results

For the Baseline, data of all children in the three replicas can be combined. Thus, we have writings from 117 children for all asymmetrical letters, except for the letters added in Replica 3 (see **Table 2**). The systematic analysis of the available writings of these 117 children, excluding data not relevant to this discussion (non-responses, other graphical productions, non-horizontal mirrors), led to 85% reversals of b (in d), 87% reversals of d (in b). Furthermore, 75% of children reversed both b (in d) and d (in b).

With respect to the non-mirror letters (i.e., excluding b-d and p-q), the weighted mean, in **Table 2**, of the left-oriented letters yields 36% reversal, and that of the right-oriented letters yields 21% reversal. If we look at the letters in a restricted sample of letters, without the mirror-letters and the insufficiently tested letters j, q, r, t, y, the weighted mean percentage reversal of the left-oriented letters yields 41% reversal, whereas that of the right-oriented letters yields 21%. Calculating for each child a percentage of reversal for left- and right-oriented letters, the paired *t*-test confirms the higher reversal of the left-versus right-oriented letters, $t(116) = 7.37$, $p < 0.001$.

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[2] This categorization is consistent with Treiman et al. (2014) assessment on adult students, with the exception of t, which is neutral in Treiman et al.

For the post-intervention writings, we pooled the data from groups C and AC because there was no learning to distinguish an asymmetrical letter and its mirror in these two groups. In addition, we verified, separately for the immediate and long-term tests, that the percentage of mirror reversals did not differ significantly in the C and AC groups (both *p*s > 0.20). We do not analyze the data in the groups T and T + S because there were very few mirror reversals in these groups. We also pooled the data obtained in groups C and AC immediately after learning or 120 days after. **Table 3** shows, in the second to last column, the number of opportunities to write a letter, with each student typically having two opportunities, one in the immediate test and one in the long-term test (but a few children were absent at one of the tests). A posteriori, the legitimacy of our pooling is supported by the very high positive correlation (Pearson's $r = 0.99$) between the mirror writing percentages for the 12 systematically studied letters in the first observation (baseline) and the same percentages calculated with the pooled data.

The percentages of mirror reversal in **Table 3** reinforce those of the baseline data in **Table 2**, since 90% of the b are reversed in d and 91% of the d are reversed in b. In addition, we counted 79% pairs (b, d) reversed in (d, b) in the 113 examined pairs.

With respect to the non-mirror letters (i.e., excluding b-d and p-q), the weighted mean, in **Table 3**, of the left-oriented letters yields 41% reversal, and that of the right-oriented letters yields 21% reversal. If we look at the letters in a restricted sample of letters, without the mirror-letters and the insufficiently tested letters j, q, r, t, y, the weighted mean percentage reversal of the left-oriented letters yields, 43% reversal, whereas that of the right-oriented letters yields 22%.

To answer the question whether visual mirror discrimination is associated with (for the symbolic icons) or explains (for the letters) reversal in writing, we analyzed the relation between the two tasks as follows.

First, we performed a linear regression of the percentage of reversed writings (restricted to the 12 letters tested in all replicates) in the baseline writing task on the number of correctly discriminated mirrored letters. For the 93 participants with data available in both tasks, the explained variance was less than 1% ($R^2_{\text{adj}} = 0.009$), and the effect of discrimination non-significant, $F(1,91) = 1.86$, $p = 0.18$. In contrast, the analogous regression on the number of correctly discriminated mirrored symbols (icons) explained 13% of the variance, $R^2_{\text{adj}} = 0.13$, and was highly significant, $F(1,91) = 14.34$, $p < 0.001$.

Second, with the reversal data in the immediate and long-term tests for the C and AC groups (as in **Table 3**), we performed similar linear regressions in the group of 40 participants with data available in both tasks. The results confirm the precedents. Mirrored letters discrimination does not explain the percentage of reversal in writing, $R^2_{\text{adj}} < 0$, $F(1,38) = 0.23$, $p = 0.63$, whereas mirrored symbols (icons) discrimination does explain it substantially, $R^2_{\text{adj}} = 0.33$, and significantly, $F(1,38) = 19.83$, $p < 0.001$.

2.3 Discussion

Preliminary, we would note that mirror invariance only predicts left-right reversal (horizontal mirror). **Tables 2**, **3** show that horizontal mirroring was indeed, and often considerably, more frequent than vertical or double mirroring. This verification may be complicated by the vertical or double mirror writings that coincide with their correct writing (this is the case for the letters c, s, and z: see **Figure 2**). But it is unrealistic to consider a correct writing as resulting from an inversion or double reversal of the displayed letter. It therefore seems relevant to focus only on horizontal mirror writing (i.e., reversing).

With respect to the models hypotheses for the crucial letters b and d, the results do not confirm the prediction of Model 1, because there are far more than 50% reversals of b and d, separately, in **Tables 2**, **3**. In addition, there are far more than 25% reversals of both b and d, simultaneously. The prediction of Model 3 is also not confirmed as both **Tables 2**, **3** show a very high percentage of b reversals when none were predicted; the prediction of many reversals of d, however, is correct. In fact, only Model 2 remains viable to explain the reversal of both b and d. Indeed, in this model, mirror-imaging arises spontaneously and intrudingly, possibly because the balance between the representations of b and d has been disturbed. Nevertheless, Corballis (2018), using the adverb "sometimes" for such intrusions, doesn't really suggest the observed, almost systematically, reversal of b and d (it is true that he did not consider the very particular conditions of writing used in the research of Torres et al., 2021).

The clear difference between reversal of the left-oriented and right-oriented letters among the non-reversible letters are rather consistent with Fischer and coworker's right orientation rule. The letters mainly contradicting this rule are "a" and "g," which were categorized left-oriented and therefore should be often reversed, and "s," which is categorized right-oriented and therefore should be rarely reversed. These letters suggest that, in fact, it is probably the dynamics of the writing that matters, not the intuitive aspect expressed in the verb "face" or "look towards" (the left for "a" and "g," or right for "s"). For example, given the two components of the handwritten letter "g," we usually starts with the loop and, then, trace the second component (a vertical line, curved at its end) on its right. Thus, the dynamics of writing runs left (the loop) to right (the line). This importance of the dynamics of writing was already noted by Fischer (2013) for the digit 4, which does not clearly face or look towards the right but was nevertheless categorized right-oriented.

The role of the direction of writing must also be taken into account to explain complete mirror writing (i.e., right-to-left writing, each letter being reversed) of the first name (Fischer and Tazouti, 2012; Fischer and Koch, 2016) or other words (Portex et al., 2018), as the sole confusion of mirrored letters cannot explain such complete mirror writing. **Figure 3** illustrates Eddy's name writing at two different times, one under spatial constraints favoring mirror writing (left side of **Figure 3**) and the other in usual writing condition (right side of **Figure 3**). This children's behavioral adaptation to the

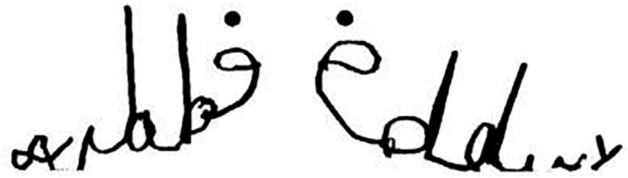

FIGURE 3 | Eddy's writing of his name, at age 6 years and 3 months, with his usual right hand in two different conditions (data from Fischer and Tazouti, 2012); note the reversal of d in b in the left part of the figure.

direction of writing in their culture suggests that the reversal of characters is also driven by underlying latent processes other than inhibition (Huster et al., 2020).

Finally, if reliable[3], the results on the relation between reversal in the writing task and mirrored images discrimination in the visual task are of great importance. This because they strongly support both the hypothesis that good visual discrimination of mirrored letters does not significantly reduce mirror reversal in writing and that the effect of visual discrimination of other mirrored symbols (icons) cannot be interpreted causally. The latter interpretation should be "predictive," not "counterfactual," with the distinction of the interpretation of regression coefficients introduced by Gelman et al. (2021). In a pedagogical perspective, a counterfactual effect would have made it possible to teach image discrimination and, as a result, to expect a reduction of reversal in writing. This is clearly not the case.

3 AN ACCOMMODATED MODEL?

Because none of the three models predicts, or "retrodicts" (McElreath, 2020), the writing data of Torres et al., we sought to develop a model by combining some of their combinable strengths into a model thus qualified as accommodated. The first and third model do not take into account a possible difference between the cerebral hemispheres. Therefore, it is possible to simply accommodate these models in making playing a differential role to the two hemispheres.

In the discussion of Corballis (2018), Fischer and Luxembourger (2018b) do not exclude that the un-oriented representation of the characters in children's memory can be supported by a differential representation of the characters in the two hemispheres. This is not exactly Corballis (2018) theory, which predicts the two representations in both hemispheres. But, since learning of a verbal material is mainly processed in the left hemisphere, we hypothesize that the strength of the mirror-image representation obtained through interhemispheric transfer is stronger in the right hemisphere than the veridic representation (cf., Corballis and Beale, 1993; Corballis et al., 2010)[4]. Thus, we suggest that when children are presented with reversible letters, or some other letters whose orientation is difficult to memorize (mainly the letters z and s, which seem to be reversible if you round the angles of the z and which, in any case, have a symmetry center), they resort to the wrong hemisphere (generally the right). This suggestion seems plausible because, with a model of complementary of the two hemispheres (Badzakova-Trajkov et al., 2016), the visual word form area (VWFA, in the left hemisphere) can recruit resources in the right hemisphere for processing mirror-reversed words when the task demands it (Ryan and Schnyer, 2007). People who are aware of a visual cue activate more the right temporo-parietal junction than people who are not (Wilterson et al., 2021). In pigeons, commissural exchange can compensate hemispheric differences in visual object discrimination and commissural interactions flexibly adjust neural processes of the left and right hemisphere (Xiao and Güntürkün, 2021). In general, visual working memory undergoes developmental changes, becoming relatively more left-lateralized in adult humans (Matejko and Ansari, 2021). Specifically, learning to mirror-read progressed from reliance upon right hemisphere dorsal stream visuo-spatial processes to a reliance upon left-hemisphere ventral stream object recognition processes in the research by Poldrack et al. (1998), and switching from plain text to mirror-reading engaged the right parietal cortex in the research by Jimura et al. (2014). The fact that the children reverse, almost systematically, the letters b and d, and, though less systematically, the letters p, q, z and s, suggest that in this (right) hemisphere the neuronal circuits of b and d representation, and of the other letters are laid down in mirror fashion. In addition, because the letter b was presented first in the Torres et al. (2021) writing test, the wrong hemisphere was initially activated and thus could intervene promptly on a later occasion. For the letters without specific orientation problem (e.g., c–e–r), the children use the other hemisphere (generally the left) and have a less strong representation of their mirror image.

Importantly, this accommodated model does not contradict many specific observations of dyslexic children. For example, that they fail to automatize mirror discrimination during visual object processing (Fernandes and Leite, 2017), or that "children with dyslexia fail to suppress symmetry generalization" (Lachmann and van Leeuwen, 2007 p. 73). Moreover, the accommodated model fits well with Mather (2001) viewing of developmental dyslexia as the outcome of learning to write the alphabet in the non-dominant (right) hemisphere.

However, a major question yet is not answered by this accommodated model: What was the role of blindfolded writing?

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[3] Our reservation comes not only from our surprising observation in the writing task, but also from some flaws in the visual task (in particular, the image-icons, half of which show axial symmetry).

[4] Without such an adaptation, Corballis (2018) theory should be paradoxical. He claims that a perfectly symmetrical organism would be incapable of saying « bee » to a *b* and « dee » to a *d*. Thus, even if an image and its mirror are represented both in the left and the right hemisphere, these representations must differ between the hemispheres.

It is obvious that writing with eyes closed is largely responsible for the curious observation that children invert both b in d and d in b. The finding by Weng et al. (2020) that brain activity may be more unstable with eyes closed than with eyes open is not explanatory, because instability is contradicted by the almost systematic reversal of b and d that we observed. Since the PET study by Kosslyn et al. (1995), we know that the primary visual cortex is activated when subjects close their eyes and visualize objects. Interestingly, Costumero et al. (2020) showed that the functional connectivity of V1 is modulated by the resting-state[5] eye condition and that V1 was positively coupled with the default mode network and sensorimotor network during closed eyes. This advantage of the closed eyes condition results partially from reducing interference from other visual inputs, thereby allowing better concentration on mental images. Indeed, eyes open and closed conditions by themselves are associated with significant changes in functional connectivity. Volitional opening the eyes perturbs the brain dynamics and functional connectivity (Jao et al., 2013; Xu et al., 2014). Closing eyes enhances brain intrinsic activity in the visual networks (Zhang et al., 2019), and increases connectivity in sensorimotor and auditory networks by allowing the brain to focus more on other senses (Agcaoglu et al., 2019). More generally, Xu et al. (2014) describe the eyes as acting as a toggle between exteroceptive and interoceptive networks.

These findings, obtained through fMRI on adult participants in resting-state, often suggest an advantage for brain intrinsic activity in the closed eyes condition. However, contrary to adults, the intrinsic functional networks does not predict cognition in children—preschoolers, early and late school-age children (Zhang et al., 2020). This leads us to verify whether eyes closing advantaged children in behavioral observations. We found only three studies in our search. All tested similarly memory recall in children. Natali et al. (2012) found that eye closure improves 11 years-old children's recall, and Mastroberardino et al. (2012) found the same but only for cued recall in 6 years-old children. The two experiments by Kyriakidou et al. (2014), on 6–12 and 9–13 years-old children, respectively, found inconsistent results. However, the experiment including 6 years-old children confirmed the advantage of the eyes closed condition and the second experiment found no difference between closed and open-eyes conditions. Thus, the eyes closed condition also seems somewhat advantageous in 6 years-old children. Why should then Torres et al.'s blindfolded writing task have a disadvantageous effect, causing systematic reversal of b and d?

Even in usual condition, the visual system must infer which external cause is most likely, given both the sensory data and prior knowledge. Born and Bencomo (2020) argue that this approach to "seeing" makes our visual systems prone to perceptual errors. In the eyes masked condition, the role of top-down feedback in the visual system will be exacerbated. For example, Götz et al. (2017) attributed eye closure disadvantage for spatial discrimination to the requirement of at least one top-down processing stage. A complex activity, such as Torres et al. (2021) letter writing task proposed to children who have already partly memorized the letters, implies certainly top-down processing. In continuity with our accommodated model previously outlined, we speculate that this top-down processing favored the intrusion of the reversed letters (d and b) from the highly activated right hemisphere in children's working visual memory. This top-down influence is consistent with, or at least does not contradict the lower brain activity in sensorimotor system areas in an eyes closed resting-state (Wei et al., 2018) and the increasing homotopic resting-state functional connectivity in sensorimotor regions with age, beginning at age 7 (Zuo et al., 2010).

4 CONCLUSION

The observation in Torres et al. (2021) data—when presented with b the great majority of the children write d, and when presented with d the same children write b—was really surprising: Why do the Brazilian first-graders systematically respond the reversed image (for b and d), rather than the image they have seen, thus following the pigeons (Mello, 1965), the monkeys with sectioned chiasmas (Noble, 1966), and the right hemisphere of the callotomized patient DDV (of Corballis et al., 2010)?

Our curious observation certainly results from the particular task the authors used, mainly from its complexity: copying a letter after a time-limited displaying of the letter (3 s) and, above all, writing without visual control, with eyes masked. This curiosity is exacerbated by the fact that visual discrimination of mirrored letters does not explain—not even correlate with—mirror writing, whereas visual discrimination of other mirrored images (icons) correlates statistically with mirror writing.

None of the three models examined can convincing explain the observation. An accommodated model integrating the fundamental component of Corballis (2018) model, that is, reversal during interhemispheric transfer in memory, accounts for the observed data. This model suggests that, in case of difficulty, children recruit the second (usually right) hemisphere, which—this is a strong assumption of the model—contains a representation of the mirror image, notably of that of the mirror-letters. For letters whose orientation is consistent with the direction of writing and which present no other difficulty, such recruitment is unnecessary and avoids children having to resort to the mirror-image of the letter they have seen, a recourse that leads them to reverse b and d in particular.

However, this accommodated model suffers from the double fact that it is based on a surprising result, which we observed in Torres et al. (2021) data but which has never been replicated (to this day), and that it is the result of an a posteriori construct generally considered to be of low scientific value. A call for replication is therefore required, but may not be heard because

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[5] If one wonders that we refer to resting-state, we would justify this reference with two complementary reasons: 1) With the discovery of the brain's default mode network, research concentrated on resting-state; 2) The brain's default mode network is important because brain's functions are mainly intrinsic and ongoing (Raichle, 2015).

the entire research of Torres et al. (2021) is very complex. Moreover, a restricted research on mirror writing and visual discrimination of symmetrical images alone is terribly frustrating because it would deprive researchers of a possible confirmation of the major and important pedagogical finding of Torres et al., that is, "a simple, low-tech, and accessible method that can efficiently unleash the reading fluency potential of first graders" and thus "can benefit millions of children worldwide" (pp. 8–9).

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: https://osf.io/643jh/https://osf.io/qc8bn.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

JPF analyzed the data, and wrote the first draft of the article. Both authors conceptualized the study, edited the article, and approved the final draft.

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ERP Correlates of Altered Orthographic-Phonological Processing in Dyslexia

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Automatic visual word recognition requires not only well-established phonological and orthographic representations but also efficient audio-visual integration of these representations. One possibility is that in developmental dyslexia, inefficient orthographic processing might underlie poor reading. Alternatively, reading deficit could be due to inefficient phonological processing or inefficient integration of orthographic and phonological information. In this event-related potential study, participants with dyslexia ($N = 25$) and control readers ($N = 27$) were presented with pairs of words and pseudowords in an implicit same-different task. The reference-target pairs could be identical, or different in the identity or the position of the letters. To test the orthographic-phonological processing, target stimuli were presented in visual-only and audiovisual conditions. Participants with and without dyslexia processed the reference stimuli similarly; however, group differences emerged in the processing of target stimuli, especially in the audiovisual condition where control readers showed greater N1 responses for words than for pseudowords, but readers with dyslexia did not show such difference. Moreover, after 300 ms lexicality effect exhibited a more focused frontal topographic distribution in readers with dyslexia. Our results suggest that in developmental dyslexia, phonological processing and audiovisual processing deficits are more pronounced than orthographic processing deficits.

Keywords: dyslexia, N170 effect, position coding, ERP, audiovisual processing, print sensitivity

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INTRODUCTION

Automatic visual word recognition requires not only well-established phonological and orthographic representations but also efficient audio-visual integration of these representations. Most children acquire these skills without any problems; however, around 5–10% of school-aged children fail to develop age-appropriate reading and spelling skills (Schulte-Körne, 2010; Galuschka and Schulte-Körne, 2016; Barbiero et al., 2019). Developmental dyslexia is characterized by a specific impairment in reading despite normal IQ, lack of any specific sensory impairment and adequate education (American Psychiatric Association, 2013). According to the phonological processing deficit hypothesis (Vellutino et al., 2004), the core problem of dyslexia is poor phonological processing which can manifest as impaired grapheme-phoneme mapping (Blomert, 2011). Skilled adult readers typically exhibit automatic grapheme-phoneme mapping wherein presentation of one code activates the other and vice versa (Harm et al., 2004); however, in readers with dyslexia speech-sound associations may never reach automatization (Vellutino et al., 2004). Thus, phonological dyslexia is characterized by impaired pseudoword reading with relatively normal word reading.

Characteristics of reading impairment may vary in dyslexia depending on the orthographic transparency of languages. In opaque orthographies reading accuracy seems to be impaired in dyslexia (English: Landerl et al., 1997; Ziegler et al., 2003), whereas in semi-transparent (German: Landerl et al., 1997; Wimmer and Schurz, 2010; Dutch: Verhoeven and Keuning, 2018) and in transparent orthographies (Spanish: Serrano and Defior, 2008; Italian: Tressoldi et al., 2001; Hungarian: Csépe et al., 2003; Landerl et al., 2013; Mohai, 2014; Finnish: Eklund et al., 2015) mainly slow reading times of pseudowords as well as spelling difficulties (Spanish: Afonso et al., 2015; German: Galuschka and Schulte-Körne, 2016) characterize the impairment. Slow pseudoword reading times may be the result of impaired grapheme-phoneme integration, whereas spelling deficits might suggest an orthographic impairment, as well. To expound this further, we will first review what is known about orthographic processing in dyslexia. Then, we will summarize the orthographic-phonological integration deficit related to dyslexia.

Extensive experience with orthographic stimuli results in highly specialized perception for print. Visually presented orthographic stimuli (e.g., words, pseudowords, consonant strings) evoke a negative peak in adults around 150–200 ms after stimulus onset over occipito-temporal brain regions. This electrophysiological component is called the N1 or N170 response (Bentin et al., 1999) and is considered to be the functional correlate of visual expertise for print. It seems that two levels of print sensitivity exists: (1) a fast, coarse-grade print sensitivity for print indexed by different processing of letter strings compared to control visual stimuli such as symbol strings or false fonts (early N1) and (2) a fine-grade print sensitivity for orthographically familiar letter sequences such as words compared to unfamiliar sequences such as pseudowords or non-words (late N1, see Eberhard-Moscicka et al., 2016).

Letter strings exhibit enhanced N1 response compared to symbol strings or false fonts (Bentin et al., 1999; Maurer et al., 2005a,b, 2010). This coarse-grade sensitivity emerges during reading acquisition. Although this is absent in kindergarten children (Maurer et al., 2005b), it emerges after one year of reading instruction (Eberhard-Moscicka et al., 2015; Varga et al., 2020) and follows an inverted U shape pattern which peaks during reading acquisition and then declines over instruction (Fraga-González et al., 2021). The N1 for print is more pronounced over the left posterior-occipital regions (Maurer et al., 2005a; Yoncheva et al., 2010), and this left lateralization is enhanced with reading experience. According to the phonological mapping hypothesis, the left lateralization is driven by automatized grapheme-phoneme mapping (Maurer et al., 2007). Typically, children show a bilateral effect for letter strings (Maurer et al., 2006; Kast et al., 2010); however, recent studies found that left lateralization can be found as early as one year (Varga et al., 2020; van de Walle de Ghelcke et al., 2021) or even half a year of reading instruction (Pleisch et al., 2019; altough lateralization is less clear for single letters, see Fraga-González et al., 2021).

As the above results indicate that reading acquisition and reading practice heavily influence coarse-grained sensitivity for print, but the presence of this print sensitivity in individuals with dyslexia is widely debated. A number of studies found evidence for attenuated N1 for print in children (Maurer et al., 2007; Araújo et al., 2012) or adults with dyslexia (Helenius et al., 1999; Mahé et al., 2012, 2013), but some studies failed to find any difference in print sensitivity between children (Hasko et al., 2012) or adults with and without dyslexia (Araújo et al., 2015). Studies reporting N1 impairments in dyslexia (Helenius et al., 1999; Mahé et al., 2012, 2013) usually included participants with more severe reading deficits compared to the control group suggesting that the degree of reading and spelling impairments can influence orthographic deficits (Mahé et al., 2012).

The fine-grade sensitivity or lexical sensitivity of the N1 is less robust and more task-dependent than coarse-grade print sensitivity. Some studies found greater N1 for pseudowords compared to words (Sereno et al., 1998; Hauk and Pulvermüller, 2004; Hauk et al., 2006; Dujardin et al., 2011; Araújo et al., 2015), while some others found greater N1 for words compared to pseudowords (Maurer et al., 2006; Kast et al., 2010; Eberhard-Moscicka et al., 2016; Faísca et al., 2019) suggesting that top-down linguistic information modulates early orthographic processing. Contrary to these results, other studies failed to find differences between the processing of word and pseudoword stimuli (Maurer et al., 2005b; Araújo et al., 2012; Hasko et al., 2013; Eberhard-Moscicka et al., 2015, 2016) suggesting that the N1 component arises at the prelexical stage of orthographic processing and is sensitive to orthographic but not to lexical constraints. The inconsistency of results probably arises due to developmental effects (adolescent: Araújo et al., 2012; grade 2: Maurer et al., 2006), differences between orthographic transparency of the language investigated (French: Bentin et al., 1999; English: Maurer et al., 2005a; Hauk et al., 2006; German: Maurer et al., 2005b), and task demands (Maurer and McCandliss, 2007; Faísca et al., 2019). Maurer and McCandliss (2007) proposed that word vs. pseudoword differences emerge when grapheme-phoneme mapping is not automatic. This argument is supported by results that show N1 fine tuning mainly in implicit reading tasks where grapheme-phoneme mapping is not required. In addition, even in these tasks, fine tuning is mostly present for readers of deep orthographies like English (Maurer et al., 2005a) and novice readers (Maurer et al., 2006).

Previous results on readers with dyslexia are even more ambiguous. For instance, 7 years old children with dyslexia showed decreased N1 amplitude to pseudowords but not to words compared to controls in one study (Wimmer et al., 2002), while adult with dyslexia showed similar lexicality effect as typical readers in another (larger N1 for pseudowords compared to words, Araújo et al., 2015). Furthermore, the results of Mahé et al. (2012) suggest that skilled adult readers show lexicality effect in the left hemisphere, while adults with dyslexia showed no lexicality effect. Finally, Kast et al. (2010) found that typically developing children showed enhanced N1 amplitude for words compared to pseudowords in a lexical decision task.

In comparison, children with dyslexia showed the opposite pattern of results, pseudowords elicited greater N1 than words. This could signify the enhanced effort to decode unfamiliar orthographic strings (pseudowords) in dyslexia. What seems to be less ambiguous, however, is that the N1 effect is usually less left-lateralized in readers with dyslexia than in skilled readers (adults: Helenius et al., 1999; Mahé et al., 2012; children: Kast et al., 2010; Araújo et al., 2012, but see Fraga-González et al., 2014).

On the other hand, for skilled reading it is not sufficient to efficiently categorize visual stimuli. Expert readers automatically identify letters and encode their position in the words they read (Grainger, 2008). This is essential in order to successfully recognize words from among the visually similar candidates (so called orthographic neighbors). For instance, to correctly recognize the word "CALM" readers must identify each letter and inhibit (substituted letter) neighbors like "CALF" or "PALM." In addition, readers also need to process letter positions to inhibit (transposed letter) neighbors like "CLAM." The latter can be problematic even for skilled readers as they sometimes confuse transposed letter words (transposed-letter effect, see Grainger, 2008). In fact, Castles et al. (2007) found that sensitivity to letter identity and letter position changes as a function of reading development. While third graders tolerate both letter identity and position mismatch between letter strings, fifth graders are sensitive to letter identity changes but still insensitive to letter position changes. Similarly, Tóth and Csépe (2017) demonstrated that children through 2nd to 4th grade show improvement in sensitivity for letter identity but not for letter position encoding.

There are two components (N1 and N250) reported in the literature that seem to capture fine orthographic differences between word pairs. First, between 100 and 200 ms after stimulus onset, the N1 component is believed to reflect visual perceptual discrimination (Vogel and Luck, 2000). In this time window, the degree of visual overlap between the prime and target items modulates ERP responses (Grainger and Holcomb, 2009; Duñabeitia et al., 2012). Thus, differences in letter identity or letter order between word pairs might result in an increased N1 response as these differences decrease the visual overlap between the word pairs. Indeed, this seems to be the case. For example, Cao et al. (2015) showed greater N1 for different word pairs than for identical word pairs. Furthermore, Duñabeitia et al. (2012) found greater N1 for targets including letter substitution compared to targets including letter transpositions. This later result suggests that letter substitution is visually more salient than letter transposition.

Second, a component between 200 and 325 ms is also sensitive to orthographic overlap (Grainger and Holcomb, 2009). The N250 peaks at around 250 ms and its distribution is largest over midline and anterior left sites. Holcomb and Grainger (2006) found for instance that N250 is greater when prime-target pairs differ in one-letter (substitution) than when they completely overlap (identical). Moreover, Duñabeitia et al. (2012) demonstrated a larger N250 for substituted letter strings in a same-different task compared to transposed letter strings (see also Dunabeitia et al., 2009). Finally, Holcomb and Grainger (2006) presented primes to their participants that could be identical, different in one substituted letter or completely different from the target. While only differences at the global word-form level were detected (identical vs. completely different pairs) in the N1 time-window (125–175 ms), finer word-form differences (identical vs. substituted letter pairs) modulated the N250 (175–300 ms) and the N400 (400–550 ms) components, too. The authors concluded that the ERP correlate of letter processing is the N250 component.

Although a number of studies examined orthographic processing in skilled readers, much less experiments investigated these processes in reading disorders. In their study, Ogawa et al. (2016) found impaired orthographic processing in adults with dyslexia. While typically reading Japanese children showed the Stroop effect for real words and their transposed-letter pseudoword pairs, readers with dyslexia showed the Stroop effect for real words only which suggests orthographic processing deficits. In another experiment Reilhac et al. (2012) compared the performance of children with and without dyslexia on a same-different task. Responses were more accurate when two letters were substituted rather than transposed in both groups. This substitution advantage was found in controls regardless of the lexicality of the letter string and was somewhat larger for pseudowords than word, but the effect was only present for words in children with dyslexia. In sum, it seems that readers with dyslexia have deficits in letter identity and position processing (Reilhac et al., 2012; Ogawa et al., 2016), but to our knowledge, no previous studies examined the electrophysiological correlates of letter identity and letter position encoding in individuals with dyslexia.

Though it seems that visual sensitivity for print (Maurer et al., 2007; Kast et al., 2010; Araújo et al., 2012; Mahé et al., 2012) and fundamental orthographic processes like letter identity and letter position encoding (Reilhac et al., 2012; Ogawa et al., 2016) can be affected in dyslexia, phonological deficits are usually more severe (Blomert, 2011; Lété and Fayol, 2013). In addition, even orthographic processes are thought to be tuned by phonology (Maurer and McCandliss, 2007; Meade, 2020); therefore, comparing deficits in orthographic processing and deficits in the integration of orthographic and phonological information is crucial.

In fact, numerous studies point to an audiovisual (AV) integration deficit in dyslexia (Froyen et al., 2011; Mingjin et al., 2012; Mittag et al., 2013; Hasko et al., 2014; Kronschnabel et al., 2014; Žarić et al., 2015; Wang et al., 2020; for a review see: Blomert, 2011). For instance, Froyen et al. (2011) reported that 11 year old children with dyslexia do not exhibit automatic integration of letters and sounds as measured by the mismatch negativity (MMN) between 100 and 250 ms in contrast to their typically developing peers (Froyen et al., 2009). Another study found (Žarić et al., 2014) that in an audiovisual oddball task deviant vowels elicited typical mismatch responses in the auditory condition even in 9-year-old children with dyslexia; however, the mismatch responses were reduced in the AV condition. In fact, children with severe dyslexia showed a small mismatch effect in the N1 time window, while less dysfluent and typical readers showed a mismatch effect in both the N1 and P2 time windows. In addition, the latency of the

MMN response was related to individual differences in reading fluency indicating impairment in grapheme-phoneme mapping. Furthermore, Žarić et al. (2015) demonstrated that the MMN latency is also related to reading gains after an extensive letter-speech sound mapping training providing further evidence for the role of deficient orthographic-phonological integration in dysfluent reading.

Although several studies provide insight into the deficits of AV integration of single letters, less is known about the AV integration of letter strings and spoken words. To investigate the latter, Kronschnabel et al. (2014) tested the audiovisual integration deficit in dyslexia by presenting congruent and incongruent three-letter audiovisual stimuli in an implicit target detection task. Although the EEG data did not reveal group differences in audiovisual integration, fMRI data indicated impaired processing of audiovisual stimuli. Moreover, despite no group differences were found during single letter processing in the EEG data, the AV integration deficit was pronounced for three-letter long strings indicating specific deficits in processing word-like stimuli (see also Mittag et al., 2013).

Moreover, a study by Jost et al. (2014) tested AV integration by presenting first-grade readers with familiar German or unfamiliar English written words along with congruent (identical) and incongruent (all letter different) auditory words. Children showed a congruency effect but only for familiar German words suggesting that the effect is modulated by lexical-semantic information. To advance results on audiovisual processing of written words, Wang et al. (2020) presented first-grade readers with congruent and incongruent audiovisual pseudowords in their fMRI study. Children did not show a congruency effect in first grade, but when re-measured in second-grade, a congruency effect emerged, and the development of the effect was related to the pseudoword reading fluency.

While it seems that both audiovisual and visual/orthographic processing can be deficient in developmental dyslexia, the relationship between the two processes should be considered, as well. As McCandliss et al. (2003) argue, the development of brain areas responsible for multimodal integration modulates the tuning of visual areas for print. In addition, the phonological mapping hypothesis (Maurer et al., 2007) also proposes that the left hemispheric lateralization of word N1 is due to automatized grapheme-phoneme integration. In line with this, several studies found association between grapheme-phoneme mapping and visual sensitivity for print. For instance, Brem et al. (2018) demonstrated that sensitivity for a novel script emerges in a two h character-sound association training regardless whether novel visual stimuli are trained with spoken syllables or spoken words which suggests that training related modulation of the visual N1 is due to phonological associations. Furthermore, in a series of experiments, Maurer and colleagues (Maurer et al., 2010; Yoncheva et al., 2010, 2015) explicitly compared the modulation of print N1 after a grapheme-phoneme focused training and a whole word focused training. The grapheme-phoneme mapping training resulted in left-lateralized N1 response whereas the whole word training resulted in right-lateralized N1 response. Even more interestingly, Fraga-González et al. (2017) reported that audiovisual integration as indexed by the MMN latency was correlated with changes in the visual N1 for words after reading fluency training in children with dyslexia. The result suggests that the severity of audiovisual integration deficit and the level of visual sensitivity for print are related and together with the above results provides further evidence that audiovisual integration might modulate print sensitivity.

Lastly, Hasko et al. (2012) explicitly tested the contribution of orthographic processing deficit and audiovisual integration deficit to reading disfluency by comparing the ERP responses of children with and without dyslexia in a visual-visual and an auditory-visual condition. The researchers found that 11 years old children with developmental dyslexia showed different N300 responses compared to control children for stimuli requiring orthographic-phonological mapping. In addition, the N300 response correlated with reading fluency. However, the groups did not differ in processing visual stimuli, which only requires orthographic processing. Similarly, children with and without dyslexia did not differ in their N170 responses, which suggests that reading deficits in dyslexia might be traced to inefficient integration of orthographic and phonological information rather than orthographic processing deficits. Nonetheless, the above study used only real words as stimuli and the task was confounded with phonological working memory skills since children had to hold the auditory reference stimulus in memory to be able to compare it the visual target stimulus.

In the current study, we aim to explore audiovisual processing of orthographic stimuli by adult readers with and without dyslexia in an implicit same-different (perceptual matching) task. Experimental paradigms used previously (such as the one-back task or the explicit same-different perceptual-matching task) are often confounded by working memory and attentional factors because participants are required to pay attention to differences between the stimulus pair. Therefore, differences between participants with and without dyslexia can result from differences in memory skills or attentional span. In our implicit same-different task, memory bias is excluded by analyzing the N1 responses to the reference stimuli and by presenting the auditory and visual stimuli concurrently in the audiovisual condition. Moreover, participants were instructed to indicate when a stimulus appeared in bold fonts; thus, the paradigm does not require reading. Furthermore, our paradigm made it possible to explore the main processes that were found to be inefficient in developmental dyslexia (fine-grade print sensitivity as indexed by the lexicality effect, orthographic coding as indexed letter identity and position coding, and audiovisual integration) in one single study.

First, we investigated whether (1) orthographic processing deficits are present in dyslexia for both words and pseudowords. Since previous studies demonstrated a lexicality effect on N1 in skilled readers but not in readers with dyslexia, we expected to find differential N1 response modulation as a function of lexicality and reading skill. Then, we examined whether (2) inefficient orthographic processing could be traced by measuring decoding of letter identity and position. To this end, participants were shown stimulus pairs that could be either identical (ID), different in the identity of one letter (letter identity neighbor, IN), or different in the position of the letters (letter position pairs, PP).

Previous studies reported deficits in letter identity and position processing in readers with dyslexia; therefore, we expected to find differential effect of the pair type on the N1, N250 as a function of reading skill. Finally, to explore whether (3) orthographic-phonological processing is more deficient than orthographic processing in dyslexia, target stimuli were presented in visual-only and audiovisual conditions. We expected to find differential effects of lexicality and pair type as a function of reading skill and modality already on the N1 and N250 components. More specifically, we expected that group differences would be greater in the audiovisual condition compared to the visual only condition.

MATERIALS AND METHODS

Participants

Twenty-seven high functioning readers with dyslexia (DL) and 31 control readers (CL) participated in the experiment; however, two participants from the dyslexia group and four participants from the control group were excluded from the analysis due to low numbers of accepted trials per condition (see details in the EEG recording and data preprocessing section). Finally, 25 participants with dyslexia [10 female, mean age 21.12 years, *SD* = 3.78, range = 18–34 years, five left-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971)] and 27 control participants (15 female, mean age 21.89 years, *SD* = 2.89, range = 18–28 years, all right handed) were included in the analysis. All participants were native Hungarian speakers and had normal or corrected-to-normal vision and intact hearing according to the screening audiometry (250–8,000 Hz). Participants with dyslexia were recruited through advertisements. All of them had been diagnosed with dyslexia during childhood and completed remediation training with a speech therapist. None of the participants except for one had a clinical diagnosis of ADHD. Control participants had no history of reading disorders. Participants' informed consent was obtained in written form from all participants, and the experimental protocol was approved by the United Ethical Review Committee for Research in Psychology.

Individual Differences Measures

Prior to the EEG experiment, the reading-related skills of all participants were assessed through the Hungarian version of the Differential Diagnosis Dyslexia Battery (Tóth et al., 2014). Reading fluency was measured by three subtasks: high-frequency word reading, low-frequency word reading, and pseudoword reading. The *reading fluency* score was calculated from the three subtasks as the correctly read items per second. The *reading accuracy* score was calculated from the three subtasks as the correctly read items. In addition, *rapid automatized naming (RAN)* with letters, digits, and objects and the *phoneme deletion* were measured, as well.

In addition, we measured s*entence reading fluency* with an in-house task in which participants read a list of 40 sentences and indicated whether the sentence's meaning is true or false. As the sentences are semantically very simple; reading speed is determined by word reading fluency rather than reading comprehension. Thus, the sentence reading fluency score was calculated as the mean log reaction time for correctly answered sentences.

To assess orthographic knowledge, participants were presented with a list of 42 sentences in a *proofreading* task. They were instructed to quickly click on the misspelled word with the mouse in every sentence. The misspellings were of three types: (1) two letter were transposed (TL), (2) one letter was substituted with another letter from the alphabet (SL1), (3) two letters were substituted with another letter from the alphabet (SL2). The proofreading score was calculated as the mean log reaction time for the correctly identified misspelled words.

Spelling was measured with an in-house multiple choice spelling test. Altogether 44 items were presented; participants used the mouse to indicate their response. Two scores were calculated: spelling accuracy (mean correct percent of responses) and spelling reaction time (mean log RT). Descriptive statistics for the groups are presented in **Table 1**.

Stimuli

In the EEG session, we employed an implicit same-different task which included blocks of word, pseudoword, character, and digit stimuli. Here we focus on words and pseudowords because only these stimuli were presented both in a visual and an audiovisual condition. Thus, two types of stimuli were used: 360 word pairs and 360 pseudoword pairs.

One hundred and eight base words were selected from the Hungarian National Corpus (HNC, Váradi, 2002) that had two different word pairs: (1) a word that differed in the position of the letters and (2) a word that differed in the identity of one letter. Thus, the reference-target pairs could be either identical (ID, e.g., MANGÓ-MANGÓ [mango]), or different in one substituted letter (letter identity neighbor, IN, e.g., MANGÓ-MARGÓ [mango-margin]), or different in the position of their letters (letter position pairs, PP, e.g., MANGÓ-MAGNÓ [mango-tape recorder]). The words were mono- and bisyllabic and did not contain digraphs or trigraphs. Mean log bigram frequency (and standard deviation) of the base words was 13.64 (1.33). In addition, 12 word triplets were selected to serve as filler items. This resulted in 360 word pairs among which 120 were three letters, 120 were four letters, and 120 were five letters long.

In addition, 108 pseudowords triplets of 3–5 letter length were created to match the word triplets. From each of the base words described above, three pseudowords were created by changing letters in the base word. The resulting pseudowords were not part of the HNC or the CELEX database. The pseudowords could be either identical (ID, e.g., ZONAT-ZONAT—from the base word "vonat" [train]), different in one substituted letter (IN, e.g., ZONAT-BONAT), or different in the position of their letters (PP, e.g., ZONAT-TAZON). Mean log bigram frequency (and standard deviation) of the pseudowords was 13.24 (1.47). In addition, 12 pseudoword triplets were created to serve as filler items. This resulted in 360 pseudoword pairs altogether (120 were three letter, 120 were four letters, and 120 were five letters long).

The word pairs and pseudoword pairs were also presented in an audiovisual condition. Thus, the target stimuli were presented visually together with an auditory stimulus. The auditory stimuli

TABLE 1 | Descriptive statistics of participants with and without dyslexia and group differences (*t*-test).

	Dyslexia (*n* = 25)		Control (*n* = 27)		*t*-value*
	Mean	**SD**	**Mean**	**SD**	
Age (years)	21.12	3.78	21.89	2.89	−0.82
Reading Fluency (item/s)	0.76	0.32	1.27	0.31	−5.84***
Reading accuracy (%)	93.16	6.38	97.36	3.3	−2.94
RAN Letter (item/s)	2.18	0.41	2.60	0.38	−3.85**
RAN Number (item/s)	2.37	0.46	2.90	0.45	−4.21**
RAN Object (item/s)	1.57	0.24	1.72	0.28	−2.09
Phoneme deletion accuracy (%)	86.23	13.59	96.99	4.82	−3.75**
Phoneme deletion speed	7.85	0.35	7.41	0.27	5.03***
Sentence reading fluency[a]	8.06	0.34	7.60	0.21	5.92***
Proofreading[b]	8.45	0.43	7.64	0.27	7.97***
Spelling accuracy (%)	47.01	7.35	62.98	12.41	−5.62***
Spelling speed	8.19	0.3	7.73	0.21	6.34***

Accuracy scores are presented as percent correct. Speed measures are expressed as log reaction times. Reading Fluency is expressed as the correctly read items per second; therefore, higher fluency score indexes faster reading.

[a] Data is missing for one participant.

*[b] Data is missing for three participants. *p < 0.05, **p < 0.01, ***p < 0.001 after Bonferroni correction.*

were digitally recorded from a male native Hungarian speaker in a soundproof room (sampling rate was 44.1 kHz presented to both ears via headphones (AKG K401) with an intensity of approximately 75 dB. Sound duration was 697 ms (*SD* = 112.96 ms, range = 444.81−1052.15 ms) for words and 683 ms (*SD* = 106.97 ms, range = 431.81−1040.54 ms). The auditory stimuli were identical to the visually presented target stimuli; therefore, for the IN and PP pairs, there was a mismatch between the visual reference and visual target and the visual reference and auditory target. The number of graphemes and phonemes in the visual and auditory stimulus were always identical. To counterbalance the stimulus presentation across conditions, two stimulus lists were prepared. In each list, half of the word (180 pairs) and half of the pseudoword (180) pairs were presented visually whereas the other half of words (180 pairs) and pseudoword (180) pairs were presented audiovisually. Thus, the lists equated lexicality (w/pw) and modality of presentation (V/AV).

Overall, 720 stimulus pairs were presented: 648 reference-target pairs and 72 filler pairs. The reference stimuli were always presented only visually, while half of the target stimuli were presented only visually (V), and the other half was presented audio-visually (AV). Stimuli were presented in 12 separate blocks according to modality (V/AV), lexicality (w/pw) and length (3/4/5 letter long). Order of the word and pseudoword blocks were randomized across participants. Visual blocks always preceded audiovisual blocks in order to avoid carry-over effects from the enhanced grapheme-phoneme mapping in the AV condition.

In each block, there were 60 stimulus pairs among which 54 were reference—target pairs and six were filler pairs. Filler items accounted for 10% of all trials and were not included in the analysis. The number of identical, transposed-letter, and substituted-letter trials was balanced within and across blocks. The order of stimuli was randomized within and across blocks. The full stimulus list is presented in **Supplementary Table 1**.

Procedure

During the EEG experiment, participants were individually tested in a soundproof, electrically shielded room. Stimulus presentation and response recording was carried out with Presentation 15.1 software; all stimuli were presented on a 22" LED computer screen with a refresh rate of 60 Hz positioned at a distance of 70 cm from the participants. The target stimulus of the filler pairs was presented in bold, and participants were required to indicate the appearance of these items by pressing a button. Before the first block of word and first block of pseudoword stimuli, there were four practice trials among which one was presented in bold. All stimuli were presented in black capital letters in DejaVu Sans Mono font on a blue-gray background. Reference stimuli were 28 font-size, whereas target stimuli were 32 font-size; targets of filler pairs were presented in bold fonts.

Each trial (see **Figure 1**) started with a blank screen displayed for 400 ms followed by a 24 font-size fixation cross at the middle of the screen for 600 ms. Then, the reference stimulus was displayed for 1,300 ms followed by a blank screen for 100 ms. Finally, the target stimulus was displayed for 1,500 ms. In the AV condition, an auditory target stimulus was also presented synchronized to the onset of the visual target stimulus.

EEG Recording and Data Preprocessing

Data was recorded with a 32-channel Easy Cap (EASYCAP GmbH, Herrsching, Germany), electrodes were positioned according to the international 10–20 system guidelines. The EEG was recorded continuously with a Cz reference, a 1,000 Hz/channel sampling rate, and a 0.01–100 Hz bandpass filter. Electrode impedances were kept below 10 kΩ. Data preprocessing was performed with Brain Vision 2.0 software

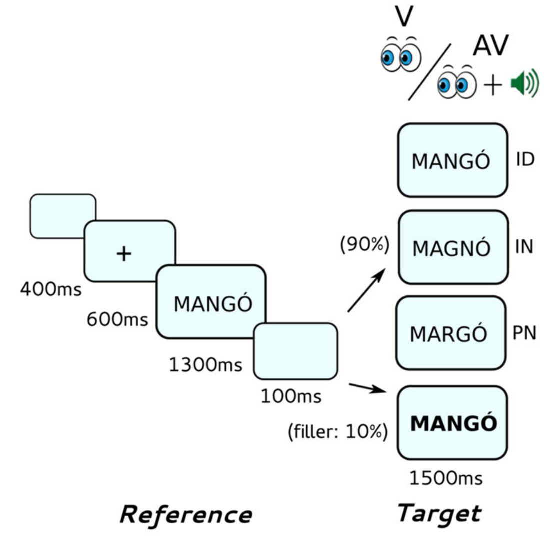

FIGURE 1 | Outline of the same-different implicit reading task. Reference stimuli were always presented visually, target stimuli were presented either visually only (V) or audiovisually (AV). Target stimuli could be either identical (ID), different in the identity of one letter (IN) or different in the position of letters (PP) compared to the reference stimuli.

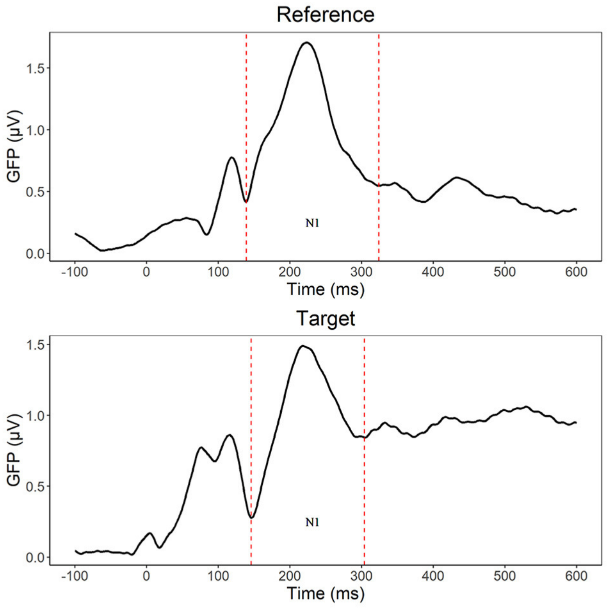

FIGURE 2 | N1 segmentation (dashed line) based on Global Field Power (GFP) separately for reference (139–324 ms) and target (146–304 ms) stimuli.

(Brain Products GmbH). First, data was filtered (0.1—30 Hz zero-phase Butterworth IIR bandpass filter, 24 dB/oct). Next, eye movements were corrected with ICA (Jung et al., 2000). The mean number of ICs and standard deviations (in parenthesis) corrected were 3.11 (1.89) for the control group and 3.6 (1.85) for the group with dyslexia. Then, data were baseline corrected (100 ms prior stimulus presentation), segmented into 600 ms epochs, and re-referenced to average reference (Lehmann and Skrandies, 1980). Finally, trials containing artifacts exceeding +/− 200 µV were rejected; the maximum-minimum voltage difference was 200 µV. In each condition, at least 38 (out of 54) artifact-free trials were required to include a participant in the analysis. Mean trial numbers and standard deviations (in parenthesis) were as following: word reference stimuli: 52.89 (1.88) for CL, 52.54 (2.09) for DL; pseudoword reference stimuli: 52.87 (1.77) for CL and 52.63 (1.99) for DL; visual word targets: 52.56 (2.08) for CL [ID: 52.44 (1.72), IN: 52.81 (2.27), PP: 52.41 (2.26)] and 52.88 (1.68) for DL [ID: 53.2 (1.35), IN: 52.72 (2.19), PP: 52.72 (1.37)]; visual pseudoword targets: 52.37 (2.84) for CL [ID: 52.58 (2.36), IN: 52.30 (3.18), PP: 52.33 (3.03)] and 52.35 (2.58) for DL [ID: 51.52 (3.38), IN: 52.6 (2.14), PP: 52.92 (1.85)]; audiovisual word targets: 52.90 (1.74) for CL [ID: 52.96 (2.23), IN: 52.78 (1.67), PP: 52.96 (1.26)] and 52.47 (2.40) for DL [ID: 52.16 (3.45), IN: 52.68 (1.68), PP: 52.56 (1.71)]; audiovisual pseudoword targets: 52.93 (2.05) for CL [ID: 52.82 (2.32), IN: 53.19 (2.24), PP: 52.78 (1.58)] and 52.43 (2.39) for DL [ID: 52.4 (2.30), IN: 52.36 (2.63), PP: 52.52 (1.69)]. The acceptable trials were averaged for participants and conditions.

Data Analysis

Data analysis was carried out using the eegR package (Tóth, 2015) available in the R environment (R Core Team, 2013). To assess the processing of word and pseudoword pairs, a Topographic Analysis of Variance (TANOVA, Lehmann and Skrandies, 1980; Strik et al., 1998) on ERP maps was computed for each time point. This approach treats ERP data as a sequence of ERP maps changing in topography and strength over time (Lehmann and Skrandies, 1980) and is sensitive to differences at particular electrodes without specifying them. ERP map strength can be characterized by the Global Field Power (GFP), which is the standard deviation of the potentials at all electrodes of an average-reference map. ERP map topography can be calculated as the difference of normalized maps (global map dissimilarities, GMD). While TANOVA on raw maps detects all systematic amplitude (GFP) differences between the maps, TANOVA on normalized maps detects only topographic differences (GMD).

In our data analysis, we ran point-to-point TANOVAs to determine whether experimental effects are due to differences in intensity (GFP) or topography (GMD). We computed GFP and GMD for each time-point, created a probability distribution (with $n = 4{,}999$ L permutation in order to control for multiple comparisons, permuted p-value, P_{perm}), and calculated a z-score of the original dissimilarity. We report the median values of z-scores and permuted p-values for those data points, which were significant at the level of 0.05.

ERP data were analyzed separately for reference and target stimuli. Reference stimuli were analyzed in a repeated measure point-to-point TANOVA with lexicality (w/pw) as a within-subject factor and with group (DL/CL) as a between-subject factor. Target stimuli were analyzed with lexicality (w/pw), modality (V/AV), and pair type (ID/IN/PP) as within-subject factors and with group (DL/CL) as a between-subject factor.

To compare the effects in the different modalities, we also ran analysis for the V and AV conditions separately.

To ease the comparison of our results with previous studies, we also performed traditional ERP analyses. Adaptive segmentation based on the GFP minima (Maurer et al., 2005b) was done for the grand averaged means. GFP was calculated separately for the reference and target pairs for adults with and without dyslexia in the time range of 0–600 ms (averaged for lexicality, pair type, and modality).

For the reference stimuli, we used repeated measures ANOVA with group (DL/CL) as between- subject factors, whereas lexicality (w/pw) and laterality (left/right) served as within-subject factors. According to the GFP segmentation, in the N1 segment, control readers exhibited the most activity at 138–337 ms (peak: 227 ms), whereas participants with dyslexia had greater activity at 140–276 ms (peak: 215 ms). Since the segmentation resulted in similar time windows for the groups, the rest of the analysis will use the general segmentation of the stimuli (139–324 ms, peak: 223 ms).

For the target stimuli, we also used repeated measures ANOVA with the same factors as in the analysis of reference stimuli, but also added the within- subject factors pair type (ID/IN/PP) and modality (AV/V). According to the GFP segmentation (see **Figure 2**), the GFP window for control group is at 147–305 ms (peak: 218 ms), whereas the time window for the group with dyslexia is at 146–290 ms (peak: 218 ms). Again, analysis will use the general segmentation of the stimuli (146–304 ms, peak: 218 ms, V targets: 140–304 ms, peak: 231 ms, AV targets: 154–292 ms, peak: 216 ms). For the letter identity and position encoding analyses, aside from the occipito-temporal sites used in the reference stimuli, we used channel clusters from the frontal-central channels (F3, P3, C3, Fz, Cz, Pz, F4, P4, C4 based on Duñabeitia et al. (2009). Lastly, we used the Greenhouse-Geiser correction to adjust critical *p* values when the assumption of sphericity is violated.

RESULTS

Behavioral Results

Filler items were included only to maintain attention during the experiment; thus, responses for these items were excluded from the EEG analysis. Mean hit rates were 0.999 ($SD = 0.001$) for the dyslexia and 0.996 ($SD = 0.008$) for the control group.

Lexicality Effect

To compare whether lexicality (word and pseudoword processing) effect occurred for both groups, we analyzed the reference stimuli (which were always presented visually).

In the GFP analysis, no effect reached the significance level (group: z-score = 0.96, $P_{\text{perm}} = 0.668$; lexicality: z-score = 0.69, $P_{\text{perm}} = 0.487$; group x lexicality: z-score = 0.51, $P_{\text{perm}} = 0.491$).

According to the GMD analysis, topography did not differ as a function of lexicality (z-score = 0.67, $P_{\text{perm}} = 0.416$) or group (z-score = 1.37, $P_{\text{perm}} = 0.101$). The group x lexicality interaction did not reach the significance level (z-score = 0.76, $P_{\text{perm}} = 0.574$). GFP curves and topographic maps are presented on **Figure 3**.

The traditional analysis in the reference stimuli (139–324 ms) showed a significant effect of laterality [$F_{(1, 50)} = 9.80$, $p = 0.003$, $\eta_g^2 = 0.03$] while the main effects of group [$F_{(1, 50)} = 2.61$, $p = 0.113$, $\eta_g^2 = 0.04$] or lexicality [$F_{(1, 50)} = 0.95$, $p = 0.334$, $\eta_g^2 = 0.001$] were not significant. In addition, laterality interacted with group [$F_{(1, 50)} = 5.82$, $p = 0.020$, $\eta_g^2 = 0.02$] (**Figure 4**) since a significant effect of laterality was observed only in controls [$F_{(1, 26)} = 14.04$, $p < 0.001$, $\eta_g^2 = 0.08$] due to greater responses in the left hemisphere, whereas the participants with dyslexia did not show any difference between the hemispheres [$F_{(1, 24)} = 0.21$, $p = 0.651$, $\eta_g^2 = 0.002$]. Meanwhile, group x lexicality [$F_{(1, 50)} = 3.27$, $p = 0.0766$, $\eta_g^2 = 0.004$], lexicality x laterality [$F_{(1, 50)} = 0.03$, $p = 0.870$, $\eta_g^2 = 0.000002$], or group x lexicality x laterality interaction [$F_{(1, 50)} = 0.13$, $p = 0.720$, $\eta_g^2 = 0.00001$] did not reach significance.

In sum, controls exhibited a more left-lateralized N1 compared to the group with dyslexia. Nevertheless, words and pseudowords are processed similarly, and readers with and without dyslexia do not differ in processing orthographic stimuli in the N1 time window.

Letter Identity and Position Encoding

To test whether readers with dyslexia process letter identity and position inefficiently, we analyzed the pair type effect (ID/IN/PP), the lexicality effect (w/pw), and the group effect (DL/CL) in the visual targets.

In the GFP analysis, the main effect of group (z-score = 3.31, $P_{\text{perm}} = 0.004$) between 185 and 380 and 493 and 600 ms indicated that controls showed greater responses than readers with dyslexia. The main effect of lexicality (z-score = 3.46, $P_{\text{perm}} = 0.005$) between 311 and 400 ms was present as word stimuli evoked greater responses than pseudoword stimuli. There was also a main effect of pair type (z-score = 3.11, $P_{\text{perm}} = 0.005$) between 144 and 235 ms and 455 and 600 ms. Based on visual inspection and the traditional analysis below, in the early time-window (144–235 ms), ID targets evoked smaller responses compared to PP or IN pairs. In the later time window (455–600 ms), IN targets evoked smaller responses than ID or PP targets. This was the case for the participants both with and without dyslexia signified by the lack of significant interactions (group x lexicality: z-score = 0.82, $P_{\text{perm}} = 0.416$, group x pair type: z-score = 0.61, $P_{\text{perm}} = 0.609$, lexicality x pair type: z-score = 0.62, $P_{\text{perm}} = 0.550$, group x lexicality x pair type: z-score = 0.67, $P_{\text{perm}} = 0.545$).

In the GMD analysis, the main effect of group (z-score = 4.49, $P_{\text{perm}} < 0.001$) between 255 and 600 ms and the main effect of pair type (z-score = 3.03, $P_{\text{perm}} = 0.006$) between 89 and 129, 142 and 206 and 273 and 600 ms was significant. Group effect was present because controls exhibited more left-lateralized responses than readers with dyslexia. Pair type effect in the early time window (142 and 206 ms) resulted from the different scalp topographies of ID vs. IN. Pair type effect in the late time window (273 and 600 ms) resulted from the different scalp topographies of ID vs. IN, ID vs. PP, and IN vs. PP pairs. No other effects were

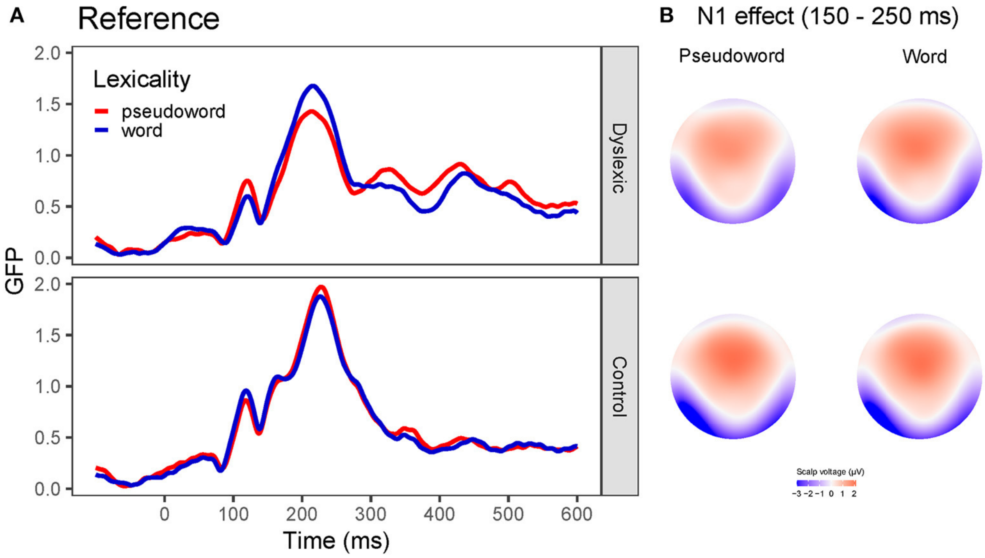

FIGURE 3 | Global field power (GFP) curves and topographic maps for the reference stimuli. Note that reference stimuli were always presented visually. **(A)** GFP for the word and pseudoword stimuli separately for the dyslexia and control group. **(B)** Topographic maps for the N1 effect for the word and pseudoword stimuli separately for the groups with and without dyslexia averaged between 150 and 250 ms.

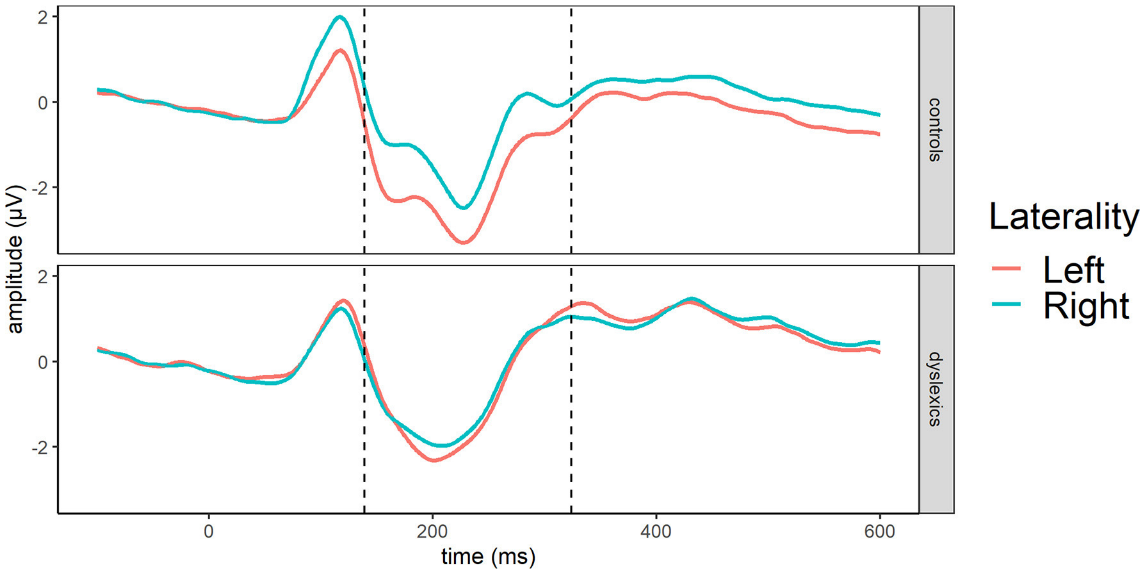

FIGURE 4 | Averages across occipito-temporal electrodes (O1, O2, P7, P8) for N1 in reference stimuli showing group and laterality interaction at GFP-based N1 segment (dashed line): 139–324 ms.

significant at any time point (lexicality: z-score = 0.76, $P_{\text{perm}} =$ 0.443; group x lexicality: z-score = 0.57, $P_{\text{perm}} = 0.467$; group x pair type: z-score = 0.56, $P_{\text{perm}} = 0.525$; lexicality x pair type: z-score = 0.78, $P_{\text{perm}} = 0.579$; group x lexicality x pair type: z-score = 0.71, $P_{\text{perm}} = 0.665$). Topographic maps and GFP curves for the pair type effect are presented on **Figure 5**.

The traditional analysis on the N1 segment on occipital-temporal sites for visual targets (140–304 ms, peak: 231 ms) revealed a significant effect on group [$F_{(1,\,50)} = 6.81$, $p =$ 0.012, $\eta_g^2 = 0.08$], wherein control participants showed more negative responses than participants with dyslexia. Moreover, the interaction between lexicality and laterality [$F_{(1,\,50)} = 5.23$, $p = 0.027$, $\eta_g^2 = 0.001$] was also significant. The interaction was present as word targets were somewhat more left-lateralized than pseudoword targets, though laterality was not significant for either the words [$F_{(1,\,50)} = 3.34$, $p = 0.073$, $\eta_g^2 = 0.01$] or the pseudowords [$F_{(1,\,50)} = 0.34$, $p = 0.561$, $\eta_g^2 = 0.0008$] when analyzed separately. The main effect of pair type was marginally

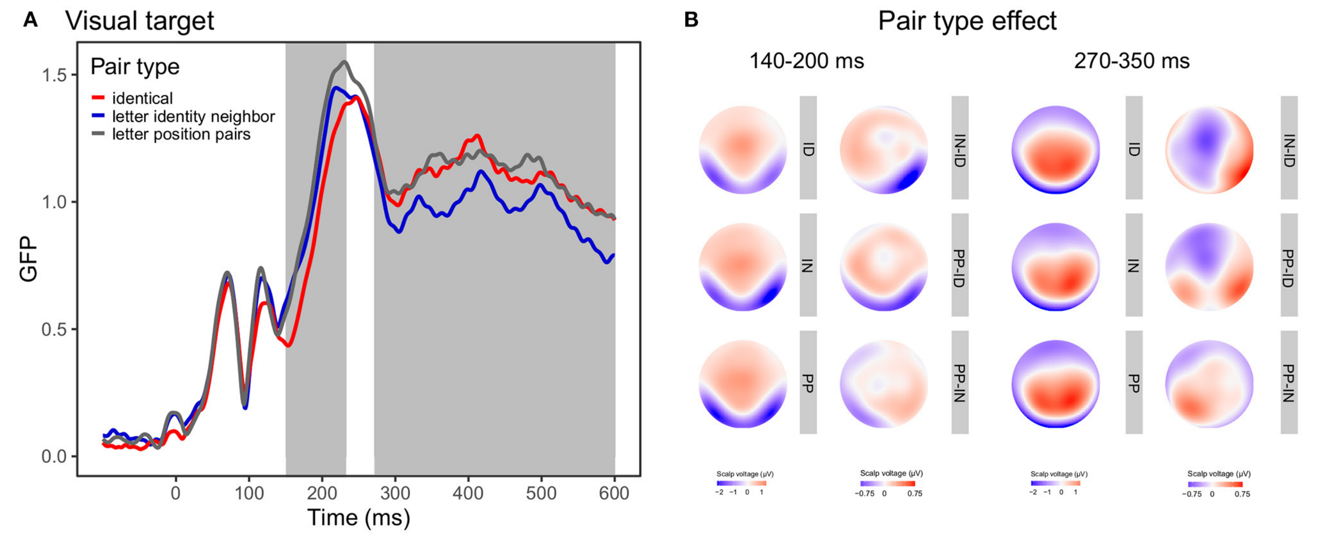

FIGURE 5 | Global field power (GFP) curves and topographic maps for the pair type effect in visual target stimuli. **(A)** GFP for the identical, letter identity neighbor, and letter position pair targets. Gray areas highlight the time windows in which the effect was significant according to the GMD analysis. **(B)** Topographic maps for the pair type conditions (ID, identical; IN, letter identity neighbor; PP, letter position pairs) and the pair type differences averaged between 140-200 ms representing the first time window and between 270–350 ms representing the second time window.

significant [$F_{(2,\,100)} = 3.04$, $p = 0.0525$, $\eta_g^2 = 0.004$]. The pair type effect suggested that ID targets elicited somewhat less negative response than PP ($p = 0.15$, $p_{bonferroni} = 0.44$) or IN ($p = 0.20$, $p_{bonferroni} = 0.61$), while PP and IN did not differ from each other ($p = 0.85$, $p_{bonferroni} = 1.0$). No other effects or interactions were significant [see (2) Letter identity and position encoding section in the **Supplementary Material**].

On the selected frontal-central sites, repeated measures ANOVA showed significant main effects on group [$F_{(1,\,50)} = 8.53$, $p = 0.005$, $\eta_g^2 = 0.10$], in which controls readers generated a bigger response than readers with dyslexia. In addition, the pair type effect was marginally significant [$F_{(2,\,100)} = 3.02$, $p = 0.053$, $\eta_g^2 = 0.005$]. Furthermore, neither the lexicality effect [$F_{(1,\,50)} = 0.50$, $p = 0.485$, $\eta_g^2 = 0.001$] nor the interactions [see (2) Letter identity and position encoding section in the **Supplementary Material**] showed any significant effect.

In sum, the group effect did not interact with either the lexicality or the pair type effect suggesting similar processing of orthographic stimuli in the visual modality despite topographic differences between the groups.

Audiovisual Processing

To test the audiovisual processing deficits in dyslexia, we compared the processing of target stimuli in the visual and audiovisual conditions.

Visual Condition

As described in the *Letter identity and position encoding* section, for visual targets there was a main effect of group (GFP: z-score = 3.31, $P_{\text{perm}} = 0.004$, 185–380 and 493–600 ms, GMD: z-score = 4.49, $P_{\text{perm}} < 0.001$, 255–600 ms), a main effect of lexicality (GFP: z-score = 3.46, $P_{\text{perm}} = 0.005$, 311–400 ms), and a main effect of pair type (GFP: z-score = 3.11, $P_{\text{perm}} = 0.005$, 144–235 ms and 455–600 ms, GMD: z-score = 3.03, $P_{\text{perm}} = 0.006$, 89–129, 142–206 and 273–600 ms), but the interactions were not significant indicating that readers both with and without dyslexia process orthographic stimuli similarly in the visual modality. Similar results emerged from the traditional analysis showing a main effect of group [$F_{(1,\,50)} = 6.81$, $p = 0.012$, $\eta_g^2 = 0.08$], a lateralized lexicality effect [lexicality x laterality: $F_{(1,\,50)} = 5.23$, $p = 0.027$, $\eta_g^2 = 0.001$], and a marginal effect of pair type [$F_{(2,\,100)} = 3.04$, $p = 0.053$, $\eta_g^2 = 0.004$].

Audiovisual Condition

As opposed to this, for the audiovisual targets, GFP analysis revealed a group main effect (z-score = 3.82, $P_{\text{perm}} = 0.001$, 190–379 ms) due to greater responses of readers without dyslexia compared to readers with dyslexia. The group x lexicality interaction (z-score = 2.35, $P_{\text{perm}} = 0.027$) between 178 and 218 ms indicated that skilled readers showed somewhat larger responses to words than to pseudowords; while readers with dyslexia did not show such a difference. In addition, a group x pair type interaction (z-score = 3.46, $P_{\text{perm}} = 0.003$) between 219 and 273 ms showed that the dyslexia group exhibited greater responses to ID targets compared to SL and PP targets, while the control group did not show a pair type effect. No other effects were significant (lexicality: z-score = 0.77, $P_{\text{perm}} = 0.400$; pair type: z-score = 0.84, $P_{\text{perm}} = 0.249$; lexicality x pair type: z-score = 0.93, $P_{\text{perm}} = 0.649$; group x lexicality x pair type: z-score = 0.65, $P_{\text{perm}} = 0.642$).

The GMD analysis revealed a group main effect (z-score = 3.57, $P_{\text{perm}} = 0.003$, 284–600 ms), a lexicality main effect (z-score = 4.34, $P_{\text{perm}} = 0.001$, 304–600 ms), and a pair type main effect (z-score = 5.47, $P_{\text{perm}} < 0.001$, 145–600 ms). Moreover, there was a group x lexicality interaction (z-score = 2.74, P_{perm} =0.011, 314–364, 386–437, 463–515, 545–595 ms) and a group x pair type interaction (z-score = 3.87, P_{perm} = 0.001, 337–403 ms). The lexicality x pair type (z-score = 0.55, P_{perm} = 0.601) and the group x lexicality x pair type interaction (z-score = 0.61, P_{perm} = 0.336) were not significant. Topographic maps and GFP curves for the group x lexicality interaction are depicted on **Figure 6**.

The traditional analysis on the N1 segment on occipital-temporal sites for AV targets (154–292 ms, peak: 216 ms) revealed a main effect of group [$F_{(1,\,50)} = 7.15$, p =0.010, $\eta^2_g = 0.09$] and a four-way interaction of group x lexicality x pair type x laterality [$F_{(2,\,100)} = 3.85$, $p = 0.025$, $\eta^2_g = 0.0007$]. As simple effect analysis indicated, the interaction was present as there was a pair type x lexicality x laterality interaction for the control group [$F_{(2,\,52)} = 3.56$, $p = 0.046$, $\eta^2_g = 0.001$] but not for the group with dyslexia [$F_{(2,\,48)} = 0.73$, $p = 0.488$, $\eta^2_g = 0.0003$]. In the control group, there was a lexicality x pair type interaction [$F_{(2,\,52)} = 3.90$, $p = 0.027$, $\eta^2_g = 0.006$] due to pair type effect only for words [$F_{(1,\,26)} = 7.80$, $p = 0.010$, $\eta^2_g = 0.02$] but not for pseudowords [$F_{(1,\,26)} = 0.50$, $p = 0.499$, $\eta^2_g = 0.002$] in the left but not in right-hemisphere [$F_{(2,\,52)} = 2.15$, $p = 0.127$, $\eta^2_g = 0.004$]. The group x lexicality interaction [$F_{(1,\,50)} = 3.12$, p =0.083, $\eta^2_g = 0.002$] just failed to reach significance in this analysis. In addition, all other effects and interactions were non-significant [see (3) Audiovisual processing section in the **Supplementary Material**].

On the selected frontal-central sites, analysis showed significant main effects of pair type [$F_{(2,\,100)} = 12.67$, $p < 0.001$, $\eta^2_g = 0.02$] due to differences between ID and IN targets [$p = 0.017$, $p_{bonferroni} = 0.05$] but not between IN and PP [p =0.41, $p_{bonferroni} = 1.0$). The group effect was marginally significant [$F_{(1,\,50)} = 3.82$, $p = 0.056$, $\eta^2_g = 0.06$]. In addition, there was a group x lexicality interaction [$F(1,\,50) = 6.70$, p =0.013, η^2_g = 0.005) since there was a lexicality effect in the group with dyslexia [$F_{(1,\,24)} = 4.72$, $p = 0.040$, $\eta^2_g = 0.006$] but not in the control group [$F_{(1,\,26)} = 2.62$, $p = 0.118$, $\eta^2_g = 0.004$]. The group x pair type interaction just failed to reach significance [$F_{(2,\,100)} = 2.91$, p =0.059, $\eta^2_g = 0.004$]. Furthermore, no other effects were significant [see (3) Audiovisual processing section in the **Supplementary Material**].

In sum, readers both with and without dyslexia process orthographic stimuli similarly in the visual modality; however, group differences emerged in the AV condition. In the TANOVA analysis, we observed main effects of group and lexicality but no interaction between the two for visual targets. On the other hand, in the audiovisual condition, controls showed a lexicality effect with greater responses for words than for pseudowords, but readers with dyslexia did not. Using the traditional analysis method we found a pair type effect for words in the left-hemisphere for audiovisual targets, but only in readers without dyslexia. However, this effect was not present for visual targets.

DISCUSSION

In our ERP study, we investigated visual and audiovisual processing of orthographic stimuli by adult readers with and without dyslexia in an implicit same-different task. Our results suggest that (1) readers with and without dyslexia exhibit similar responses to words and pseudowords, (2) readers with and without dyslexia process letter identity and letter position similarly in the visual modality despite topographic differences between the groups, and (3) readers with and without dyslexia exhibit different responses when orthographic stimuli are presented audiovisually. The above results indicate that in developmental dyslexia, orthographic-phonological processing deficits are more pronounced than orthographic processing deficits *per se*.

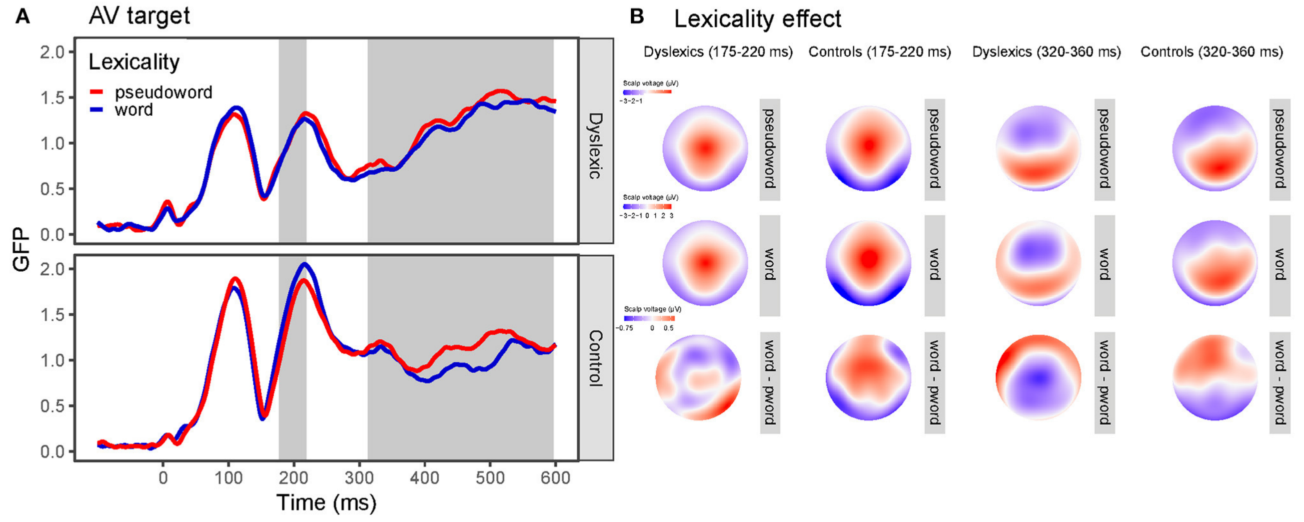

FIGURE 6 | Global field power (GFP) curves and topographic maps for the visual and audiovisual target stimuli. **(A)** GFP for the word and pseudoword targets separately for the dyslexia and control group. Gray areas highlight the time windows in which the effect was significant according to the GFP (first area) and the GMD (second area) analysis. **(B)** Topographic maps for the word and pseudoword targets and their difference (lexicality effect) separately for the dyslexia and control group for the time window where GFP (175–220 ms) and GMD (320–360 ms) differed between the groups.

Adult With and Without Dyslexia Did Not Show Lexicality Effect

According to our results, orthographic processing is not inefficient in developmental dyslexia. We investigated word and pseudoword processing and expected to find an N1 lexicality effect modulated by reading skill. However, this was not the case as none of the groups showed a lexicality effect. This result is in contrast with some previous studies which reported lexicality effect on N1 in skilled readers but not in readers with dyslexia (Mahé et al., 2012, 2013) but rather supported studies that failed to find differences between the processing of word and pseudoword stimuli (Maurer et al., 2005b, 2006, 2008; Kast et al., 2010; Araújo et al., 2012; Hasko et al., 2013; Eberhard-Moscicka et al., 2015). According to Maurer and McCandliss (2007) lexicality effect occurs when grapheme-phoneme mapping is not automatic, such as in deep orthographies, in novice readers or when an implicit reading tasks is employed. In implicit reading tasks, only those readers can apply grapheme-phoneme mappings whose grapheme-phoneme mappings are fully automatized; therefore, we expected to find lexicality effect only in the group with dyslexia but not in the control group as their grapheme-phoneme mapping should be highly automatized. Therefore, the lack of lexicality effect for skilled readers in our study could be explained by their highly automatic grapheme-phoneme mapping which allows them to read simple pseudowords as efficiently as real words. However, based on the above argument, we expected to find differential processing for words and pseudowords in the dyslexia group whose reading difficulties are characterized by sluggish grapheme-phoneme mapping. Contrary to our hypothesis, the group of readers with dyslexia did not show the lexicality effect either. Visual inspection of the GFP curves (**Figure 3**) suggests somewhat larger responses for words compared to pseudowords in the N1 time window; however, this difference failed to reach significance in the analysis. Our participants were speakers of a highly transparent language (Hungarian); thus, this could suggest that participants with dyslexia in our study did not have fully automatized grapheme-phoneme mapping, but their decoding is automatic enough due to the shallow orthography of Hungarian so that no lexicality effect could be detected. Our experiment used short, simple pseudowords; however, it is possible that inclusion of longer and more complex pseudowords would result in a stronger lexicality effect especially for the group with dyslexia.

More interestingly, the analysis revealed no group difference in the N1 time window. This is somewhat surprising as most studies conducted with participants with dyslexia reported less left-lateralized effect (Helenius et al., 1999; Kast et al., 2010; Dujardin et al., 2011). However, when the effect was analyzed by applying traditional ERP analysis methods, a significant group x laterality effect emerged in the N1 time window. This indicates that the participants with dyslexia in our study do not have a fully left-lateralized N1 response; however, the difference between the groups is not substantial enough to be detected by the data-driven TANOVA. Although we could not detect differences in orthographic processing it is possible that those group differences are subtle enough so that we cannot capture them in an implicit task.

Taken together, readers with dyslexia process words and pseudowords similarly as typical readers albeit their N1 responses might be less left-lateralized indicating less automatic orthographic-visual mapping but relatively intact orthographic processing.

Letter Position and Letter Identity Encoding Is Similar in Readers With and Without Dyslexia

To provide further evidence whether inefficient orthographic processing is the main culprit of reading deficits in dyslexia, we compared letter identity and letter order processing of readers with and without dyslexia. In the implicit same-different paradigm, participants were shown stimulus pairs that could be either identical (ID), different in one letter (letter identity neighbor, IN), or different in the position of the letters (letter position pairs, PP). In contrast to our hypothesis that adults with dyslexia show less efficient processing of letter identity and letter order, our results suggest that orthographic processing is similar between the groups.

As opposed to the expected interaction between group and pair type, we found only a main effect of pair type and a main effect of group, but no interaction between them. We are not aware of any previous study that investigated letter identity and letter position coding in adults with dyslexia using EEG, although, previous behavioral studies suggested deficits in letter identity and position processing in dyslexia (Reilhac et al., 2012; Ogawa et al., 2016). However, we did not find any difference in letter identity and letter order processing when word and pseudoword pairs were presented in the visual modality. Furthermore, our results showed that the pair type effect was modulated neither by the lexicality of the stimulus nor by the reading skill of the participants. This result is in contrast with the study of Reilhac et al. (2012) which found a substitution advantage over transposition in controls for both words and pseudowords but in children with dyslexia, the effect was only present for words. Probably, the differences found by Reilhac et al. (2012) arose from the explicit nature of their same-different task. In our paradigm, participants performed a simple feature-detection task which did not require detection of repetition. Thus, the task is less affected by short-term memory load, attentional demands, and strategic top-down effects. It is possible that group differences would emerge when the task requires to hold items in memory or to make strategic decisions. In line with this idea, group differences were found in letter position encoding in a task which used an explicit (naming) task (Ogawa et al., 2016). In addition, when a masked priming paradigm is used (Lété and Fayol, 2013), children with dyslexia show similar performance as same-age peers. This suggests that differences between readers with and without dyslexia in letter identity and letter order processing are not necessarily due to impaired visual word processing, but could be due to attentional factors.

Indeed, visual attentional difficulties have been debated as one of the characteristics in some groups with dyslexia (Valdois et al., 2004). Difficulties in distributing attention during parallel processing could affect letter identification within strings (Reilhac et al., 2012) or ordering of letters leading to sequencing errors (Valdois et al., 2004). Moreover, attentional difficulties may influence parallel processing speed, thus putting more effort in a supposedly automatized task and affecting reading performance (Valdois et al., 2004). Therefore, future studies could explore how much attentional differences contribute to letter identity and position encoding explicitly comparing implicit and explicit reading tasks.

Our results present that groups with and without dyslexia show a similar pair type effect in two time windows. Between 140 and 230 ms identical pairs evoked smaller responses compared to letter identity neighbor or letter position pair targets. In addition, identical targets exhibited different topography. This is in line with previous studies reporting different N1 for identical word pairs compared to different word pairs (Holcomb and Grainger, 2006; Cao et al., 2015). Although Holcomb and Grainger (2006) found that only coarse differences (such as identical vs. different in all letters) modulated N1 responses, they used a time window of 125–175 ms. In a later time window (175–300 ms), they also detected finer word-form differences (identical vs. substituted letter pairs). We applied a data-driven approach of analysis which requires no preselection of specific channels or time windows. The result of TANOVA indicated a time window that partly overlaps with the time windows used by Holcomb and Grainger (2006) which can explain the discrepancies. In addition, Duñabeitia et al. (2012) found greater N1 for substituted letter targets compared to transposed letter targets. Our study replicates these results as letter identity neighbors evoked somewhat smaller responses than letter position pairs. In the later time window (270–600 ms) the identical, letter identity, and letter position pairs showed topographic differences; letter identity neighbors evoked smaller responses than identical or letter position pairs. This is consistent with previous results reporting differential processing of identical and one-letter different prime-target pairs (Holcomb and Grainger, 2006). Duñabeitia et al. (2012) demonstrated larger responses for substituted letter strings than transposed letter strings in a same-different task. It should be noted, however, that they compared two-letter different and transposed letter word pairs, whereas we used one-letter different substitution neighbors. In addition, they found the difference between 200 and 325 ms; whereas the pair type effect in our study was observed in a later time window corresponding to the P3 component.

Compared to the reference stimuli, analysis of the visual targets showed lexicality effect due to greater responses for words compared to pseudowords. Many studies reported greater N1 for pseudowords compared to words (Hauk and Pulvermüller, 2004; Hauk et al., 2006; Dujardin et al., 2011; Araújo et al., 2015); however, the lexicality effect in our study occurred in a later time window (300–400 ms) and is probably related to semantic processing of the real words.

In addition, we found a group main effect. Although control readers showed larger and more left-lateralized responses compared to readers with dyslexia, this difference occurred regardless of stimulus lexicality or pair type. Topographic differences are in line with previous results reporting bilateral N1 response for readers with dyslexia but left-lateralized response for typical readers (Helenius et al., 1999; Kast et al., 2010). As the phonological mapping hypothesis (Maurer and McCandliss, 2007) suggests, left lateralization is driven by automatized grapheme-phoneme mapping which explains why readers who struggle with fluent reading exhibit bilateral responses. Strikingly, the group effect was weak in the reference stimuli; however, target processing enhanced the difference. This could indicate that group differences partly originate from automatic matching of the reference and the target. Namely, the difference extends to later time windows such as the P3 time window which is known to reflect attentional processing related to subsequent memory and stimulus discrimination (Polich, 2007). The divergence, therefore, could signal a general attentional, memory-related difference between the groups.

To summarize, group and lexicality effects were enhanced in the visual targets suggesting that automatic matching of the reference and target stimuli can modulate these effects. In addition, a robust pair type effect was present for adults both with and without dyslexia which signifies that orthographic processing deficit *per se* does not characterize reading deficits in developmental dyslexia.

Audiovisual Processing Deficits Are More Pronounced Than Orthographic Processing Deficits in Dyslexia

Finally, to investigate whether inefficient orthographic-phonological processing characterizes developmental dyslexia, we presented target stimuli in an audiovisual condition. We assumed that if audiovisual processing is deficient in dyslexia, group differences will be greater in the audiovisual condition compared to the visual only condition. Indeed, our results confirmed this hypothesis. While in the visual condition the dyslexia and control participants showed similar visual word processing as signified by the lack of group x lexicality and group x pair type interaction, in the audiovisual condition group differences emerged.

In the audiovisual condition reading skills modulated the effect of lexicality. Between 178 and 218 ms skilled readers showed larger N1 responses to words than to pseudowords; while readers with dyslexia did not show such a difference. In addition, readers with and without dyslexia showed differential topographic distribution for words and pseudowords after 300 ms due more localized anterior distribution lexicality effect in participants with dyslexia. Previous studies provided mixed results on the emergence and direction of the lexicality effect (no effect: Maurer et al., 2005b, 2006; Araújo et al., 2012; Hasko et al., 2013; Eberhard-Moscicka et al., 2015; greater N1 for words: Maurer et al., 2006; Mahé et al., 2012; Eberhard-Moscicka et al., 2016; greater N1 for pseudowords: Hauk et al., 2006; Dujardin et al., 2011; Araújo et al., 2015) and several factors were proposed which could account for the discrepancies (developmental effects: Eberhard-Moscicka et al., 2016; orthographic depth: Maurer and McCandliss, 2007; and task demands: Faísca et al., 2019). Our study adds to the above results providing evidence that the N1 lexicality effect is not detectable when orthographic stimuli are presented visually in a highly transparent language in an implicit task regardless of reading skills. However, the effect is present when words are presented audiovisually but only for skilled readers. Thus, greater responses to words in our control sample can indicate that audiovisual presentation of words engages reading-related processes automatically. These findings are in accordance with the results of Varga et al. (2020) who reported enhanced N1 effect for audiovisual presentation compared to visual only presentation in typically developing children.

Furthermore, there were group differences in the pair type effect, too. Between 219 and 273 ms, readers with dyslexia exhibited larger responses to identical targets compared to different (letter identity neighbor or letter position pairs), while the control group did not show a pair type effect. In addition, readers with and without dyslexia showed differential topographic distribution from 330 ms. It seems that when the task requires audiovisual processing, the mismatch between the reference and the target stimuli is enhanced for adults with dyslexia. This result seems counterintuitive at first; however, it should be noted that in our paradigm, the auditory stimuli were always identical to the visually presented target stimuli. Therefore, the pair type effect reflected a mismatch between the visual reference and the audiovisual target. Skilled readers showed a robust pair type effect in the visual condition; however, this effect disappeared when the target was presented audiovisually. One possible explanation is that the simultaneous presentation of the same linguistic stimulus in both the visual and audiovisual modality resulted in a prompt integration between the visual target and the auditory target (which were the same) which overrode the integration between reference and target stimuli (which differed). On the other hand, readers with dyslexia showed a pair type effect in the visual condition which was enhanced by the audiovisual presentation. That is, for them probably no automatic integration between the visual target and the auditory target occurred, but the integration between reference and target stimuli was augmented. This hypothesis is supported by previous studies reporting that readers with dyslexia fail to show automatic audiovisual integration when the visual letters and the speech sound are presented simultaneously; however, a weak and late effect of mismatch appeared when the letter appeared 200 ms before the speech sound (Froyen et al., 2011).

Finally, this study provides further support for the findings of Hasko et al. (2012). The researchers tested whether German children with dyslexia demonstrate more severe deficits in a task requiring orthographic-phonological integration than in a task requiring only orthographic processing. They found no group difference in the visual-visual matching task, but children with dyslexia showed different N300 responses when auditory-visual matching was required for word pairs. Our study extends the above finding investigating adult readers with dyslexia in an implicit reading task. Different pair type effect for participants with and without dyslexia could suggest different auditory-visual matching even though this matching was not required by the task. Our results seemingly posit that audiovisual processing deficits can be detected even when the task does not explicitly require grapheme-phoneme binding. Moreover, the results of Hasko et al. (2012) could generalize to pseudoword stimuli since we found the same pattern of results for both word and pseudoword pairs. In addition, not only auditory-visual matching (as in Hasko et al., 2012) but (implicit) visual-auditory matching (as in the present study) is inefficient in developmental dyslexia. Though Hasko et al. (2012) used an explicit auditory-visual matching task where they compared an auditory reference and a visual target whereas our implicit same-different task compared a visual reference and an auditory/visual target, both studies found group differences. Direction of stimulus matching could serve as a future direction of investigation, since the visual-auditory direction is more relevant to reading as graphemes are mapped to phonemes, while the auditory-visual direction is more relevant to spelling as phonemes are mapped to graphemes. Thus, further research could directly compare whether the visual-auditory direction (as in reading) or the auditory-visual direction (as in spelling) is more impaired in dyslexia.

Limitations

Some limitations of the present study should be noted. First, we did not obtain any measures of IQ; thus, we cannot exclude that group differences result from differences in IQ. However, we believe this is not the case as the groups were recruited with similar level of education and it is not clear how IQ would influence implicit reading skills. Nevertheless, group differences in our study warrant caution as IQ was not controlled.

Second, our study includes five left-handed participants with dyslexia. Although most people have left-hemispheric dominance for language and print processing, left-handed individuals show atypical lateralization more often than right-handed individuals (8 vs. 15%, respectively (Szaflarski et al., 2012). As the incidence of left-handedness in developmental dyslexia is slightly higher than in typical readers (Vlachos et al., 2013), relationship between lateralization and reading difficulties arises. Our results suggested that readers with dyslexia exhibit less left-lateralized N1 responses; however, this could be due to the inclusion of left-handed individuals. Therefore, any lateralization differences between the groups should be interpreted with caution as handedness may confound results.

Third, group differences that result from the comparison of visual and audiovisual processing could be driven by either differences in phonological processing or differences in phonological processing in audiovisual integration. Our experiment does not allow differentiating between the two alternative explanations. Though impaired phonological processing and impaired orthographic-phonological mapping seem to be related (Blomert, 2011), future studies should follow up by comparing the audiovisual condition to both visual and auditory unimodal conditions to further investigate audiovisual integration in developmental dyslexia.

Conclusion

In conclusion, in an implicit same-different task we could not demonstrate any orthographic processing deficit such as fine-grained print sensitivity or letter identity and letter position encoding deficit in adult readers with dyslexia. However, we found group differences in audiovisual stimulus processing suggesting that in dyslexia phonological and orthographic-phonological processing deficits are more fundamental than orthographic-visual deficits.

DATA AVAILABILITY STATEMENT

The dataset used in this study is available at: https://osf.io/6bt8g/?view_only=b1c6684655da4e9194b1e36b0f7430b9.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by United Ethical Review Committee for Research in Psychology. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

DT and VC: conceptualization. DT: experimental task preparation. DC: data collection. VV, KA, DC, and DT: analysis. VV: writing—original draft. VV, KA, DT, DC, and VC: writing—revision and editing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.723404/full#supplementary-material

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From Hand to Eye With the Devil In-Between: Which Cognitive Mechanisms Underpin the Benefit From Handwriting Training When Learning Visual Graphs?

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Cognitive science has recently shown a renewed interest on the benefit from training in handwriting (HW) when learning visual graphs, given that this learning experience improves more subsequent visual graph recognition than other forms of training. However, the underlying cognitive mechanism of this HW benefit has been elusive. Building on the 50 years of research on this topic, the present work outlines a theoretical approach to study this mechanism, specifying testable hypotheses that will allow distinguishing between confronting perspectives, i.e., symbolic accounts that hold that perceptual learning and visual analysis underpin the benefit from HW training vs. embodied sensorimotor accounts that argue for motoric representations as inner part of orthographic representations acquired *via* HW training. From the evidence critically revisited, we concluded that symbolic accounts are parsimonious and could better explain the benefit from HW training when learning visual graphs. The future challenge will be to put at test the detailed predictions presented here, so that the devil has no longer room in this equation.

Keywords: sensorimotor training, handwriting, letter processing, reading, visual analysis

INTRODUCTION

Literacy is an exquisite example of human ingenuity. Written scripts are composed by *graphs*[1], i.e., artificial two-dimensional geometric-like shapes (cf. Chang et al., 2018) that are arbitrary but, when learning to read, become visual counterparts of linguistic units as phonemes, syllables, or morphemes (e.g., letters in the Latin alphabet, kanas and kanjis in Japanese), and gears of written words (e.g., Pelli et al., 2003; Grainger, 2018). Reading thus bridges visual object recognition and language.

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[1] The term graph is preferable to letter because it applies to orthographic characters of any written system and not just to alphabets (cf. Chang et al., 2018). In the present work we also adopt the term *visual graph* when referring to the visual component of these orthographic units given that graphs (e.g., letters) have multiple facets (i.e., visual, phonological, motor).

Along with reading development, a hierarchically organized, orthographically tuned circuitry is built along the *visual ventral stream,* originally dedicated to visual recognition of familiar objects (for a review, see Dehaene et al., 2015). Skillful graph and visual word recognition depend on fast access to abstract orthographic representations (usually called *abstract or symbolic letter identities*) which are not determined by physical (visual, low-level), phonological, or motor similarity and are underpinned by the left *ventral occipitotemporal* cortex, *vOT* (Dehaene et al., 2005; Rothlein and Rapp, 2014). Readers' immunity to physical differences of *allographs* (visual forms of the same graph) is found in different scripts: e.g., in Latin alphabet, A and a; in Japanese kanas, イand い; in Arabic abjad, ﺠ and ﺝ (e.g., Bowers, 1996; Carreiras et al., 2013; Kinoshita et al., 2019). It depends on long-term changes in the perceptual space of graphs, which are consequence of learning to read. For example, B is physically equidistant to both p and b, and hence, without any experience, observers would be as fast in discriminating the pair B-p as the pair B-b. However, readers are slower in discriminating the pair B-b in consonance with the degree of perceptual similarity of graph representations (Lupyan et al., 2010; for recent evidence with training on an artificial script, see, Wiley and Rapp, 2021). This example demonstrates that learning to read is an ecological example of perceptual learning (Gibson, 1969, 1970; Dehaene et al., 2005; Goldstone and Byrge, 2015).

Probably because learning to read puts heavy demands on visual processing, the observation that motor training *via handwriting, HW* (that is, writing by hand) benefits more subsequent visual graph recognition than other learning experiences has been startling since the earliest studies (Jeffrey, 1958; Williams, 1969, 1975; Jensen and King, 1970; Koenigsberg, 1973). The advantage from HW training when learning visual graphs is robust. It is found in different written systems and types of scripts (for a recent meta-analysis, see Araújo et al., 2021; e.g., Jensen and King, 1970; Guan et al., 2011; Cao et al., 2013b; Li and James, 2016; Xu et al., 2020; Vinci-Booher et al., 2021). It is especially strong for *highly confusable* graphs which share visual features and in the most extreme the whole shape, differing only by orientation, such as *mirror images* (e.g., d and b) or rotations in the image plane (i.e., *plane rotation*: e.g., N and Z, or n and u) (Hendrickson and Muehl, 1962; Williams, 1969, 1975; Torres et al., 2020). It is found relative to *visual-only* (e.g., looking at) and to *motor control* (e.g., typewriting on a keyboard, pointing to, circling) training, regardless of training in phonological correspondences, adoption of natural or artificial scripts, amount of training (single vs. multiple training sessions), and age of learners (Araújo et al., 2021; for an overview, see James, 2017; e.g., Williams, 1969; Longcamp et al., 2006, 2008; James, 2010; Bara and Gentaz, 2011; Guan et al., 2011; Suggate et al., 2016; Labat et al., 2020; Mayer et al., 2020; Seyll et al., 2020). Note that control training often leads to improvement in subsequent visual graph recognition as well, but HW training usually excels it (Longcamp et al., 2006; Kiefer et al., 2015; Labat et al., 2020; Mayer et al., 2020; Fernández-López et al., 2021).This benefit from HW is impressive because it corresponds to a *transfer* effect (Gilbert and Li, 2012): performance in an untrained (non-motor) visual recognition task on the new graphs is enhanced *via* HW training, indicating that neural plasticity is not restricted to the brain underpinnings of the graphomotor task but extends to those of visual graph recognition at the left fusiform gyrus in the vOT (Longcamp et al., 2008; James, 2010).

It is consensual that writing by hand, stroke by stroke, establishes a connection between the visual percept of the graph and the motor plan for creating it, resulting in a sensorimotor experience that influences learning to read. Most research has provided descriptive insight only, occasionally legitimating evidence-based programs (e.g., Bara et al., 2016; Mayer et al., 2020; Torres et al., 2020) given that HW is a worldwide strategy in literacy instruction (e.g., Tan et al., 2005; Bara and Gentaz, 2011; Itaguchi et al., 2015; Xu et al., 2020). However, this benefit from HW training does not necessarily imply that knowledge on how to write the graphs (that is, on motoric representations) is the underlying mechanism. This (premature) conclusion confuses the expression of a learning experience with the underlying cognitive representations and processes (Norris and Cutler, 2021).

In fact, explanatory insights have been rare (notwithstanding recent exceptions: Li and James, 2016; Zhai and Fischer-Baum, 2019; Seyll et al., 2020; Vinci-Booher et al., 2021; Wiley and Rapp, 2021). We thus came to have misgivings about the underlying mechanism: Why does HW training benefit visual graph recognition? Is it due to perceptual learning and visual segmental analysis regardless of the motor act (e.g., Williams, 1975; Courrieu and de Falco, 1989; Seyll et al., 2020)? Or does it depend on internal motor simulation (e.g., Longcamp et al., 2008, 2016) such as that of stroke order during visual graph recognition (e.g., Parkinson and Khurana, 2007; Itaguchi et al., 2015)?

It is time to put the phenomenon into perspective, confronting potential explanations, in order to bring to light the underlying cognitive mechanism. In the present work, we critically review evidence from pioneering research (e.g., Hendrickson and Muehl, 1962; Pick, 1965; Williams, 1969; Jensen and King, 1970; Koenigsberg, 1973) to more recent functional resonance imaging (fMRI) studies (e.g., Longcamp et al., 2006; James and Atwood, 2009; James, 2010; Cao et al., 2013b; Vinci-Booher et al., 2021). Our aim is to aggregate this research, adopting a theoretically based perspective that has hitherto been largely missing. Specifically, we consider the two alternative theoretical frameworks (about conceptual representations, and hence, not exclusive of letter representations) that can be associated with most research on the benefit from HW training even if this theoretical discussion has often been dismissed (e.g., Bara and Gentaz, 2011; Labat et al., 2020; Torres et al., 2020). The debate between these two theoretical perspectives is about the *nature* of cognitive representations, that is, about their *format* (i.e., the nature of the code used to represent information) and not about their content (that is, which information is stored; for a critical discussion, see, e.g., Glenberg et al., 2013; Barsalou, 2016; Goldinger et al., 2016; Machery, 2016; Mahon and Hickok, 2016).

On the one hand, *embodied* cognitive accounts (also called grounded or situated cognition: e.g., Allport, 1985; Barsalou, 2008; Glenberg et al., 2013) hold that the content and the format of cognitive representations is isomorphic: sensory concepts have a sensorial format and action concepts have a motor format.

Therefore, representations of graphs and of written words would not be symbolic but rather *sensorimotor*. During visual graph recognition, the graphic motor programs acquired *via* HW would be *reactivated* or *simulated* because they would be an inner part of graph representations. This sensorimotor mechanism would be responsible for the benefit from HW training in visual graph recognition (e.g., Bara and Gentaz, 2011; Longcamp et al., 2016; Labat et al., 2020; Xu et al., 2020). Action-perception coupling *via* HW training would be critical for the development of the reading-specialized circuitry (Longcamp et al., 2008; James and Atwood, 2009) because reading would involve a gesture decoding system, located within a region of the left *dorsal premotor cortex, PMd* (Brodmann Area 6; e.g., Longcamp et al., 2008; Nakamura et al., 2012; Cao et al., 2013b).

On the other hand, *abstractionist, symbolic* accounts (e.g., Goldinger et al., 2016; Machery, 2016; Mahon and Hickok, 2016) do not deny the role of sensorimotor experiences when learning to read but hold that abstract representations are not reducible to, and hence differ from, modality-dependent ones. In what regards visual graph processing, ample behavioral, neuroimaging, and neuropsychological evidence (e.g., Rapp and Caramazza, 1997; Dehaene et al., 2005; Lupyan et al., 2010; Dufor and Rapp, 2013; Wiley and Rapp, 2021) shows that symbolic, amodal graph identities are core representations in reading and writing in alphabetic and non-alphabetic scripts (e.g., Carreiras et al., 2013; Rothlein and Rapp, 2014; Kinoshita et al., 2019). These abstract orthographic representations are connected *via* bidirectional links to the input (visual) and output (motor) systems, with automatic spreading of activation between them (Rapp and Caramazza, 1997; Dufor and Rapp, 2013). HW training would thus assist on the emergence of abstract orthographic representations due to activation dynamics (that is, because activation cascades automatically) and not because motoric representations were an inner part of orthographic representations. In this vein, HW training would benefit subsequent visual graph recognition due to the operation of a *perceptual learning* mechanism, resulting in long-lasting changes in the perception of the trained graphs (e.g., Gibson, 1969, 1970; Williams, 1975; Courrieu and de Falco, 1989; Goldstone and Byrge, 2015; Seyll et al., 2020).

Both frameworks predict that HW training benefits more subsequent visual graph recognition than other learning experiences. However, they disagree about the nature of the representations and about the putative mechanisms underpinning the HW benefit. In this work, we highlight some of the loose ends that research has left and present our theoretical framework and hypotheses. Before our proposal, we start by pinpointing the cognitive components involved in HW, to then discuss three promising theoretical accounts framed by the symbolic cognitive framework (i.e., the perceptual variability and the visual analysis hypotheses) and by the embodied cognitive framework (i.e., the stroke processing hypothesis). For each hypothesis, we first present critical positive evidence and next the evidence that questions it. Note, however, that it is not our aim to provide an exhaustive literature review but one that is unbiased and tackles the critical evidence for the present discussion. We also detail the predictions that follow, because, like the devil, unveiling the underlying cognitive mechanisms is on the details.

WHY IS HANDWRITING SO SPECIAL? THREE THEORETICAL PROPOSALS LOOKING FOR THE COMMON DENOMINATORS

Learning to read is often accompanied by proxies of HW as copying and tracing (Kiefer et al., 2015; Mayer et al., 2020). It is a multisensory experience bridging visual graphs with speech sounds and motor gestures (Pegado et al., 2014). Consequently, letters have multiple codes (i.e., visual, motor, phonological) and are involved both in reading and in writing, which in turn also comprise multiple types of representations (Abbott and Berninger, 1993; Rothlein and Rapp, 2014). Therefore, the cognitive mechanisms and representations involved in a transfer effect from HW training to visual graph recognition are not straightforward. It is undeniable that HW training has effects in writing and might also have in other abilities beyond the written domain (Abbott and Berninger, 1993). However, the scope of the present work is on the benefit from HW training on subsequent visual recognition of graphs. We are isolating a specific challenge that is posed when learning to read, that is, the emergence of abstract graph identities, which can be distinguished from other challenges posed in orthographic processing during reading development (e.g., transposed letter effect; phonological consistency).

The first strategy to enlighten the transfer effect from HW training to visual graph recognition is by process decomposition. The rationale here is that of the perceptual expertise literature (Curby and Gauthier, 2010): the training task is a vehicle for encouraging differences in processing and/or in representation of graphs, and transfer effects from training to testing tasks depend on the common denominators (Gilbert and Li, 2012). Such rationale is not only optimal to theory testing but can also readily translate into education. By identifying the key components of this benefit, other tasks besides HW can be used to optimize learning to read. Furthermore, given that HW is becoming an obsolete task in the digital era, its inclusion in school activities depends on the contribution of HW to other facets of literacy beyond writing *per se* (Wiley and Rapp, 2021). For unveiling this cognitive mechanism, we need to isolate the common denominators, that is, which representations and processes in the learning experience are critical to subsequent visual graph recognition and reading. To this aim, we first consider the cognitive components involved in HW.

Handwriting is a perceptual-motor multi-component task that involves a plethora of processes, including balance, eye-hand coordination, focused attention, visual processing, fine coordination of hand movements, and precise motor control of spatial and temporal constraints (Waterman et al., 2015; Julius et al., 2016). Behaviorally, HW is characterized by *legibility* and *fluency* (i.e., accuracy and speed in reproduction). It is underpinned by a frontoparietal associative striatum-cerebellar circuitry that also engages attention and executive processes (Makino et al., 2016; Palmis et al., 2017; Vinci-Booher et al., 2019). Therefore, at first sight, multiple possible mechanisms could be involved in a transfer effect to visual graph recognition and reading (for a similar discussion, see, Wiley and Rapp, 2021).

Notably, the temporal course of HW learning reveals two aspects that could be key for unveiling the underlying cognitive mechanism. Like other forms of motor learning, HW follows a well-characterized temporal course of two phases, both dependent on the *cortical-cerebellar* loop (the primary motor, somatosensory, dorsal premotor, and parietal cortices, the thalamus and cerebellum) and the *cortico-striatal* loop (composed by the same motor cortical areas, the thalamus and basal ganglia; Makino et al., 2016; Palmis et al., 2017). It begins with a *fast-learning phase* of rapid improvement but with slow and highly variable graph reproduction. Movements are overly guided by the visual stimuli, with exploration of multiple motor behaviors, contingently to the resulting visual output (Maldarelli et al., 2015). Next, in a *slow-learning* phase, refinement of graph reproduction occurs over a longer time course. HW becomes legible, fluent, and highly stereotyped but still relies more on visual feedback than proprioceptive (tactile and kinesthetic) feedback (Palmis et al., 2017). Thus, the two key aspects are that, during the first phase, HW is accompanied by highly variable visual outputs, and hence, perceptual variability of the graphs to-be-learned is maximum, and in both learning phases visual processing is prevalent.

This temporal course also highlights the first loose end of this topic of research. Most studies on the benefit from HW training when learning visual graphs likely tap mostly into the first phase of motor learning. These studies were usually short-term, many with a single training session of 1–3 min (e.g., Naka and Naoi, 1995; Suggate et al., 2016) to 20–25 min (e.g., Jensen and King, 1970; Guan and Wang, 2017) and subsequent visual graph recognition was tested immediately or 24 h post-training (e.g., Williams, 1969; James and Atwood, 2009). From the 50 studies meta-analyzed by Araújo et al. (2021), half had just one or two training sessions (of less than 30 min) and only six studies had more than seven training sessions (e.g., Kiefer et al., 2015; Mayer et al., 2020). Follow-up testing has been rare, although post-training gains are kept after at least one week (Longcamp et al., 2006, 2008; Cao et al., 2013b; Seyll et al., 2020; Vinci-Booher et al., 2021). Note, however, that when children were trained on real letters, uncontrolled post-training exposure could have been involved in the follow-up results (e.g., Longcamp et al., 2005). More important to the present work, in these training studies HW is always preceded, accompanied, and followed by visual graph processing, and hence, visual perceptual processes seem to be critical. This observation agrees with fMRI evidence showing enhancement of functional activity in occipitotemporal regions for HW with ink vs. without ink (Vinci-Booher et al., 2019). Therefore, in short-term training studies, HW training is contingent to visual pattern learning, and hence, its benefit could be due to perceptual learning of graphs (Williams, 1975; Courrieu and de Falco, 1989).

The first two hypotheses discussed here, that is, the *perceptual variability* (James and Engelhardt, 2012; Li and James, 2016) and the *visual analysis* (Koenigsberg, 1973; Courrieu and de Falco, 1989; Seyll et al., 2020) hypotheses are framed by symbolic accounts of cognitive representations (e.g., Goldinger et al., 2016; Machery, 2016; Mahon and Hickok, 2016). Both were originally proposed in studies with preliterate children, and hence, with learners that had no previous reading expertise in any script (we return to this point in Section "The nature of graph representations"). These hypotheses are not mutually exclusive but focus on different operations of perceptual learning. As aforementioned, this mechanism is responsible for the emergence of symbolic graph identities (Gibson, 1969; Dehaene et al., 2005; Goldinger et al., 2016) as expressed by faster discrimination of the pair B-p than B-b by Latin-alphabet readers (Lupyan et al., 2010). In fact, this example illustrates the two perceptual challenges that a learner faces, each one emphasized by one of the two symbolic hypotheses discussed below.

The Perceptual Variability Hypothesis

First, *category learning* is used to abstract away over perceptual differences between allographs (e.g., B and b), giving rise to the formation of abstract letter identities at the left vOT (Dehaene et al., 2005; Rothlein and Rapp, 2014). These representations are the gateway for letter and visual word recognition across reading development (Grainger, 2018). Fast access to them is demonstrated by the observation of equivalent facilitation in recognition of written words preceded by identical items written in a different case, regardless of visual similarity of allographs: i.e., same magnitude of cross-case identity priming for e.g., <ROSE > preceded by as for <KISS> preceded by <kiss> (e.g., Bowers, 1996). It could thus be the case that, due to the high perceptual variability inherent to graph reproduction, HW training would assist on extraction of perceptual invariants (Kirk, 1980) relevant for the emergence of abstract letter representations. In other words, during HW, learners are exposed to variable (messy) visual stimuli more than in other types of training without a graphomotor activity (James and Engelhardt, 2012; Li and James, 2016). Thus, HW training could broaden graph categories at the left vOT due to *perceptual variability* (James and Engelhardt, 2012; Li and James, 2016): "experiencing visual variability would be more important for letter learning and subsequent visual recognition than experiencing the motor variability" (Vinci-Booher and James, 2020, p. 3).

Indeed, regardless of training including HW or not, children exposed to more variable instances of graphs show better reading abilities (Bara et al., 2016) and larger post-training gains in subsequent categorization of these graphs (Li and James, 2016). Nonetheless, when instances of new graphs are more variable by using a hampering writing tool (e.g., vibrating or conic-shape pen), learners show smaller post-training gains that those who used a regular pen (Suggate et al., 2016; Seyll and Content, 2020). However, a trade-off might have occurred between exposure to more variable instances of graphs and the attentional resources demanded by (difficult) motor reproduction with a hampering tool. In this regard, more conclusive evidence has been provided by Wiley and Rapp (2021). When adults were exposed to the same number of variable instances of Arabic letters, those trained *via* HW still showed faster learning rates of these letters than participants trained in visual or motor control conditions (Wiley and Rapp, 2021). Thus, albeit relevant, perceptual variability might not be the sole (or even the core) operation.

The Visual Analysis Hypothesis

Second, learners become able to isolate diagnostic features *via differentiation*, leading to between-category expansion (e.g., B and p; Gibson et al., 1962). The most fascinating consequence of perceptual learning is that stimuli that were at first indistinguishable became discriminated, as happens with mirror images (e.g., b and d), which are originally processed as equivalent percepts due to *mirror-image invariance*. This property of the ventral visual stream is inherited from evolution: natural objects are often symmetric, and hence, for fast identification (i.e., whether an item is a tiger or a kitten) there is no advantage in discriminating mirror images which are just profile views of the same item (Bornstein et al., 1978; Logothetis et al., 1995; Pegado et al., 2014; Dehaene et al., 2015). However, mirror-image discrimination must be accomplished when learning a script with mirrored graphs as the Latin alphabet (e.g., p and q) or Japanese hiragana (e.g., ち and さ) (Gibson et al., 1962; Kaufman, 1980; Kolinsky et al., 2011; Fernandes et al., 2016, 2021; for recent evidence on the role of the writing direction in mirror-image processing during lexical access, see, e.g., Soares et al., 2019, 2021).

The benefit from HW training could be because HW enhances awareness of the critical, distinctive features of graphs (Williams, 1969, 1975). *Visual features* are image components that are detected independently and are unaffected by the presence of other features; they are the primitives of visual object recognition (e.g., Pelli et al., 2003, 2006; Dehaene et al., 2005; Grainger, 2018). Therefore, the benefit from HW could be due to enhancement of visual-feature based processing, which in turn grounds efficient visual graph recognition (Gibson et al., 1962; Pelli et al., 2006; Grainger, 2018). This *visual analysis hypothesis* was the first proposed (for an early review, see, e.g., Kaufman, 1980), has recently seen a revival (Seyll et al., 2020), and is the one which gathers more corroborating evidence.

Handwriting training would foster discrimination of fine-grained visual configurations (Mayer et al., 2020). Therefore, as long as training engages explicit segmentation and visual discrimination, even if the graphomotor action is out of the equation, we would still get the same magnitude of gains in graph recognition. The empirical evidence available is coherent with this prediction. Indeed, explicit (non-motor) training on the distinctive features of highly confusable graphs is critical for facilitating graph recognition and subsequent letter-sound learning (Pick, 1965; Tawney, 1972; Samuels, 1973; Nelson and Wein, 1974). There is no added value of HW when visual training is fully focused on diagnostic features like orientation (e.g., d and b; Koenigsberg, 1973; Williams, 1975) nor when visually segmented graphs are presented to the learner (Courrieu and de Falco, 1989; Seyll et al., 2020). Visual exposure is not enough; training must imply visual analysis (e.g., Caldwell and Hall, 1969; Samuels, 1973; Spectorman et al., 1977).

Although appealing, most of the corroborating evidence is behavioral, and only a few studies have directly compared (non-motor) visual analysis training with HW training (Williams, 1969, 1975; Koenigsberg, 1973; Courrieu and de Falco, 1989; Seyll et al., 2020). Nonetheless, this theoretical account is also coherent with eye-movement patterns showing strong inspection of the visual item before copying it (Maldarelli et al., 2015) and transient enhancement at the left vOT for graphs learned *via* HW, immediately after training (James, 2010; James and Engelhardt, 2012; Vinci-Booher et al., 2021). Nonetheless, given that this hypothesis has not been directly tested in neuroimaging studies, it is still unknown whether such visual segmental training could lead to the same long-term neurocognitive changes in visual graph processing found after HW training, including those outside the vOT.

The Stroke Processing Hypothesis

Notably, other mechanism could be involved. Along training, HW becomes automatic (legibility reaches a plateau by 2nd-grade, but HW only becomes automatic around the 3rd-grade, between 8 and 11 years of age; Waterman et al., 2015; Julius et al., 2016; Palmis et al., 2020). One generates similar graph shapes with different limbs and execution modes, suggesting that *abstract*, *effector-independent* motoric representations are involved. These representations specify graphs in terms of *strokes*, that is, units of movement defined by velocity vectors. Strokes can be segmented based on the occurrence of pen velocity minima, as happens, for example, when lifting off the pen because the beginning and end of the movement segment corresponds to an interruption (Rapp and Caramazza, 1997; Julius et al., 2016; Palmis et al., 2017). These representations are underpinned by the *PMd,* also known as a *graphemic motor image center* (see, e.g., Roux et al., 2009), whose damage often leads to *agraphia*, a specific writing disorder, with HW impairment (e.g., Kurosaki et al., 2016). This brain region is involved in transforming abstract motoric identities into motor plans (Dufor and Rapp, 2013). During HW by fluent readers, the PMd is specifically responsive to letter shape but not to letter identity (i.e., when shape changes; e.g., d and D). Naturally, HW training leads to the emergence of these motoric representations, which are necessary for legibility and fluency in subsequent writing tasks (Naka and Naoi, 1995; Kiefer et al., 2015; Wiley and Rapp, 2021). In this sense, the specificities of the sensorimotor learning experience are relevant for the emergence of motoric representations. However, it does not necessarily imply that these motoric representations are the ones responsible for the transfer effects from HW training to visual graph recognition. The point of dispute here regards the format of cognitive representations, on which embodied and symbolic cognitive accounts diverge.

The *stroke processing hypothesis* (e.g., Tan et al., 2005; Parkinson and Khurana, 2007; Itaguchi et al., 2015) was originally framed by an embodied cognitive account (e.g., Allport, 1985; Barsalou, 2008; Glenberg et al., 2013). According to it, the graphic motor programs acquired *via* HW would be reactivated during subsequent visual graph recognition because motor plans would be core of sensorimotor graph representations (Longcamp et al., 2008, 2016; James and Atwood, 2009;

James and Gauthier, 2009; Labat et al., 2020). This hypothesis has been especially emphasized in logographic written systems because these graphs tend to be complex and with non-linear configurations (e.g., Chang et al., 2018), and hence, stroke simulation would be particularly relevant (Tan et al., 2005; Itaguchi et al., 2015): "writing facilitates recognition for both Chinese characters and English letters because (1) writing adds additional motor-related information to the representation system, which is wired together with visual input and enhances the activation of visual information during the recognition stage" (Cao et al., 2013b, p. 1671).

This hypothesis is appealing and has gathered considerable positive evidence, which we present next. However, it also has important limitations that have not hitherto been discussed in a systematic manner. Therefore, in the following Subsections "The nature of graph representations," "Learners who are already experts in reading and HW," and "Stroke processing is not about stroke order" we discuss the three caveats that question it.

Most enthusiasm with sensorimotor accounts and the stroke processing hypothesis has come from fMRI evidence during visual presentation of written stimuli. Such neuroimaging studies have found functional activity at the PMd and functional connectivity between frontal and/or parietal regions (within the writing network; e.g., Roux et al., 2009) and the vOT (part of the visual ventral stream and a core region of the reading network; e.g., Dehaene et al., 2005) in two populations: (i) In fluent adult readers presented with graphs or words written in the script on which they are experts (Longcamp et al., 2003; Nakamura et al., 2012; Vinci-Booher and James, 2020). (ii) In learners presented with visual graphs immediately after training (e.g., Longcamp et al., 2008; James and Atwood, 2009; James, 2010; James and Engelhardt, 2012; Vinci-Booher et al., 2016). This fMRI evidence has been interpreted as reflecting the involvement of motor representations during perception, because reading and writing would depend on sensorimotor representations of graphs (Longcamp et al., 2016; Vinci-Booher et al., 2016). Visual graph recognition would thus involve a gesture decoding system. Note, however, that fMRI evidence does not allow establishing causal inferences. We discuss this caveat in section "The nature of graph representations."

Positive behavioral evidence was found with beginning readers. Indeed, copying of pseudographs by Chinese beginning readers was a reliable predictor of reading performance, even after controlling for general processing speed and phonological awareness (Tan et al., 2005). Adults learning Chinese as second language also showed larger post-training gains in hanzi categorization, not only after HW training, but also after training in an *animation* condition, where stroke order was presented unfolding but without a motor action involved (Xu et al., 2013). Furthermore, the post-training gains in graph naming by 2nd-grade Chinese children were similar (and larger than in control training) after HW training as after *kusho* training (air-writing training; Xu et al., 2020). Additionally, fluent adult readers of logographic scripts like Chinese or Japanese often adopt kusho and show better identification of decomposed kanjis when simultaneously doing kusho than when writing circles in the air or holding still (Itaguchi et al., 2015). However, this behavioral evidence regards participants that had already some prior (pre-training) knowledge of graphs. The effects of kusho training do not necessarily imply the involvement of motoric representations in visual graph recognition. These two aspects are discussed in section "Learners who are already experts in reading and HW."

A *stroke order* effect has been reported in Latin-alphabet readers. When letters were presented as a sequence of strokes (dynamic unfolding, stroke-by-stroke), letter identification was faster in the consistent (left-to-right) than in inconsistent (right-to-left) stroke order (Parkinson and Khurana, 2007; Parkinson et al., 2010). Coherently, fluent readers show worse letter recognition when simultaneously writing another letter than when drawing a geometric shape. This *motor interference* by letters suggests that incongruent graphic motor programs were activated, interfering with visual graph recognition (James and Gauthier, 2009). In some patients with *alexia* (a specific reading disorder), HW also seems to facilitate letter recognition (e.g., Seki et al., 1995; Lott et al., 2010).The role of stroke processing was recently shown by Schubert et al. (2018) in Patient NGN (with a severe deficit in reading and in cross-case letter matching but with spared copying of letters and other symbols). When presented with letters comprising dots, Patient NGN showed worse letter identification for a static letter or a dynamic random one (not mimicking strokes) than for *dynamic* letters (dots presented in a continuous sequence along letter strokes) either in *consistent* or *inconsistent* orders. Note, however, that stroke processing is not the same as stroke order; the former is about the unit of movement and primitive of motor representations, while the latter is about the motoric program (the sequence of strokes) involved in graph reproduction. We return to this point in section "Stroke processing is not about stroke order."

The Nature of Graph Representations

It is undeniable that sensorimotor accounts and the reviewed fMRI evidence are appealing. They are easy to understand and at first sight might seem *parsimonious*: they are brief, refer to observables, and have possible generality (Epstein, 1984; Vandekerckhove et al., 2015). However, fMRI evidence is correlational. It does not provide a causal explanation *per se* and neither does the mere reference to action-perception coupling due to brain-body-environment interaction (e.g., Longcamp et al., 2006; James and Atwood, 2009; Bara and Gentaz, 2011; Labat et al., 2020; Xu et al., 2020). To go beyond observation, it is necessary to bridge the evidence with psychological processes and mechanisms (Norris and Cutler, 2021).

Indeed, in at least some of the training studies on new graphs that have favored a sensorimotor account (e.g., Longcamp et al., 2005, 2006; James and Atwood, 2009; Bara and Gentaz, 2011), the benefit from HW training could be as easily explained by a perceptual learning hypothesis without reference to a sensorimotor mechanism, given that none of these studies has tested or discarded this alternative. Furthermore, even the most promising evidence for the stroke processing hypothesis, which has come from fMRI evidence of functional connectivity between visual and motor brain regions when learners were presented with graphs trained *via* HW (relative to control) immediately after training (e.g., Longcamp et al., 2008;

James and Atwood, 2009; James, 2010; James and Engelhardt, 2012; Vinci-Booher et al., 2016) is limited. Indeed, Vinci-Booher et al. (2021) recently showed that such immediate enhancement in functional connectivity is temporary and not causally related with post-training gains in visual graph recognition, given that it was already gone (no functional connectivity observed) one week after training although the post-training gains in visual graph recognition were kept. These transitory effects are well accommodated by symbolic accounts considering the dynamics of activation spreading (Mahon and Hickok, 2016). Indeed, as aforementioned, ample evidence (Rapp and Caramazza, 1997; Dehaene et al., 2005; Lupyan et al., 2010; Dufor and Rapp, 2013; Rothlein and Rapp, 2014) shows that symbolic, amodal graph identities and sensorial and motor representations are independent but linked by bidirectional connections. Therefore, sensorimotor activity during letter perception would be about the dynamics of information flow rather than about the format of mental representations (Goldinger et al., 2016; Machery, 2016; Mahon and Hickok, 2016). In other words, visual graph recognition and graph production (writing) are related by means of abstract orthographic representations (e.g., Rapp and Caramazza, 1997; Rothlein and Rapp, 2014). Contrary to what some authors advocate (e.g., Longcamp et al., 2008, 2016; Cao et al., 2013a,b), when the evidence reported as favoring this hypothesis is thoroughly considered, it is unlikely that motoric representations and motor simulation during letter perception are responsible for the benefit from HW training in visual graph recognition.

Neuropsychological studies are also enlightening in this regard. Damage in brain regions responsible for HW does not necessarily lead to deficits in visual graph recognition and reading, even in Chinese (e.g., Bi et al., 2009; Kurosaki et al., 2016). Moreover, if graph representations were sensorimotor in format, then richer multisensory experiences would lead to larger post-training gains in graph recognition. However, the evidence says otherwise (Labat et al., 2020; Mayer et al., 2020; Xu et al., 2020; Araújo et al., 2021).

Critically, symbolic accounts have recently gained further support. A recent multi-session study demonstrated that HW training leads to the emergence of motoric representations but, importantly, also assists in the emergence of symbolic orthographic representations, which are dissociable from the former (Wiley and Rapp, 2021). In this study, three groups of participants learned Arabic letters along with their names and sounds. All were exposed for the same duration to multiple instances of dynamic letters (mimicking the stroke order) and to visually similar and visually dissimilar allographs: (e.g., ط and ـط; ك and ک, respectively), while performing an active task during training: (i) HW *via* copying; (ii) *typing* on a keyboard, where each allograph was presented on a specific key (hence, this motor control training comprised physically based discrimination including between allographs); (iii) *visual* by performing a same-different matching task (*different*-response trials corresponded to non-letter, familiar symbols, e.g., %, ?, #, and *same*-response trials to the letter being trained but in smaller size; hence, this visual training comprised a symbol/non-symbol categorization task). The most interesting result was found in a same-different matching task presented to participants at pre- and post-training. In this task, in *different*-response trials participants were presented with different graphs, which could be either different letters of Arabic (e.g., ط and ك) or allographs (ک and ك). At post-training, the HW group showed sensitivity to motoric similarity but also to symbolic identity (i.e., slower *different*-response for allographs than for different graphs; cf. Lupyan et al., 2010). Furthermore, visual training also led to the emergence of symbolic representations in the absence of motoric ones.

Learners Who Are Already Experts in Reading and Handwriting

The second caveat stems from the fact that most positive evidence was found with participants who were not naïve on the graphs to be learned. In some studies, participants had already (at least some) knowledge of the script, given that they were beginning readers, either children (Tan et al., 2005; Xu et al., 2020) or adults learning Chinese as second language (who knew ∼180–450 hanzis, whereas fluent readers usually know ∼3000 hanzis; Cao et al., 2013a,b; Xu et al., 2013). Research with fluent adult readers (Parkinson and Khurana, 2007; James and Gauthier, 2009; Parkinson et al., 2010) or with alexic patients exposes the same caveat (Lott et al., 2010; Itaguchi et al., 2015; Schubert et al., 2018; Xu et al., 2020), given that such studies do not provide evidence on the mechanisms involved in learning the new graphs.

Research with kusho does neither provide conclusive evidence. Kusho or "air writing" corresponds to writing without visual feedback, and hence, to be successful in kusho, one needs to already know the visual form of graphs. In other words, for fluent readers kusho necessarily implies writing from memory; for learners, kusho training always occurs along with presentation of visual graphs (e.g., Itaguchi et al., 2015; Xu et al., 2020). In studies with fluent readers, the effects of kusho could thus be consequence of access to abstract letter identities (e.g., Itaguchi et al., 2015). Furthermore, the literate adults examined by Itaguchi et al. (2015) were asked to perform kusho while being presented with visually decomposed graphs, and hence, the effect could rather be about visual analysis. This alternative also applies to studies with learners. Indeed, Xu et al. (2020) found the same benefit in graph naming after HW training as after kusho training by the youngest group of 2nd-graders, and in both trainings, children were required to write the visual graph which was simultaneously presented on the screen. Therefore, the same motoric processes and the same explicit visual segmental analysis were operating in both conditions.

Pre-training knowledge of the graphs to-be-learnt might have a moderator role in the size of the benefit driven by HW. Specifically, post-training gains in visual graph recognition seem to be larger for children with less reading skills (Williams, 1969; Xu et al., 2020). Second-grade readers showed the same large post-training gains after HW as after kusho training and only for 4th-graders HW training was no longer as effective as kusho training (Xu et al., 2020). More important, when preliterate children (without pre-training knowledge) and first-grade beginning readers were trained on graphs (letter-like), only preliterate children showed larger post-training gains after HW than after a control training, whereas first-graders did not show any effect of type of training. More important, in this study, preliterate children showed even larger post-training gains after a (non-motor) training in mirror-image discrimination than after HW training (Williams, 1969; for a similar advantage from this visual-discrimination training over HW training see, Williams, 1975). This point is specifically about prior knowledge on the script to-be-learned and not about age (but see, Longcamp et al., 2005). Indeed, we known that, regardless of age of literacy acquisition, learning to read leads to the same benefit in orientation processing and mirror-image discrimination (e.g., Kolinsky et al., 2011; Fernandes et al., 2016) and visual graph recognition becomes underpinned by the vOT (e.g., Dehaene-Lambertz et al., 2018; Hervais-Adelman et al., 2019). The point here is that we cannot assume that evidence from participants with prior knowledge of the script can speak about the mechanisms involved when learning these visual graphs.

This observation also highlights a second loose end of this topic of research, which regards whether post-training gains in new (unknown) graphs by literate participants would generalize to those elicited in preliterate or illiterate participants (Naka and Naoi, 1995; Xu et al., 2020; Vinci-Booher and James, 2020; Vinci-Booher et al., 2021). This loose end is not specific to the stroke processing hypothesis, given that other accounts have also provided evidence with learners that had prior reading expertise in another script (Seyll et al., 2020; Vinci-Booher et al., 2021). However, this point is raised by this hypothesis because this is the only proposal that confuses evidence about visual graph recognition by fluent adult readers (i.e., with prior knowledge on these graphs) with evidence about learning of new (unknown) graphs (e.g., Parkinson and Khurana, 2007; Longcamp et al., 2016). More important, in training studies with adults (even if these studies adopted highly controlled, novel, artificial scripts; for a discussion on the advantages of artificial scripts, see, e.g., Chetail, 2017), HW on the first script was already automatic (Waterman et al., 2015; Julius et al., 2016; Palmis et al., 2020). In contrast, studies with preliterate children were conducted with learners for whom the HW training implied learning of the visual graphs plus learning of the HW task itself. The message here is that we do not know whether: (a) different cognitive mechanisms underpin the benefit from HW training by naïve participants (preliterate children or illiterate adults) and by readers (who are experts in letter and HW in a first script and for whom generalization might apply, if possible); or (b) the same mechanism is involved but the time course of the HW benefit might be modulated by reading expertise in another, first script. Surprisingly, although silent, the literature seems to have implicitly assumed the latter, given that studies with preliterate children have significantly longer training programs and on less graphs than those with literate adults (Araújo et al., 2021).

In fact, indirect evidence suggests that the mechanism is likely the same for learners that are either fully naïve or experts in another script; only the time course seems to differ. After phonological training (without HW), preliterate children and literate adults show similar enhancement in vOT response for the learned graphs (Brem et al., 2010, 2018). In what regards learning HW (in an invented-letter task), the same learning curve, the same improvement slope in consolidation (24 h post-training) and retention (follow-up after 2 weeks) was found in 5–6-year-old preliterate, 7–8-year-old beginning readers, and adults, although preliterate started with the lowest performance (Julius and Adi-Japha, 2015). When copying single letters, preliterate children took more time to complete the task, but both adults and children spent similar time inspecting the letter (in number and duration of fixations) before writing it down. Yet, children still inspected the visual item during writing, whereas adults showed a larger decrease in fixations (Maldarelli et al., 2015).

Stroke Processing Is Not About Stroke Order

Finally, it is becoming clear that evidence for a stroke effect is weak. In what regards, a stroke order effect, if there is motor simulation (re-instatement) during visual graph recognition, then presenting a consistent stroke order would prime perceptual end states (Parkinson and Khurana, 2007; Parkinson et al., 2010). Consequently, action-inconsistent sequences would interfere with visual graph recognition. It is not possible to predict facilitation in the former condition without predicting interference in the latter. This is the rationale of motor interference paradigms which are a credible evidence for a potential role of stroke processing in graph recognition by fluent readers (James and Gauthier, 2009).

Therefore, full examination of stroke order effects requires a proper baseline. Only then we can attest whether action-inconsistent sequences, which would activate incompatible graphic motor programs, and hence, incongruent graph representations, would interfere with visual recognition of a different graph (James and Gauthier, 2009). In fact, in studies with such baseline, action-inconsistent sequences did not interfere with visual graph recognition. For example, adult readers showed faster graph categorization when letters were primed by an inconsistent stroke order than by a static letter or a dynamic neutral circle (Parkinson and Khurana, 2007, Experiments 1 and 3). Thus, the inconsistent stroke order did not hinder graph recognition, it actually facilitated it, albeit less than the consistent stroke order. The same observation applies to the results of Patient NGN (Schubert et al., 2018) who showed an advantage in letter naming of dynamic letters. If such advantage was due to stroke order processing, then his letter recognition would have been hampered in the dynamic reversed (inconsistent stroke order) relative to the baseline condition. Instead, the inconsistent stroke order still led to better letter naming than the static condition. To be clear, both stroke orders led to better letter naming (accuracy: 89.4% for consistent stroke order; 80.3% for inconsistent stroke order; 73.7% for static letters) even though the inconsistent stroke order is unusual because it is contrary to the direction of writing (Simner, 1981). Notably, the results of Patient NGN even show that for 12 out of the 26 uppercase letters examined, the inconsistent order led to either better or as good performance as the consistent stroke order. If these results were about stroke (movement, dynamic) processing, then the inconsistent order would be compatible with a different letter, and hence, would interfere with visual graph recognition.

Likewise, when preliterate 5-year-old children were trained on new graphs *via* HW either with a self-defined or with a predefined stroke order, both groups showed similar post-training gains in graph recognition. More important, there was no advantage in visual recognition of dynamic graphs presented in the same (consistent) stroke order relative to a novel, inconsistent one (Merritt et al., 2020). The results by Wiley and Rapp (2021) also suggest that stroke processing is not the locus of the benefit from HW training. On the one hand, motoric representations derived from HW training differ from symbolic letter identities. On the other, dynamic training (mimicking stroke sequence) was not enough to lead to the emergence of abstract representations, given that all groups were exposed to dynamic graphs during training, but the group trained *via* typing did not show any hint of abstract letter representations after training (in contrast to what was found after training in HW or in visual categorization).

In sum, the overview of the literature presented in this second section shows that the stroke processing hypothesis is weak and sensorimotor representations are not able to explain the advantage from HW training when learning visual graphs. In fact, the available evidence, even the one that at first sight might seem compatible with sensorimotor representations can be accommodated by a perceptual learning mechanism. In the next section, we detail our proposal, integrating it with the available evidence. We also propose how to disentangle and to test the role of visual features and of strokes (motoric features) in future research. **Table 1** presents a summary of the hypotheses derived and the predictions that follow from our perspective.

OUR PROPOSAL: DISENTANGLING STROKES FROM VISUAL FEATURES

Stroke representations are not necessarily motor, gestural in format. In fact, sensorimotor representations are already a transduction (Machery, 2016). The emphasis by Rapp and colleagues (e.g., Rapp and Caramazza, 1997; Dufor and Rapp, 2013; Rothlein and Rapp, 2014) in the abstract, amodal quality of these representations highlights their symbolic nature, which gives them computational fitness (Mahon and Hickok, 2016). Indeed, the PMd, sometimes referred as a motor center (Roux et al., 2009; Longcamp et al., 2016), is involved in serial sublexical orthographic processes shared by writing and by pseudoword reading (Pattamadilok et al., 2016). From the reviewed evidence, it is clear that the benefit from HW is not about the motor act itself (e.g., Courrieu and de Falco, 1989; Xu et al., 2013, 2020). Our proposal is that the benefit from HW training when learning visual graphs is about computations over symbolic representations (for a similar proposal and supporting empirical evidence, see Wiley and Rapp, 2021). Whether these regard strokes (units of movement, primitives of HW), visual features (image components, primitives of visual object recognition), or both must first be seriously discussed. Several authors have pointed out that visual analysis and dynamic movement could be involved (e.g., Courrieu and de Falco, 1989; Cao et al., 2013a; Merritt et al., 2020; Vinci-Booher and James, 2020), but few studies tried to disentangle them.

What If Stroke Processing Were Involved in the Benefit From Handwriting Training?

We propose that if stroke processing were a core mechanism, then it would be about multi-system interplay, where top–down information from motor (and also possibly from phonological) system (Pegado et al., 2014) would assist subsequent graph recognition due to automatic spreading of activation within the orthographic network. If the benefit from HW is about top-down processes, then it would take time to evolve and, even when established, it would occur at a later stage in processing.

Indeed, Vinci-Booher and James (2020) have suggested that an extensive amount of experience may be required for parietal-frontal regions to develop a functional response during letter perception. Such top–down effects could also explain why the benefit from HW training is sometimes labile (that is, not always observed even in well-controlled studies: e.g., Naka and Naoi, 1995; Kiefer et al., 2015). Note, however that such flexible expression already suggests that stroke processing might not be a core operation. This mechanism is also incompatible with the observation of a benefit from HW training after a single training session of less than 20 min by preliterate children (e.g., Li and James, 2016; Guan and Wang, 2017) and of larger gains in post-training graph recognition in learners who are naïve to graphs or have less reading experience (Williams, 1969; Xu et al., 2020). Regarding the temporal course of a putative top–down effect of stroke processing during visual graph recognition, such effect would occur at a later time-window, whose assessment implies the adoption of high-temporal resolution methods as eye movement recordings or electroencephalography (EEG). However, to our knowledge, no study has hitherto examined this hypothesis.

Note that such stroke processing would be especially relevant for highly confusable graphs like mirror images (e.g., d and b), whose discrimination would be facilitated by bidirectional connections between abstract graph representations and the different motoric representations (Pegado et al., 2014; Longcamp et al., 2016). This prediction is compatible with the available evidence. However, it is also compatible with the operation of a perceptual learning mechanism (for a discussion, see also, Araújo et al., 2021).

Perceptual Learning and Visual Segmental Analysis Might Be a Parsimonious Account

Given the inconsistent evidence, we propose that rather than about stroke processing, another mechanism could be responsible for the benefit from HW training. From the evidence reviewed thus far both the stroke processing hypothesis and the perceptual variability hypothesis are limited. However, the visual analysis hypothesis is promising, given that none of the available evidence is incompatible with it. The major problem of this hypothesis is that few studies have systematically examined it, while testing the alternatives. We join other authors (e.g., Gibson, 1970; Williams, 1975; Kaufman, 1980;

TABLE 1 | Summary of our proposal.

Putative mechanism	Symbolic representations involved	Predictions	Refuting evidence	Future directions
Stroke processing (motoric primitives)	Abstract motoric	Dynamic letter presentation during training facilitates subsequent visual graph recognition	- Courrieu and de Falco, 1989; - Wiley and Rapp, 2021.	Effects of dynamic graphs vs. static decomposed graphs
		Multi-system interplay, top–down effects from abstract motoric representations ⇒ late effects in training (in a later phase)	- Benefit of HW in very short, single session training (e.g., Naka and Naoi, 1995; Suggate et al., 2016); - Larger benefit from HW training in naive participants (Williams, 1975; Xu et al., 2020).	- Manipulation of training regime: single vs. multi-session training (prediction: smaller benefit early on and for single-session training); - Potential involvement of sleep; - Time-course of HW training effects: EEG or eye-tracking methods.
		Larger benefit from HW training on highly confusable graphs (e.g., d and b) because of different motor representations ⇒ mirror-image letters (e.g., p and q) would lead to smaller interference than motoric similar letters (e.g., P and R).	(still untested)	Concurrent manipulation of visual vs. motoric similarity.
Perceptual learning (visual analysis)	Abstract graph identities	HW is a natural way of promoting detailed visual analysis and learning of diagnostic features, leading to emergence of abstract graph identities ⇒ visual analysis and HW trainings result from operation of the same mechanism.	None (all studies where visual analysis vs. HW trainings show the same magnitude of benefit in graph recognition (e.g., Williams, 1969; Seyll et al., 2020).	- Bayesian statistics; - Multivariate pattern analysis of brain responses with EEG; - Training naïve vs. literate participants; - Manipulation of script proximity (e.g., diagnostic features, writing direction); - Generalization effects to untrained graphs.
		Larger benefit from HW training on highly confusable graphs (e.g., d and b) because of visual segmental analysis ⇒ mirror-image letters (e.g., p and q) would lead to larger interference than motoric similar letters (e.g., P and R)	(Still untested)	Concurrent manipulation of visual vs. motoric similarity.

Courrieu and de Falco, 1989; Mayer et al., 2020; Seyll et al., 2020) and in what regards the benefit from HW training when learning visual graphs, we propose that HW is a vehicle for optimizing perceptual learning of the new visual graphs.

Letter recognition involves perceptual processes based on the extraction of elementary visual features (Pelli et al., 2003, 2006). Letter knowledge, the gateway for reading across reading development (Grainger, 2018), comprises knowledge of the letter form and of phonological correspondences. Letter discrimination is a very low-order aspect of reading, but it precedes decoding graphs into phonological counterparts: "the discovery of distinguishing characteristics and the extraction of invariant orders, both set up as relational observations, are the ultimate prerequisites for learning to read. It is only after such discriminations are learned that recognition and production (writing) can be achieved" (Kaufman, 1980, p. 57).

The visual system is highly solicited during HW, and hence, HW is an optimal vehicle for perceptual learning. To become able to successfully reproduce a graph, HW must rely on a detailed and explicit visual analysis of the graph, especially of diagnostic features, and their relationship in shape, orientation, and visuospatial arrangement (Courrieu and de Falco, 1989; Seyll et al., 2020). One must learn the features that are critical to become able to differentiate visual graphs (Gibson et al., 1962; Gibson, 1969, 1970). This is all about perceptual learning, which establishes a deep relationship between perception and experience (Gilbert and Li, 2012; Goldstone and Byrge, 2015). Furthermore, this proposal agrees with evidence on eye movement patterns during copy of single letters by preliterate children and literate adults (Maldarelli et al., 2015).

We are not arguing that motor learning is not part of the learning experience promoted by HW, but rather that the benefit from HW training when learning visual graphs is especially because HW is a natural way of promoting detailed visual analysis (Seyll et al., 2020). The rationale is that the benefit from HW is because this training implies visual analysis, facilitating the creation of perceptual representations that then underpin visual graph recognition. Therefore, even when training is non-motor, without a graphomotor task, if it taps into graphs' diagnostic features, then the gains will be as large as the benefit from HW training.

The available evidence, since the earliest studies until the most recent ones (e.g., Williams, 1969; Seyll et al., 2020), fully agrees with this prediction. When training implies visual discrimination of distinctive features of graphs, either *via visual composition* (where participants are presented with several individual features and select those that compose the graph: Seyll et al., 2020), *segmental, non-dynamic* (where the presented graph is decomposed into its static features: Courrieu and de Falco, 1989), *match-to-sample* (where learners select from a set, including mirror images and plane rotations, which one corresponded to the graph, with feedback on response: Williams, 1969, 1975), the gains in visual graph recognition are similar (or even larger: Williams, 1969, 1975) to those after HW training.

To the best of our knowledge, no study showed significantly larger benefits from HW training when compared to non-motor visual segmental conditions requiring explicit visual analysis or attending to distinctive features of graphs. Furthermore, all the available evidence on which HW training led to the larger benefit in subsequent visual graph recognition can be accommodated by a visual analysis account.

Notably, perceptual learning and visual analysis can also accommodate evidence that at first sight seems compatible with a stroke processing's explanation (Parkinson and Khurana, 2007; James and Gauthier, 2009; Parkinson et al., 2010; Schubert et al., 2018). Not only the stroke processing hypothesis has serious limitations (as discussed in section "The stroke processing hypothesis") but, more important, for all studies in which visual feature and stroke processing were not disentangled, either one could be the key factor because many graphs are similar both in visual features and in strokes. Indeed, most studies suffer from this fundamental ambiguity regarding similarity (Rapp and Caramazza, 1997). For studies that did not find stroke interference relative to the static baseline (e.g., Parkinson and Khurana, 2007; Schubert et al., 2018), the visual analysis' explanation is credible. Regardless of stroke order being consistent or not, the presentation of decomposed visual items (e.g., in Parkinson and Khurana, 2007; Parkinson et al., 2010; Itaguchi et al., 2015; Schubert et al., 2018) necessarily implies presentation of separate visual features, enhancing visual analysis of graphs, as happens in HW training (e.g., Williams, 1969; Courrieu and de Falco, 1989; Seyll et al., 2020).

Mere visual exposure to highly confusable graphs is not enough. When trained on mirror-image graphs, learners who were trained on graphs' shape only (not on the diagnostic feature) showed worse subsequent visual graph recognition than learners whose training focused on orientation (the diagnostic feature; Pick, 1965; Caldwell and Hall, 1969, Experiment 1; Williams, 1969; Tawney, 1972; Samuels, 1973; Spectorman et al., 1977). More interesting, these pioneer studies showed that such focus in diagnostic features leads to *generalization* from the trained graphs to novel, untrained ones, including real letters (Pick, 1965; Tawney, 1972; Nelson and Wein, 1974). Non-motor visual training can thus boost mirror-image discrimination. This is not a paradox because mirror-image invariance is a perceptual bias (Bornstein et al., 1978; Kolinsky et al., 2011). It is not a low-level visual property computed in early visual occipital areas (Dehaene et al., 2005). Indeed, mirror images (e.g., d and b) have very different retinal projections. Their perceptual equivalence occurs at a higher level (like that of structural description of non-linguistic objects), underpinned by the vOT (Logothetis et al., 1995; Dehaene et al., 2015).

More important, visual analysis promoted by HW could also explain the supposed motor interference by letters, given that the two properties were intertwined (James and Gauthier, 2009). We all agree that graphs are not just visual objects, but graph shapes, graph names, and graph motor plans are representational dimensions that are dissociable (Rothlein and Rapp, 2014; Zhai and Fischer-Baum, 2019; Wiley and Rapp, 2021). Therefore, to test our alternative, one must manipulate the similarity of concurrent letters within-trial in terms of visual features and in terms of strokes. If HW assists in visual segmentation, then greater interference would be found for letter pairs that share more visual features, regardless of their (dis)similarity in strokes. If it is about activation of motoric representations, then pairs composed of highly confusable letters as mirror images (e.g., p and q), which share visual features except orientation but do differ in motor strokes, would elicit significantly less interference than letters that are visually less similar but closer in stroke composition (e.g., P – R). The acid test is one in which visual feature processing and stroke processing are confronted (see **Table 1**).

Although this strategy has been rare, such studies are particularly revealing (Courrieu and de Falco, 1989; Zhai and Fischer-Baum, 2019; see also Rapp and Caramazza, 1997). Indeed, Zhai and Fischer-Baum (2019) showed that visual similarity of graphs was the best predictor of kanji recognition (in a same-different matching task) for adults who were either readers of Chinese or not (the latter were Latin-alphabet readers of English). It was only for Chinese readers that phonology and semantics also tended to be significant predictors. Stroke processing was never a reliable predictor of kanji discrimination. In fact, even when stroke similarity was the only predictor considered (and even when it included as parameters: sequence of component strokes, shared first stroke, stroke bigram familiarity, stroke-motor features), it was still not a reliable predictor. Bayesian statistics further demonstrated that stroke similarity had no contribution at all for kanji discrimination either by naïve or expert observers (Zhai and Fischer-Baum, 2019). However, these results speak to the mature reading system and not to the benefit that HW training could have when learning visual graphs.

In this regard, the results of the training study by Courrieu and de Falco (1989) with 3–6 years old preliterate children are especially revealing. Relative to a control visual-only group (non-segmental non-dynamic), the group trained on letters *via* HW showed similar post-training gains in visual letter recognition as the groups trained on letters presented broken down into static visual features either without HW (segmental non-dynamic group) or with HW training (segmental dynamic group). There was no added value of HW; the key factor was visual analysis *via* segmental training and not stroke processing. These results also highlight another aspect that deserves to be examined in future studies, which regards whether dynamic stimuli without HW (which has been used in some research to mimic stroke order without a motor action; e.g., Parkinson and Khurana, 2007; Schubert et al., 2018; Merritt et al., 2020) could fully elicit visual segmental analysis. To our knowledge no study has yet compared these two training conditions, that is, dynamic unfolding vs. static visual decomposition of graphs. However, the results of Wiley and Rapp (2021) suggest that dynamic unfolding is not enough given that when learners were exposed to dynamic letters, training *via* typewriting did not lead to the emergence of symbolic graph representations. It was only training *via* visual categorization of graphs (graph/non-graph decision) or *via* HW which led to the emergence of symbolic representations. Note that the visual (active) training in Wiley and Rapp (2021) did not focus on either decomposed or diagnostic features of graphs; it just involved symbol/non-symbol categorization. Indeed, pioneer research has clearly shown that visual training only leads to the same benefit as HW training when the former is fully focused on diagnostic features like orientation (e.g., d and b; Koenigsberg, 1973; Williams, 1975) or when visually segmented graphs are presented during training (Courrieu and de Falco, 1989). Mere visual exposure is not enough to elicit visual segmental analysis (e.g., Pick, 1965; Caldwell and Hall, 1969, Experiment 1; Williams, 1969; Tawney, 1972; Samuels, 1973; Spectorman et al., 1977).

DISCUSSION

Cognitive science has recently shown a renewed interest in the role of HW training when learning to read (for an overview, see, James, 2017). Indeed, a large body of empirical evidence supports the advantage from HW training relative to control training in subsequent visual graph recognition (Araújo et al., 2021; for an overview, see, James, 2017; e.g., Williams, 1969; Longcamp et al., 2006, 2008; James, 2010; Bara and Gentaz, 2011; Guan et al., 2011; Suggate et al., 2016; Labat et al., 2020; Mayer et al., 2020; Seyll et al., 2020). However, the nature of the underlying cognitive mechanism has been elusive and rarely addressed (Gibson, 1970; Williams, 1975; Kaufman, 1980; Li and James, 2016; Zhai and Fischer-Baum, 2019; Mayer et al., 2020; Seyll et al., 2020; Vinci-Booher et al., 2021). The available theoretical proposals have hitherto been unspecified. Therefore, it was not fully clear which predictions would follow and which patterns of performance would empirically distinguish them. In this work, we presented the most promising theoretical accounts, detailed their predictions, and critically revisited key empirical evidence.

We join other authors (e.g., Gibson, 1970; Kaufman, 1980; Courrieu and de Falco, 1989; Mayer et al., 2020; Seyll et al., 2020) in the proposal that HW training is a vehicle for perceptual learning of visual graphs. Visual segmental analysis would be the key element in HW training by highlighting diagnostic features of visual graphs which then would assist the emergence of perceptual representations to be involved in subsequent visual graph recognition (see also Wiley and Rapp, 2021).

Although beyond the scope of the present work, the theoretical proposals discussed here have implications for the nature of mental representations. Embodied and symbolic cognitive accounts are two perspectives with dramatically different approaches in this regard. Note that both proposals are able to accommodate the available fMRI evidence (e.g., Longcamp et al., 2003, 2008; James and Atwood, 2009; James, 2010; James and Engelhardt, 2012; Nakamura et al., 2012; Vinci-Booher et al., 2016, 2021; Vinci-Booher and James, 2020) but they do differ on the cognitive mechanisms responsible for such effects. According to the embodied sensorimotor accounts, the fronto/parietal regions within the writing network are activated when viewing graphs or written words because these regions underpin motoric representations that are core of orthographic (sensorimotor) representations (e.g., Parkinson and Khurana, 2007; Longcamp et al., 2008, 2016; James and Atwood, 2009; Cao et al., 2013b; Itaguchi et al., 2015). According to symbolic accounts, the observed motor activation is rather due to information spreading throughout the orthographic system; it is coactivation, not causation (e.g., Rapp and Caramazza, 1997; Rothlein and Rapp, 2014; Mahon and Hickok, 2016). In fact, from the reviewed literature, we must conclude that there is no compelling evidence that embodied representations are necessary for understanding the benefit from HW training in visual graph recognition (for a meta-analysis and discussion, see, Araújo et al., 2021). In fact, the recent results of Wiley and Rapp (2021) show that HW training leads not only to the emergence of motoric representations but also of dissociable symbolic orthographic representations.

The present work has also raised several questions to be addressed in future research. We thus present further predictions and future directions that could be enlightening in what regards the mechanism underpinning the benefit from HW training when learning visual graphs. First, although the idea of a perceptual learning mechanism *via* visual analysis seems parsimonious, it is mainly corroborated by behavioral evidence showing that this type of visual training leads to either similar or even larger post-training gains than HW training (e.g., Williams, 1969, 1975; Koenigsberg, 1973; Courrieu and de Falco, 1989; Li and James, 2016; Seyll et al., 2020). In the present work, we discussed how this visual analysis hypothesis could explain prior evidence which did not test it nor considered it. We also presented the arguments in favor of this proposal, considering detailed predictions. However, we must acknowledge that even if the behavioral effects are the same, the benefit from visual segmental analysis and HW trainings might result from different neurocognitive mechanisms. Cognitive, neural, and behavioral changes when learning visual graphs will be closed intertwined and all are relevant for understanding the underlying mechanism. At the cognitive level, we believe that the predictions presented here, especially those regarding the opposition between stroke and visual feature processing, will be especially revealing (see **Table 1**). In what regards the neural implementation, a promising technique to address the underlying mechanism is *multivariate pattern analysis* of brain responses, especially when adopted with high-temporal resolution techniques as EEG (King and Dehaene, 2014). Such classification algorithms could assist in accomplishing three aims: (i) determining the temporal course of emerging representations of graphs in the brain; (ii) testing whether the brain pattern of response is able to predict post-training gains in visual graph recognition; (iii) testing whether one can predict which type of training the participants were in (e.g., HW vs. visual analysis) based on patterns of brain responses to visual graphs after training. Achievement of these aims would be especially revealing on whether the similar benefits from HW training and visual segmental training (e.g., Courrieu and de Falco, 1989; Seyll et al., 2020) do reflect the operation of the same neurocognitive mechanism and on whether top–down effects related with a late stage of processing would be involved in the benefit from HW training (see **Table 1**). In this regard, convergence across methods will provide a better characterization of the components involved. This line of research is thus relevant to the future development of our framework.

Second, we also discussed two loose ends of this topic that hopefully will be considered in future research. We are hardly the first to consider them, for which the earliest studies contributed with deep insights (e.g., Tawney, 1972; Williams, 1975; Kaufman, 1980; Kirk, 1980), albeit these pioneer works have (surprisingly) been underestimated by recent research. On the one hand, *training regime* (i.e., total amount, frequency, and duration of training) has been overlooked (although with references by Jeffrey, 1958; Longcamp et al., 2006), probably because the benefit from HW has been found both in single and multiple session training (e.g., Williams, 1969; Li and James, 2016; Mayer et al., 2020; Seyll and Content, 2020). However, the nature of graph representations may change as a function of training regime, which would agree with the different patterns of fMRI activation found when children (6-year-old beginning readers and 8-year old) and adults (fluent readers) viewed letters (Vinci-Booher and James, 2020) and the observation that functional connectivity between visual and motor brain regions found immediately after HW training were already gone after one week (Vinci-Booher et al., 2021).

Notably, a manipulation of training regime could also be key in hypothesis testing. If the benefit from HW training were about stroke processing, it would take time to develop, and hence, the benefit relative to control training would increase along sessions. Alternatively, if the benefit from HW training is due to visual analysis, then the largest difference relative to control training would occur early on, which would dissipate with stabilization of graph representations. Nonetheless, whenever testing of visual graph recognition occurs multiple times along training, then the contribution of testing for the learning curve must be controlled to ensure that it is not confounded with the independent contribution of training (for this kind of strategy, see, Wiley and Rapp, 2021). Training along multiple sessions also allows for the involvement of sleep, which is relevant in perceptual learning and visual discrimination (Stickgold et al., 2000). Indeed, sleep has a significant role in the stability of post-training gains in mirror-image discrimination of graphs after HW training (Torres et al., 2020). In this vein, follow-up assessment is of critical importance (Longcamp et al., 2005, 2008; Vinci-Booher and James, 2020; Vinci-Booher et al., 2021). However, very few studies included a follow-up and with a disperse interval, from one week to several months. When the new graphs were real letters, these studies also had the possible confound of uncontrolled post-training exposure (e.g., Longcamp et al., 2005).

On the other hand, when learners are already experts in reading and HW in their first script, a literacy-specific network is already established. Therefore, they might rely on it when learning new graphs. The research has suggested, however, that this might not be the case. Indeed, neurocognitive and behavioral effects of leaning a new script are similar in (literate) adults and (preliterate) children, even though besides reading skills there is also an age/maturation confound in this comparison (James and Atwood, 2009; Brem et al., 2010; James, 2010; James and Engelhardt, 2012; Brem et al., 2018; Vinci-Booher et al., 2021). Additionally, the earliest studies have examined possible generalization effects from the graphs trained *via* HW to novel, untrained graphs, and found that such generalization occurred and assisted subsequent learning of letter-sound correspondences (Pick, 1965; Tawney, 1972; Nelson and Wein, 1974). However, since then this generalization effect has not been considered, leading to several questions. For example, could generalization effects depend on the type of diagnostic features of the new script and whether these features resemble or not those of the first script? And if this were the case, with which time course?

These questions also highlight the link between the studies on the benefit from HW training when learning visual graphs and the field of perceptual expertise. Indeed, perceptual expertise can be contrasted to other forms of perceptual learning as it is characterized by robustness and generalization to new contexts and to new items within the expertise domain (Curby and Gauthier, 2010). This field has systematically focused on the interaction between participant (naïve vs. expert), item (novel vs. old), and task demands (individuation vs. categorization), which are all known to be important in development and in expression of expertise.

In fact, the benefit from HW training when learning visual graphs is, in our view, a paradigmatic example of perceptual and of motor expertise. Note that, in literate adults, HW is highly automatic; it consists of rapid sequences of short movements with fast changes in direction, resulting in high-quality, stable, and consistent reproduction of graphs. It is clearly an ecological example of motor expertise like playing a musical instrument (Palmis et al., 2017; Calmels, 2020). Therefore, the convergence with research from perceptual and motor expertise could be fruitful for a deeper understanding of the cognitive mechanism underpinning the benefit from HW training in visual graph recognition (see, e.g., Folstein and Monfared, 2019). This research is also relevant for the expertise literature, given that it is easier to study expertise in a domain with many participants and where relevant stimuli is widely available.

In summary, the investigation of the cognitive mechanism underpinning the benefit from HW training when learning visual graphs goes beyond its realm. It can provide insights into the principles, limits, and possibilities of learning of cultural activities. It is also relevant for generation of testable hypotheses about interactions between training modes and performance benefits. In a broader scope, it also speaks to the nature of cognitive representations. Finally, it has relevance for Education and public policy because it can translate in better designing of literacy programs. When learning visual graphs, HW involves multiple components. Thus, we can no longer advocate the adoption of HW as a holistic school activity. The critical processes can and should be separated in order to implement the best educational strategies in literacy instruction.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: OSF Preprints. doi: 10.31219/osf.io/quywt; https://osf.io/wzdxn/.

AUTHOR CONTRIBUTIONS

TF and SA conceptualized together this work, critically revised the manuscript, and prepared the revised version. TF has the first authorship and wrote the first draft of the manuscript. Both authors approved the final version submitted and the revised version.

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ORIGINAL RESEARCH
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Audiovisual Learning in Dyslexic and Typical Adults: Modulating Influences of Location and Context Consistency

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Learning to read involves efficient binding of visual to auditory information. Aberrant cross-modal binding skill has been observed in both children and adults with developmental dyslexia. Here, we examine the contribution of episodic memory to acquisition of novel cross-modal bindings in typical and dyslexic adult readers. Participants gradually learned arbitrary associations between unfamiliar Mandarin Chinese characters and English-like pseudowords over multiple exposures, simulating the early stages of letter-to-letter sound mapping. The novel cross-modal bindings were presented in consistent or varied locations (i.e., screen positions), and within consistent or varied contexts (i.e., co-occurring distractor items). Our goal was to examine the contribution, if any, of these episodic memory cues (i.e., the contextual and spatial properties of the stimuli) to binding acquisition, and investigate the extent to which readers with and without dyslexia would differ in their reliance on episodic memory during the learning process. Participants were tested on their ability to recognize and recall the bindings both during training and then in post-training tasks. We tracked participants' eye movements remotely with their personal webcams to assess whether they would re-fixate relevant empty screen locations upon hearing an auditory cue—indicative of episodic memory retrieval—and the extent to which the so-called "looking-at-nothing behavior" would modulate recognition of the novel bindings. Readers with dyslexia both recognized and recalled significantly fewer bindings than typical readers, providing further evidence of their persistent difficulties with cross-modal binding. Looking-at-nothing behavior was generally associated with higher recognition error rates for both groups, a pattern that was particularly more evident in later blocks for bindings encoded in the inconsistent location condition. Our findings also show that whilst readers with and without dyslexia are capable of using stimulus consistencies in the input—both location and context—to assist in audiovisual learning, readers with dyslexia appear particularly reliant on consistent contextual information. Taken together, our results suggest that whilst readers with dyslexia fail to efficiently learn audiovisual binding as a function of stimulus frequency, they are able to use stimulus consistency—aided by episodic recall—to assist in the learning process.

Keywords: cross-modal binding, looking-at-nothing, paired associate learning, visual-phonological associations, webcam-based eye-tracking, developmental dyslexia (DD), episodic memory, reading

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INTRODUCTION

Quickly binding visual forms to phonological forms is a fundamental skill in the initial stages of grapheme-phoneme learning, providing a foundation for the later development of integrated visual-phonological representations that are crucial for skilled reading. Most children are able to convert written letters and words into sounds effortlessly, and later retrieve them as a single audiovisual unit, eventually becoming proficient readers. However, some struggle to form novel audiovisual mappings, a difficulty that can persist well into adulthood (Blau et al., 2009; Jones et al., 2013b, 2018). Readers with developmental dyslexia exhibit indications of less-integrated grapheme-phoneme representations (Blau et al., 2009, 2010; Blomert, 2011; Warmington and Hulme, 2012; Aravena et al., 2013, 2018; Žarić et al., 2015), a deficit owing in part to their comparatively poorer cross-modal binding skills (Aravena et al., 2013; Jones et al., 2013b, 2018; Žarić et al., 2015; Albano et al., 2016; Toffalini et al., 2018, 2019; Garcia et al., 2019). Despite the well-known link between audiovisual integration and ultimate reading attainment, the cognitive mechanisms underlying typical and atypical cross-modal binding ability are not yet fully understood. Here, we examine how adults with dyslexia and typical readers may differ in their reliance on episodic memory cues as they acquire novel cross-modal bindings that vary in location-related and contextual consistency over the course of the learning process.

Learning to read requires establishing new representations in memory: not only separate representations for novel visual/orthographic and phonological forms, but also correspondences between them. A commonly used task to tap the acquisition of novel visual-phonological mappings is cross-modal *paired associate learning* (PAL; e.g., Warmington and Hulme, 2012; Wang et al., 2017; Jones et al., 2018; Calabrich et al., 2021), in which participants must learn that a given visual symbol is associated with a particular phonological sequence (typically a pseudoword). This learning process is thought to emulate the associative mechanisms underpinning grapho-phonological mappings in the early stages of literacy development (Hulme et al., 2007; Warmington and Hulme, 2012). An extensive body of research demonstrates that readers with dyslexia are generally more error prone on such cross-modal PAL tasks, relative to typical readers (Messbauer and de Jong, 2003; Warmington and Hulme, 2012; Litt and Nation, 2014; Wang et al., 2017; Jones et al., 2018; Toffalini et al., 2018), and, crucially, performance on PAL tasks correlates with individual differences in reading skill (Hulme et al., 2007; Warmington and Hulme, 2012). In particular, visual-verbal PAL ability is a unique predictor of both word recognition and non-word reading (Warmington and Hulme, 2012).

Whilst PAL tasks are useful in showing the relationship between visual-verbal learning and reading ability, such paradigms do not typically elucidate the learning mechanisms that distinguish good and poorer performance in PAL and reading. However, in other learning contexts, the ability to track simple statistics, such as stimulus repetition and sequences is a strong predictor of reading ability (Ahissar, 2007), and poorer readers are liable to forget previous exposures to perceptual stimuli (Jaffe-Dax et al., 2015, 2016, 2017), potentially leading to "noisier" processing of a current stimulus. We can therefore reasonably extrapolate that statistical tracking, implicating episodic memory and associated decay, may play an important role in determining the effectiveness with which audiovisual associations can be created and established over repeated exposures. Indeed, learning audiovisual stimuli requires accurate encoding of temporal and spatial characteristics in order to appropriately bind visual and phonological features and to create a composite representation. Temporal and spatial properties, commonly encoded in episodic memory, share patterns of neural activity, and can be used as cues to aid memory retrieval when required (Tulving, 1972; El-Kalliny et al., 2019). In the context of language, episodic memory of the context in which a word is encountered plays an important role in acquisition (Stark and Stark, 2016). Through repetition and rehearsal, representations become gradually less episodic and more abstract, representative of an amalgam of consistent stimulus properties, with the result that specific episodic details, such as spatial and temporal properties, become less and less relevant (Squire and Zola, 1998; Stark and Stark, 2016). In literacy acquisition, this process also entails a gradual increase in automatization of print reading, such that phonology is eventually accessed automatically and without recourse to an effortful retrieval process, implicating episodic memory resources (LaBerge and Samuels, 1974; Ehri and Saltmarsh, 1995; Ehri, 2005; Jones et al., 2013a,b, 2018).

Recently, Jones et al. (2018) examined the role of statistical learning mechanisms and episodic memory in the context of a PAL task, in which groups of readers with dyslexia and typically reading adults learned to associate a sequence of unfamiliar characters (i.e., Mandarin Chinese characters) with consistently paired pseudowords. As participants attempted to retrieve each target's corresponding pseudoword, their eye movements were tracked on the now-blank screen to examine whether they consulted the spatial location of the target item in order to support retrieval. Such "looking-at-nothing" behavior would imply re-activation of integrated memory representations: re-activating one of the target features, such as its phonological representation, may automatically drive the memory system to re-activate other features as well, including its visuospatial location, mechanistically or epiphenomenally producing eye movements toward that location (Altmann, 2004; Ferreira et al., 2008; Scholz et al., 2011; Johansson and Johansson, 2020; Kumcu and Thompson, 2020) when rebinding the multiple features again. Although such looking-at-nothing movements can suggest both successful memory encoding and reactivation in the earliest stages of learning, they also become less frequent as learners consolidate a memory representation, presumably abstracting away such details (Spivey, 2007; Scholz et al., 2011). For readers with dyslexia in Jones et al. (2018) study, fixating a target's former location within the current trial was associated with greater recall accuracy (which nevertheless stayed well below par, compared with the typical reader group), and fixating a distractor's former location was associated with lesser recall accuracy, both compared to a no-fixation baseline. For typical readers, in contrast, fixating a target's former location within the current trial was only associated with greater recall accuracy when it had also appeared in the same location in a previous trial. Thus, whilst readers with dyslexia showed sensitivity to location information for only the current trial, typical readers showed a sensitivity to longer-range statistical regularities over multiple exposures. This pattern suggests that typical readers use spatial location as a cue to retrieve such bindings, even when location information is task irrelevant, and this ability may specifically be impaired in readers with dyslexia (Jones et al., 2013b, 2018; Albano et al., 2016; Toffalini et al., 2018).

Audiovisual learning is therefore modulated by the statistical sensitivity and associated episodic memory usage that individuals of different reading abilities bring to bear on the task. However, we are yet to discover how specific stimulus configurations during learning affect learning efficiency in dyslexic and typical readers. In general, presenting multiple items in a temporally adjacent format increases the association between these items (El-Kalliny et al., 2019). However, isolating and retrieving *individual* memories encoded in temporal proximity can only succeed if the distinct memories were separated in neural space during encoding (Sheehan et al., 2018; El-Kalliny et al., 2019). In other words, our ability to discriminate between different past experiences that share similar features largely depends on the brain's capacity to store *distinct* activity patterns to represent *each* of these experiences (Madar et al., 2019). Readers with dyslexia have been shown to benefit from having novel cross-modal bindings presented in a fixed temporal order (Toffalini et al., 2018), but, to the best of our knowledge, there is no comprehensive study of how stimulus configurations during learning affect typical and dyslexic readers' capacity to learn reading-related items. This is an important next step, since dyslexic readers' reduced ability to create stable representations over multiple exposures is plausibly related to their inability to identify an item as distinct from other items presented in temporal and spatial proximity.

In the present study, we examine whether specific statistical properties of stimulus exposures differentially affect learning in adults with and without developmental dyslexia. To this end, we designed a PAL task (adapted from Jones et al., 2018), in which we manipulated the consistency of the spatial and contextual stimulus properties during encoding. We created arbitrary associations between monosyllabic pseudowords—following English phonotactics (e.g., /gɔp/)—and Mandarin Chinese characters (e.g., 日). Our participants were unfamiliar with both the visual and auditory stimuli, thus ensuring an arbitrary relationship between these visual-verbal bindings, and simulating the early stages of orthography-to-phonology mapping.

In terms of accuracy, we predicted that, compared with typical readers, readers with dyslexia would show generally higher error rates, and a shallower function of learning (Messbauer and de Jong, 2003; Aravena et al., 2013; Jones et al., 2013b, 2018; Albano et al., 2016; Toffalini et al., 2018, 2019; Garcia et al., 2019). Further, whilst we predicted that consistently presenting targets in the same spatial location and/or in the context of the same alternatives would generally decrease error rates, we suspected that these consistency effects would disproportionately benefit readers with dyslexia: though previous work indicates that readers with dyslexia are less likely to track single-feature statistics (e.g., location) over multiple exposures (Jones et al., 2013b, 2018; Toffalini et al., 2018), providing *both* spatial (i.e., item screen location) *and* contextual consistencies (i.e., item co-occurrences) might prove particularly advantageous to help impaired readers bootstrap degraded representations/poorer retrieval of individual items. Indeed, readers with dyslexia are known to engage in chunking strategies such as whole word memorization in order to avoid phonological sequencing, which is problematic in dyslexia (Ullman and Pullman, 2015).

To consider the possible role of implicit memory retrieval, we estimated participants' reference to episodic detail *via* a looking-at-nothing paradigm. During the main training and recognition task, we made novel use of webcam-based technology (WebGazer.js: Papoutsaki et al., 2016) to remotely track participants' eye movements as they viewed a blank screen immediately after hearing an auditory cue. Even though the use of webcam-based eye tracking in behavioral science is still in its infancy, previous investigations have demonstrated the method's suitability to detect fixations reliably and to replicate in-lab findings with minimal reduction in data quality (Bott et al., 2017; Semmelmann and Weigelt, 2018). With this approach, we sought to ascertain whether looks to relevant blank screen locations would modulate recognition accuracy. Following previous work (Jones et al., 2018), we predicted that readers with dyslexia would have a stronger tendency to make errors following fixations to blank screen locations previously occupied by distractor items. We also expected repetition to diminish the link between accuracy and looking-at-nothing behaviors for all participants, reflecting direct access to increasingly abstracted memory representations (Richardson and Spivey, 2000; Ferreira et al., 2008; Scholz et al., 2011; Wantz et al., 2016). Finally, our factorial manipulation allows us to consider higher-order interactions, but it is challenging to derive and evaluate specific predictions for such interactions, and robustly assessing such interactions would require more power than our study provides (Button et al., 2013); as a compromise, we note such interactions but consider them primarily as invitations for future research.

In addition to the main training and recognition task, we collected three additional measures of item learning. We added (1) cued-recall trials at regular intervals in the main training task to test participants' ability to recall and verbalize the specific pseudoword associated with a given character. Moreover, to probe participants' longer-term memory, we tested participants' ability to (2) recall, and (3) recognize the bindings in two separate tasks administered approximately 10 min after the main task. This approach allowed us to assess whether the episodic memory effects of spatial and contextual cues carried over and differentially modulated longer term retention of the bindings for the two reading groups. Due to the gradual consolidation process engendered by repeated exposures, we predict that performance in the subsequent post-training cued-recall and recognition tests would be less strongly modulated by episodic memory cues. We also predicted overall higher error rates in recall than in recognition, given that recognition is wont to succeed even when recall fails (Tulving, 1982).

MATERIALS AND METHODS

Participants

Thirty-five readers with dyslexia (age: *M* = 28.17, *SD* = 7; 23 females) and thirty-five typical readers (age: *M* = 23.55, *SD* = 6.14; 19 females) were tested remotely. All participants were native speakers of British English, recruited through Bangor University and Prolific.[1] A similar level of education was reported in both groups (dyslexia: *M* = 15.8 years, *SD* = 2.37; typical: *M* = 14.8 years, *SD* = 2.11; *p* = 0.09), and none of the participants reported any history of psychiatric and/or neurological diseases, visual and/or hearing impairments, or any other risk factors. Group membership (i.e., typical reader or individual with dyslexia) was confirmed *via* a battery of literacy tests. All participants provided informed consent, were naïve to the purpose of the experiment, and were unfamiliar with the experimental stimuli. Participants received course credits or payment for their time. The experiment was approved by Bangor University's Ethics Committee.

Literacy and General Cognitive Ability Measures

Participants' group membership was validated *via* a battery of eight short tests: (1) *Adult Reading Questionnaire* (ARQ, Snowling et al., 2012); (2) word reading efficiency and (3) phonemic decoding efficiency subscales of the *Test of Word Reading Efficiency* (TOWRE, Torgesen et al., 1999); (4) letter and (5) digit versions of the *Rapid Automatized Naming* (RAN) subtest from the *Comprehensive test of Phonological Processing* (CTOPP, Wagner et al, 1999); (6) *Similarities* subtest from the *Wechsler Adult Intelligence Scale* (WAIS, Wechsler, 1981) as an index of verbal intelligence quotient (IQ); (7) *Matrix Reasoning* from the *Wechsler Abbreviated Scale of Intelligence* (WASI, Wechsler, 1999) as an index of non-verbal IQ; and (8) computerized forward and backward digit span tests in which participants first saw sequences of digits and were then prompted to type the digits in the same or reverse order. Tests 1–5 were administered shortly before the main training and recognition task, whereas the remaining were administered immediately after the main task.

Stimuli

Thirty-six consonant-vowel-consonant (CVC) pseudowords (e.g., /gɔp/) were arbitrarily matched to thirty-six Mandarin Chinese characters (e.g., 日), as in Jones et al. (2018). The pseudowords followed English phonotactic rules and were generated with Wuggy (Keuleers and Brysbaert, 2010), a multilingual pseudoword generator. The auditory stimuli were recorded by a female native speaker of British English and digitized at 44.1 kHz on Praat (Boersma and Weenink, 2021). Each Mandarin Chinese character was consistently presented with the same CVC pseudoword over the course of the experiment.

Procedure

The experiment was programmed and deployed online on Gorilla Experiment Builder (Anwyl-Irvine et al., 2020). It included three tasks, presented in the same order to all participants: (1) training, *via* a six-block recognition task with interspersed cued-recall trials; (2) a single-block cued-recall test; and (3) a single-block recognition test.

Access to the experiment was restricted to desktop and laptop users only; mobile phones and tablets were disallowed. Participants were instructed to wear earphones or headphones, to place their computers on a desk, and to do the tasks individually in a quiet and well-lit room. To minimize distraction and correct for varying screen sizes and resolutions, participants were prompted to activate the full screen mode on their computers before proceeding to the experimental tasks. On average, participants sat 546.03 mm (*SD* = 101.02) from their computer screens as estimated by the Virtual Chinrest task (Li et al., 2020). The entire testing session lasted approximately 130 min, including background tests, experimental tasks, and calibrations. A time limit of 180 min automatically rejected any participants exceeding this threshold.

Eye-tracking measures were assessed *via* WebGazer.js (Papoutsaki et al., 2016) with an ideal sampling rate of approximately 60 Hz, dependent on each participant's monitor's refresh rate (Anwyl-Irvine et al., 2020). Before each task, participants completed a 5-point calibration procedure. A series of pictorial instructions demonstrated appropriate head position during calibration and experimental tasks. Failure to calibrate at least one of the points (i.e., if the estimate for a point was too close to another) resulted in an automatic repetition of the calibration procedure. To account for participants' potential head drift and body repositioning, re-calibration was performed in the middle of each experimental block (i.e., after 18 trials), and before the onset of each new block in training. Eye-tracking estimates with face confidence values (i.e., a score ranging from 0 to 1 estimating the webcam-based eye-tracking machine learning model's confidence level in detecting a human face) lower than 0.5 were excluded from the analyses. In the two post-training tests, eye-tracking measures were recorded for exploratory purposes only and are not reported here.

Training: recognition (with interspersed cued-recall trials)

Training emulates Calabrich et al. (2021) main paradigm, originally based on Jones et al. (2018) cued-recall paradigm. Each training trial consisted of an encoding phase and a testing phase. Each trial began with a 1,000-ms fixation cross, followed by three Mandarin Chinese characters presented in black on a white background. The three characters were displayed in triangle formation (see **Figure 1A**), each occupying 20 × 20 units of Gorilla Experiment Builder's (Anwyl-Irvine et al., 2020) screen space. Each character's color changed from black to red synchronously with auditory presentation of its corresponding pseudoword. The order in which character/pseudowords were highlighted/presented was fully counterbalanced across trials. At the end of this encoding phase, a 1,000-ms blank screen was followed by a visual backward masking phase: hash symbols and numbers, presented in pseudorandomized order, momentarily

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[1] www.prolific.co

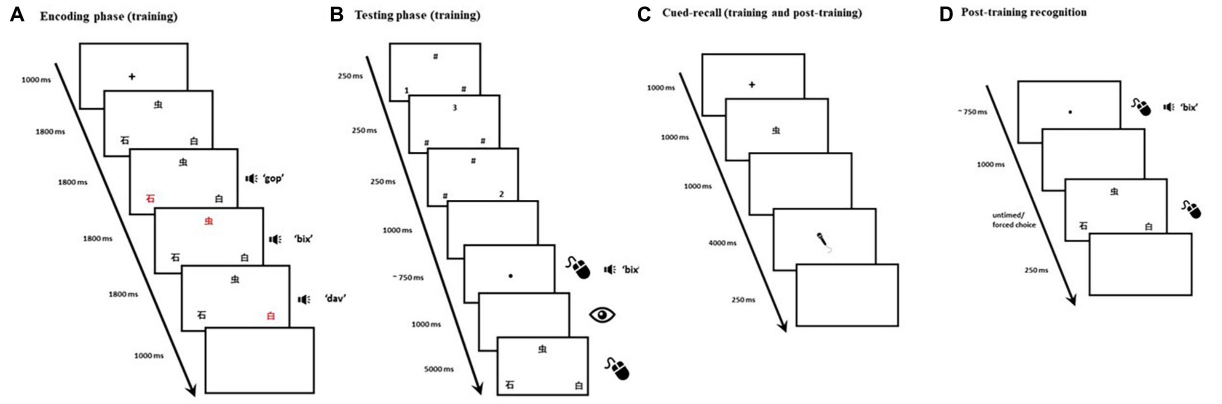

FIGURE 1 | Panels **(A,B)** depict the timeline of a single trial in the main training and recognition task. The encoding phase **(A)** was immediately followed by backward masking and then by the testing phase **(B)**. Panel **(C)** depicts the timeline of a single cued-recall trial (both training and post-training). Panel **(D)** depicts the timeline of a single trial in the post-training recognition test. The eye depicts recording of onscreen fixations, the microphone depicts when a verbal response was expected, and the mouse illustrates when a click was expected.

replaced the characters to minimize visible persistence (see **Figure 1B**). The onset of the testing phase was signaled by the appearance of a small black dot presented in the center of the screen. A click on the black dot would play the auditory cue that corresponded to the target (i.e., one of the three pseudowords from the encoding phase). If no clicks were detected within 10 s, the trial would terminate. The requirement to click the black dot had the secondary purpose of introducing an inconspicuous attention check: if, in three consecutive trials, no clicks had been detected, the participant would be automatically excluded from the experiment as this would constitute a strong indication that their computer had been left unattended mid-task. A 1,000-ms blank screen followed the black dot, during which participants' eye movements were recorded. The three Mandarin Chinese characters then reappeared, and a mouse-click was expected: participants were instructed to select the character that corresponded to the auditory cue. In order to minimize auditory localization bias and encourage our participants to attend to both visual *and* auditory features of the stimuli, the characters' screen position changed in two thirds of the trials once they reappeared in the testing phase. The characters remained on the screen for 5,000 ms, or until a mouse-click was detected, whichever occurred first. A 250-ms blank screen was presented, at which point the trial ended. A total of 216 trials were evenly distributed over 6 blocks. Block and trial presentation were randomized across participants to avoid order effects.

As in Calabrich et al. (2021), we orthogonally manipulated two binomial factors in the encoding phase: (1) *Location consistency*: whether a visual-phonological association was consistently presented in the same spatial location throughout the experiment, and (2) *Context consistency*: whether a visual-phonological association consistently co-occurred with the same items throughout the experiment. As a result, half of the 36 Mandarin Chinese characters were always presented in the same screen position across different trials (i.e., six items would only appear in the top middle, six in the bottom left, and six in the bottom right), whilst the other half could appear in any of three possible screen locations with equal probability. Similarly, half of the stimuli would always appear within a specific triplet (i.e., a target item along with the same two distractors, e.g., items A, B, and C would always be presented together in each occurrence—taking turns as targets and distractors across different trials—and would never co-appear with any other items over the course of the experiment), whilst the remaining would not have any fixed co-occurrences. For each participant, each binding was therefore assigned to one of four trial types: (1) *Inconsistent Location/Inconsistent Context*, (2) *Inconsistent Location/Consistent Context*, (3) *Consistent Location/Inconsistent Context*, and (4) *Consistent Location/Consistent Context*. Each binding appeared three times in each block: once as a target, and twice as a distractor. Each 36-trial block thus contained nine pseudorandomly ordered trials of each type.

We added cued-recall trials at regular intervals (i.e., every six recognition trials) within each block. In each cued-recall trial, 1 of the 36 Mandarin Chinese characters appeared in the center of the screen (see **Figure 1C**). Upon seeing this visual cue, participants were required to articulate the corresponding pseudoword. The target item for each of the interspersed cued-recall trials ($N = 36$) was randomly selected from one of the six preceding recognition trials. The purpose for the interspersed cued-recall trials was twofold: (1) to ensure participants were actively attempting to store the items in their memory beyond the temporal boundaries of each recognition trial, and (2) to afford participants the opportunity to practice saying the pseudowords aloud, since they would later be tested on their ability to recall the cross-modal bindings in the post-training cued-recall test. Participants were prompted to recall each binding once over the course of the task.

To familiarize the participants with the experimental procedure, training was preceded by a practice block with four recognition trials and one cued-recall trial, using additional filler stimuli. Participants were provided with feedback after each practice trial, and were given the option of repeating the practice block if needed. Participants were encouraged to take short breaks between blocks, and were instructed to resume to the same position upon their return. Re-calibration ensured that accurate eye-movements were detected following these breaks.

Post-training cued-recall test

As in Calabrich et al. (2021), a cued-recall test followed training. The post-training cued-recall test consisted of a single block with 36 randomly ordered trials (see **Figure 1C**), testing each of the previously trained bindings. A 1,000-ms fixation cross started each trial, which was then followed by a Mandarin Chinese character presented centrally for 1,000 ms in black on a white background. As in training, each character occupied 20 × 20 units of Gorilla Experiment Builder's screen space. A 1,000-ms blank screen followed, and then a drawing of a grayscale microphone, presented in the center of the screen, indicated that the voice recording had started and a verbal response was required. Participants were instructed they would have 3 s to provide a response. However, to ensure that the onsets of participants' responses were not inadvertently trimmed due to potential delays in the activation of the audio recording, voice recording effectively started 1,000 ms before the microphone was shown. A 250-ms blank screen then appeared, ending the trial.

Post-training recognition test

A single-block recognition test, comprising the same visual-auditory stimuli from the previous tasks, was administered immediately after the post-training cued-recall test. It consisted of 36 randomly ordered three-alternative forced-choice trials. These were similar to the recognition trials in the training task but lacked the encoding phase. Each trial began with a black dot presented on a white background in the center of the screen (see **Figure 1D**). Upon clicking on the dot, participants would hear one of the 36 target pseudowords. A 1,000-ms blank screen would follow, and three equidistant Mandarin Chinese characters would be presented in the same triangle formation as training. Participants were instructed to select the character which corresponded to the auditory cue they had just heard. A 250-ms blank screen was presented, at which point the trial ended.

Data Analysis

To enable comparisons of eye movements across different screen sizes, we used normalized coordinates in our eye-tracking analyses wherein −0.5 and 0.5 always refer to the center of the screen regardless of their size (Gorilla Experiment Builder; Anwyl-Irvine et al., 2020). We performed fixation detection on the normalized data for each individual participant *via* the "detect.fixations" function in the "saccades" v0.2.1 library (von der Malsburg, 2019) in R v4.0.0 (R Core Team, 2020). Due to the noisier and low-frequency nature of webcam-based eye-tracking data, we set the "smooth.coordinates" parameter to "TRUE" to suppress noise, and set the "smooth.saccades" to "FALSE" to detect short saccades more reliably (von der Malsburg, 2019).

We used confirmatory logistic mixed effects regression, *via* the glmer:binomial function in the lme4 v1.1-23 library (Bates et al., 2015) in all analyses. All models included maximal random effects structures (Barr et al., 2013) reverting to a "parsimonious" approach in the case of convergence errors (Bates et al., 2015). In all models, *subject* and *item* were included as random effects. For the recognition trials from the training task—our richest source of data—we modeled error rate as a function of six fixed effects and their interactions: (1) Group membership (*Group*, i.e., typical reader = −0.5, individual with dyslexia = 0.5); (2) Context consistency (*Context*, i.e., whether a target consistently co-occurred with the same distractors over the course of the task; consistent = −0.5, inconsistent = 0.5); (3) Location consistency (*Location*, i.e., whether a target consistently appeared in the same screen location over the course of the task; consistent = −0.5, inconsistent = 0.5); (4) Repetition effects [*log(Block)*, i.e., Blocks 1–6; log-transformed]; (5) The presence of looking-at-nothing behavior (*FixatedAnyROI*, i.e., whether participants re-fixated any of the regions of interest (ROI) upon hearing the auditory cue; no = −0.5, yes = 0.5); and (6) Primary fixation (*PrimaryFixation*, i.e., the dominant region of interest fixated upon hearing the auditory cue; target = −0.5, distractor = 0.5, none = 0.0), conceptually nested within *FixatedAnyROI*. All predictors were contrast-coded and centered. In our pre-registration of this study, we conducted a power analysis using the simR library (Green and Macleod, 2016) to estimate a sample size with sufficient power for the interaction of primary theoretical interest (Group × Context × Location). Thus, when reporting the findings below, we signpost significant higher order interactions that should be interpreted with caution.

In the cued-recall trials embedded in the training task, and in the subsequent post-training tests of cued-recall and recognition, we modeled error rate as a function of the following three factors and their interactions, as described above: (1) Group membership, (2) Context consistency, and (3) Location consistency. Cued-recall errors were defined as any mis-articulations that deviated from the correct pseudoword in at least one phoneme. Recognition errors were defined as any trial in which a participant clicked on a non-target character.

RESULTS

Literacy and General Cognitive Ability Measures

Background measures for both groups are summarized in **Table 1**. Participants with self-reported dyslexia diagnoses scored significantly higher on the ARQ (Snowling et al., 2012) than those without such diagnoses. As a group, readers with dyslexia correctly read significantly fewer words and pseudowords than did the typical readers. Similarly, typical readers were significantly faster at naming digits and letters than readers with dyslexia. There were no significant group differences on verbal and non-verbal IQ measures, nor on forward and backward digit span measures.

Training

Recognition Task

A total of 491 (3.24%) recognition trials timed out (i.e., no mouse click was detected) and were thus excluded, leaving the 14,629 trials for the behavioral analyses summarized in **Table 2**. Distributed across these behaviorally valid trials, the webcam-based eye tracking technique provided a total of 900,837 eye-tracking estimates in our screen of interest. We excluded approximately 3% of these estimates (N = 28,080) due to suboptimal face detection values (i.e., face_conf < 0.5). The noise suppression and short saccade detection filtering excluded about 16% of the data, leaving a total of 12,145 trials (6,130 dyslexic; 6,015 typical) containing both the behavioral and eye tracking measures required for our planned analyses. In these trials, readers with and without dyslexia fixated ROIs for targets and distractors in similar proportions [$\chi^2(1) = 0.02, p = 0.88$].

Error patterns common to both groups

As illustrated in **Figure 2**, both typical readers and readers with dyslexia benefited from stimulus repetition, making fewer errors in each successive block [odds ratio: 0.32:1, $\beta_{log(Block)} = -1.13$, $SE = 0.08$, $p < 0.001$]. Participants made fewer recognition errors in context-consistent conditions, when a target consistently appeared with the same distractors (odds ratio: 1.35:1, $\beta_{Context} = 0.30$, $SE = 0.13$, $p = 0.018$). As illustrated in **Figure 3A**, participants also showed some tendency to make fewer errors in location-consistent conditions, when a target consistently appeared in the same screen location (odds ratio: 1.20:1, $\beta_{Location} = 0.19$, $SE = 0.13$, $p = 0.153$), but this effect was diminished for trials in which they fixated the former location of either a target or distractor (odds ratio: 0.39:1, $\beta_{Location \times Context \times FixatedAnyROI} = -0.94$, $SE = 0.48$, $p = 0.049$). Repetition also interacted with location consistency to modulate the general looking-at-nothing effect, as illustrated in **Figure 3B**: when a target appeared in varied screen positions, looking at any of the three blank ROI was associated with lower recognition error rates in the early blocks,

TABLE 1 | Group scores on literacy and general cognitive ability measures.

Test	Measure	Group performance				*t*	*p*	Cohen's *d*
		Dyslexic *N* = 35		Typical *N* = 35				
		M	*SD*	*M*	*SD*			
TOWRE	Word reading rate[a]	74.60	19.26	90.63	9.25	4.42	< 0.001	−1.05
	Pseudoword reading rate[a]	41.11	11.24	53.97	7.27	5.68	< 0.001	−1.35
CTOPP	RAN digits[b]	16.46	4.1	13.31	2.61	3.82	< 0.001	0.91
	RAN letters[b]	17.23	4.09	13.51	2.34	34.11	< 0.001	1.11
WAIS	Verbal IQ[c]	22.66	4.14	23.31	3.74	0.69	0.488	−0.16
WASI	Non-verbal IQ[c]	18.50	6.7	20.69	3.92	1.64	0.105	−0.39
ARQ	Risk of reading impairment[d]	23.09	5.17	13.30	5.57	7.57	< 0.001	−1.82
	Forward digit span[e]	5.27	1.7	6.03	1.76	1.80	0.076	−0.43
	Backward digit span[e]	4.26	1.7	5.06	1.76	1.92	0.059	−0.46

[a] *Number of correctly read items within 45 s.*
[b] *Raw scores in seconds.*
[c] *Raw scores.*
[d] *Higher scores represent greater likelihood of reading disability.*
[e] *Discontinue rule: two incorrectly typed responses in a row.*

TABLE 2 | Summary of subject-weighted mean error proportions in the training recognition task and interspersed cued-recall trials, post-training recognition and cued-recall tests.

		Context															
		Consistent								Inconsistent							
		M				*SD*				*M*				*SD*			
		TR[a]	TCR[b]	PTR[c]	PTCR[d]	TR	TCR	PTR	PTCR	TR	TCR	PTR	PTCR	TR	TCR	PTR	PTCR
Location	Consistent (dyslexic)	0.173	0.567	0.225	0.679	0.132	0.209	0.213	0.203	0.227	0.744	0.241	0.753	0.112	0.226	0.173	0.232
	Consistent (typical)	0.091	0.435	0.082	0.489	0.072	0.229	0.136	0.294	0.110	0.542	0.140	0.493	0.089	0.222	0.167	0.294
	Inconsistent (dyslexic)	0.191	0.676	0.171	0.673	0.128	0.196	0.200	0.222	0.244	0.621	0.216	0.716	0.138	0.208	0.190	0.245
	Inconsistent (typical)	0.107	0.520	0.104	0.466	0.085	0.212	0.155	0.223	0.123	0.430	0.098	0.428	0.098	0.230	0.126	0.273

[a] *Training recognition.*
[b] *Training cued-recall.*
[c] *Post-training recognition.*
[d] *Post-training cued-recall.*

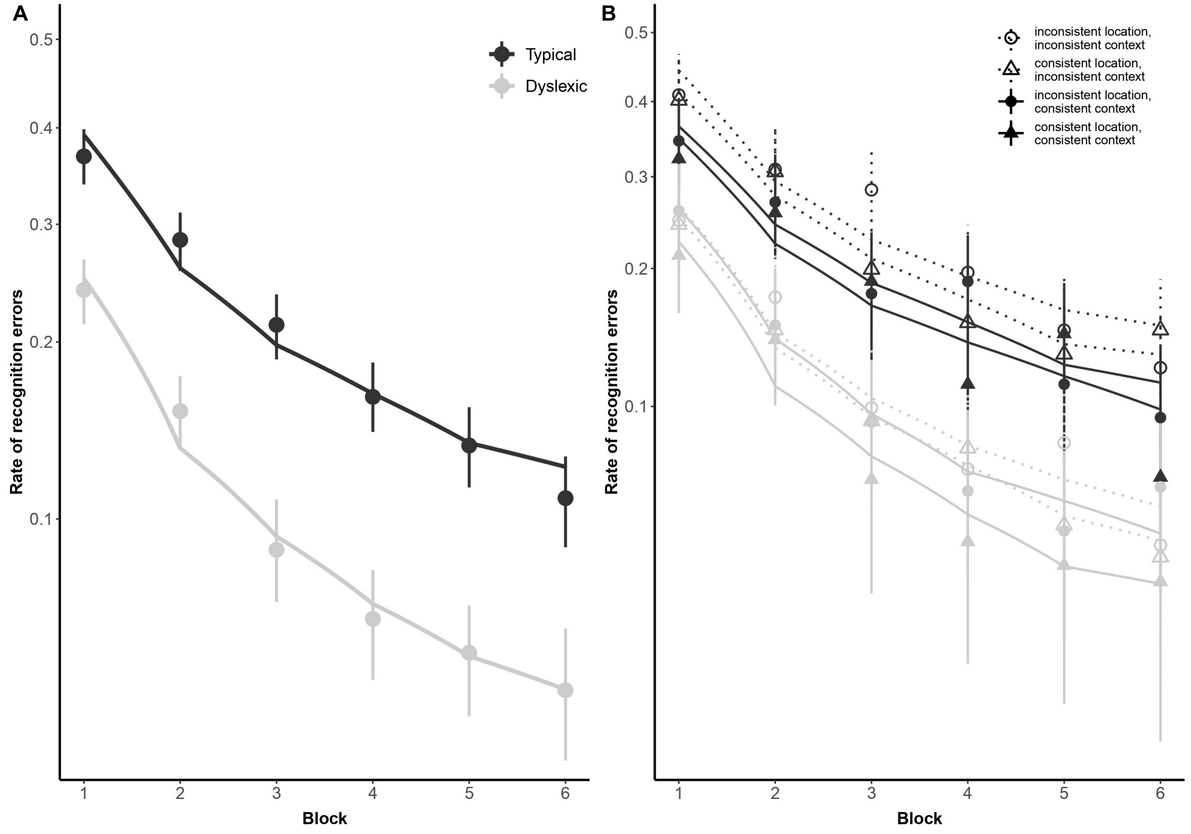

FIGURE 2 | Subject-weighted mean recognition error rates as a function of reading ability and repetition in the training and recognition task. Panel **(A)** depicts overall recognition error rates for readers with dyslexia and typical readers, whereas panel **(B)** outlines the same data broken down by trial type (i.e., whether context and/or location was kept consistent during encoding). The *y*-axis is logit-scaled in both plots to match logistic regression error analyses. Point ranges represent bootstrapped confidence intervals, and lines represent logistic regression model fits.

but this pattern reversed in later blocks [odds ratio: 2.33:1, $\beta_{log(Block) \times Location \times FixatedAnyROI} = 0.85$, $SE = 0.36$, $p = 0.018$].

Group effects

As illustrated in **Figure 2**, typical readers made significantly fewer errors than readers with dyslexia (odds ratio: 2.72:1, $\beta_{Group} = 1.00$, $SE = 0.22$, $p < 0.001$), but there was no significant difference in how the two groups performed as a function of repetition [odds ratio: 1.30:1, $\beta_{log(Block) \times Group} = 0.26$, $SE = 0.15$, $p = 0.069$]. We predicted a stronger tendency for readers with dyslexia to err more when fixating screen locations previously occupied by distractors, as previously observed by Jones et al. (2018). However, this interaction did not come out significant in our study (odds ratio: 1.08, $\beta_{Group \times PrimaryFixation} = 0.08$, $SE = 0.47$, $p = 0.864$). Similarly, contrary to our prediction that spatial *and* contextual consistency would jointly decrease recognition error rates in general, albeit with a disproportionately stronger effect for readers with dyslexia, these two-way and three-way interactions also did not reach significance in the present study (odds ratio = 0.89:1, $\beta_{Context \times Location} = -0.12$, $SE = 0.26$, $p = 0.650$; odds ratio = 1.18:1, $\beta_{Group \times Context \times Location} = 0.17$, $SE = 0.29$, $p = 0.563$).

Our analysis yielded a higher-order interaction involving reading ability and eye movements. Specifically, a five-way interaction between block, group, context consistency, location consistency, and ROI fixation [odds ratio: 44.78:1, $\beta_{log(Block) \times Group \times Location \times Context\ x\ FixatedAnyROI} = 3.80$, $SE = 1.38$, $p = 0.006$; see **Figure 4**]. This interaction suggests differential sensitivity to presentation details, but we report it with caution because we did not anticipate the precise form of this interaction and, as noted earlier, the analysis lacks the necessary power to properly assess it (Button et al., 2013).

Cued-Recall Trials

Due to a playback error which rendered some of the audio files unintelligible, we excluded 82 (3.25%) of the cued-recall trials that were interspersed in the training task, leaving the 2,438 analyzable trials (1,210 dyslexic; 1,288 typical) summarized in **Table 2**. Overall, readers with dyslexia incorrectly recalled bindings more frequently than typical readers (odds ratio: 2.28:1, $\beta_{Group} = 0.82$, $SE = 0.19$, $p < 0.001$). As illustrated in **Figure 5A**, location-consistency and context-consistency significantly interacted (odds ratio = 0.35:1, $\beta_{Context \times Location} = -1.04$, $SE = 0.39$, $p = 0.007$), such that location-consistency only benefited recall during training when context was also consistent, but the strength of this interaction did not significantly differ between groups (odds ratio = 0.80:1, $\beta_{Group \times Context \times Location} = -0.22$, $SE = 0.37$, $p = 0.549$).

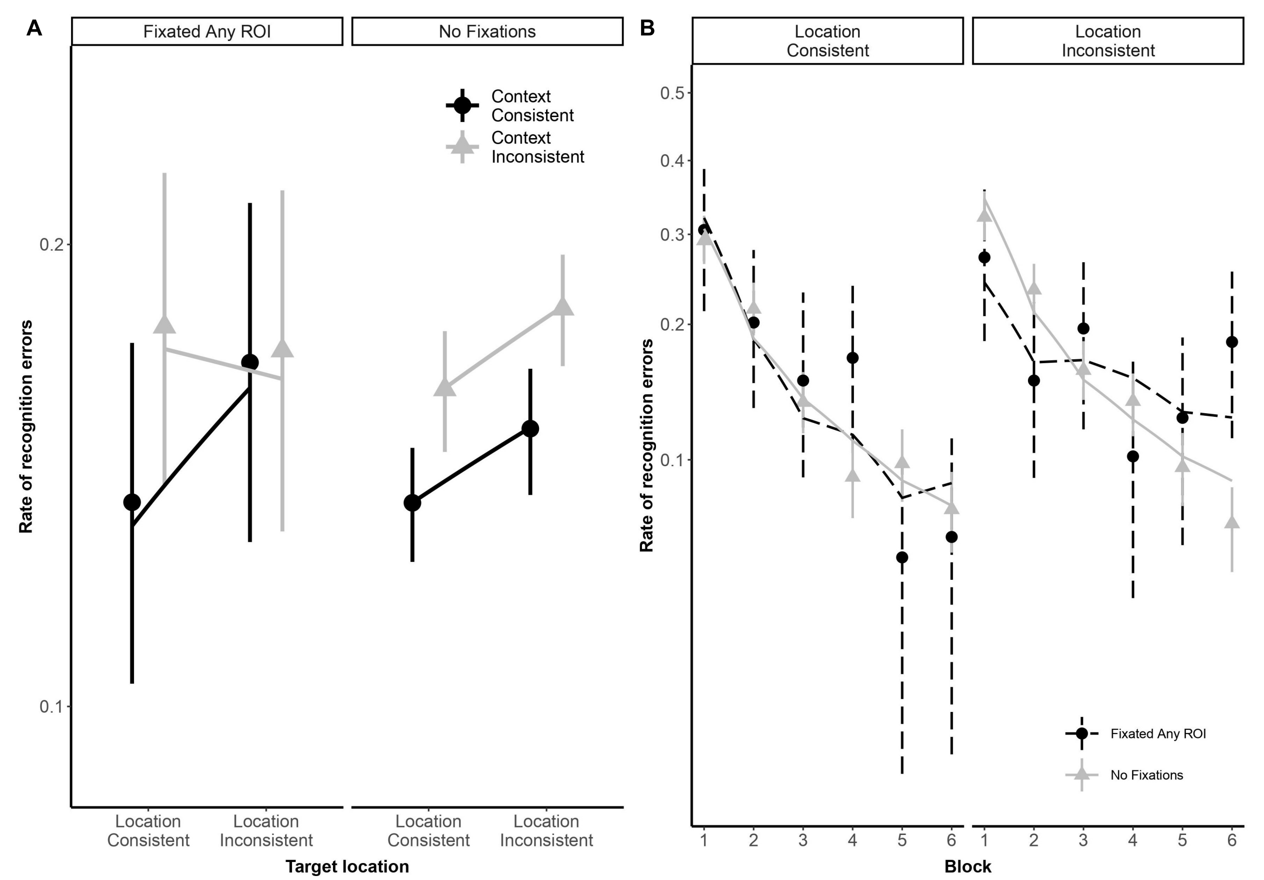

FIGURE 3 | Panel **(A)** shows subject-weighted mean recognition error rate as a function of context and location consistency in trials where participants looked at any of the three regions of interest (ROI), depicted by the "FixatedAnyROI" facet, compared to trials in which looking-at-nothing behavior did not emerge. Panel **(B)** shows subject-weighted mean recognition error rate as a function of repetition (i.e., blocks) and location consistency. In both panels, the *y*-axis is logit-scaled to match logistic regression error analyses. Point ranges represent bootstrapped confidence intervals, and lines represent logistic regression model fits.

Post-training Cued-Recall Test

We excluded 224 (8.88%) trials from the post-training cued-recall test, due to the playback error noted above, leaving the 2,296 trials (1,113 dyslexic; 1,183 typical) summarized in **Table 2**. Overall, readers with dyslexia incorrectly recalled bindings more frequently than typical readers (odds ratio: 3.50:1, $\beta_{Group} = 1.25$, $SE = 0.28$, $p < 0.001$), but as illustrated in **Figure 5B** they benefited more from having consistently appeared with the same distractors during the training phase (odds ratio = 1.48:1, $\beta_{Group \times Context} = 0.39$, $SE = 0.2$, $p = 0.047$).

Post-training Recognition Test

Accuracy in the post-training recognition test is summarized in **Table 2**. Readers with dyslexia incorrectly recognized bindings more frequently than typical readers (odds ratio: 2.71:1, $\beta_{Group} = 0.99$, $SE = 0.33$, $p = 0.003$). No other effects or interactions approached significance.

A summary with the significant effects and interactions observed in all models can be found in **Table 3**. A complete list with all the effects and interactions can be found in the **Supplementary Material**.

Response Times

Although our predictions and power analyses concerned only accuracy data, for completeness, we also ran an analogous analysis of the response time data, reported in the **Supplementary Material**. In sum, although readers with dyslexia were generally slower at recognizing the bindings during training, response times for the accurate responses did not significantly differ between the two groups. In the post-training recognition test, however, typical readers accurately recognized the bindings significantly faster than readers with dyslexia.

DISCUSSION

Efficient cross-modal binding (e.g., mapping letters to letter sounds) is fundamental in the initial stages of literacy acquisition (Seidenberg and McClelland, 1989; Harm and Seidenberg, 1999), and this skill appears to be impaired in children and adults with developmental dyslexia (Blau et al., 2009; Jones et al., 2013b, 2018). Here, we examined whether dyslexic readers' ability to track stimulus consistencies across multiple exposures might contribute to their impaired audiovisual learning (relative to

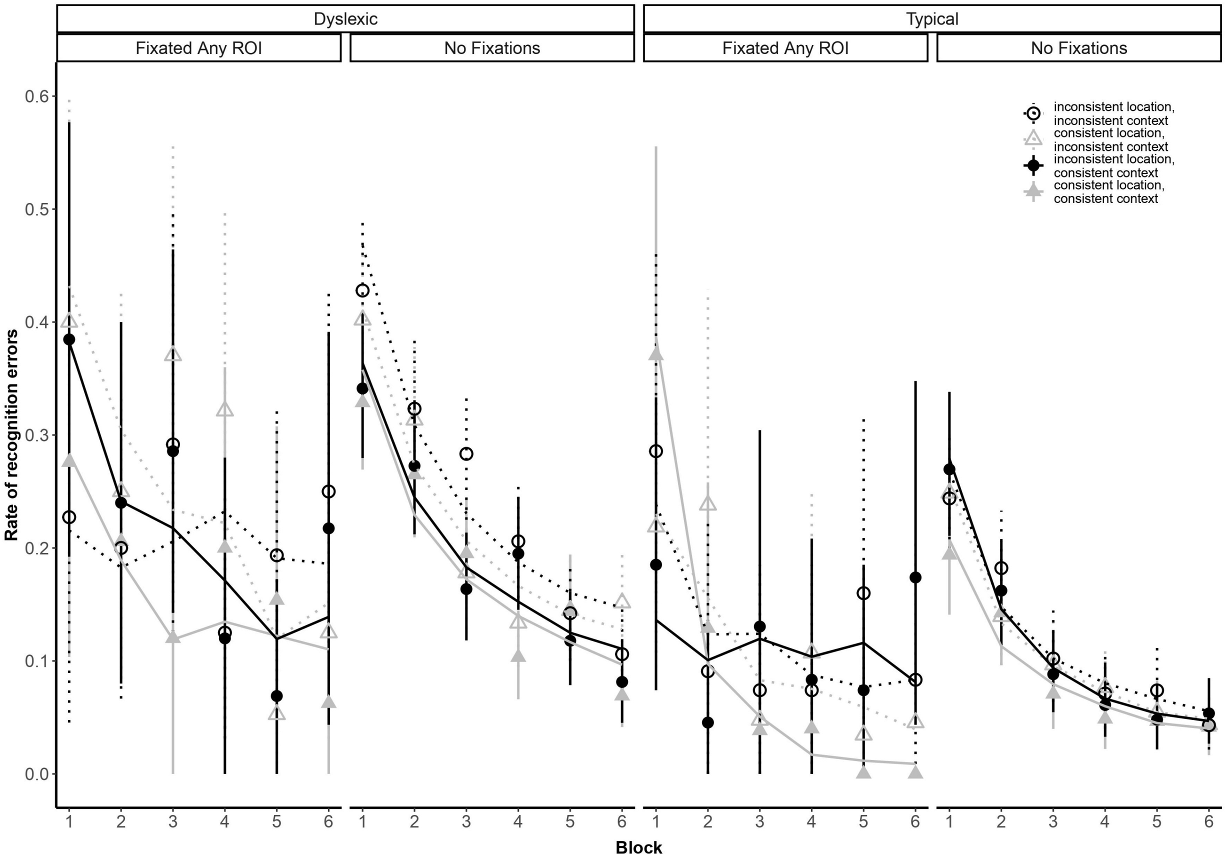

FIGURE 4 | Subject-weighted mean recognition error rate as a function of repetition (i.e., blocks), group membership, context and location consistency, and whether participants looked at one of the three regions of interest (ROI). Point ranges represent bootstrapped confidence intervals, and lines represent logistic regression model fits.

typical readers), more generally considering the contributions of statistical learning and associated episodic memory processes to the acquisition of novel cross-modal bindings. Our experiment simulated the incremental process of letter-sound acquisition by repeatedly presenting participants with arbitrary visual-phonological associations. We were primarily motivated by (1) the specific question of how episodic memory cues, such as consistent spatial and contextual properties, might modulate readers' acquisition of these novel bindings, and (2) more generally identifying differences in the learning characteristics of typical and dyslexic readers. This section is structured according to these objectives. To briefly summarize our main findings, we show that whilst all participants used stimulus consistencies in order to improve learning, readers with dyslexia may show a particular reliance on stimulus co-occurrence.

How Statistical Consistencies Impact Cross-Modal Binding for All Participants

We examined the extent to which reliance on the consistency (or inconsistency) of spatial and contextual stimulus properties—presented across multiple exposures and trials—modulated binding performance. These effects were examined in the context of the main training task, but also in the recognition and recall post-tests. We also examined the extent to which participants would execute looks toward relevant blank screen locations previously occupied by targets, and their effect, if any, on recognition accuracy during the training task.

During training, all participants benefited from a target's repeated presentation as part of the same three-stimulus set (i.e., context consistency; see El-Kalliny et al., 2019). Moreover, context interacted with location and screen fixations to modulate error rates: whilst *inconsistent* contexts were overall detrimental to recognition (see above), recognition accuracy in these trials nevertheless improved in location-consistent trials, in which items were consistently presented in the same screen location. However, this pattern was predominantly observed in trials where participants *did not* fixate any of the relevant ROI. We suggest that since relevant spatial information had presumably already been encoded along with the bindings, re-fixating the empty screen locations in search of spatial retrieval cues may have been redundant, or even deleterious to performance.[2] This relationship

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[2] Note that characters' position was changed between encoding and testing phases in 2/3 of all trials during training, to avoid strategic responses. Pilot data suggested that when the positions were congruous across the two phases, participants appeared to rely more on their ability to localize the sound source (i.e., top, bottom left, and bottom right), rather than on their ability to bind the sound to its corresponding visual stimulus, pushing performance to ceiling during the main

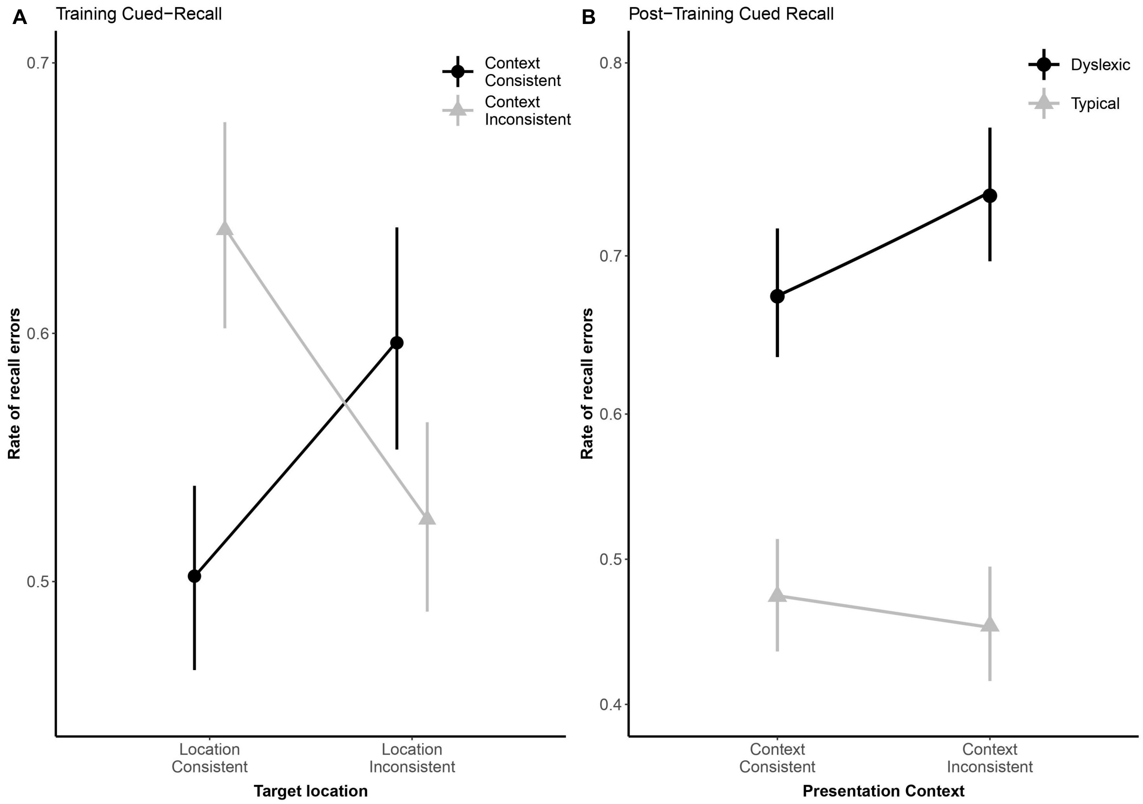

FIGURE 5 | Panel **(A)** shows subject-weighted mean recall error rate as a function of context and location consistency in the cued-recall trials interspersed in training. Panel **(B)** shows subject-weighted mean recall error rate as a function of reading ability and context consistency in the post-training cued-recall test. In both panels, the *y*-axis is logit-scaled to match logistic regression error analyses. Point ranges represent bootstrapped confidence intervals, and lines represent logistic regression model fits.

is further modulated by stimulus repetition: recognition for stimuli presented in *inconsistent* screen locations was found to be more accurate when participants did fixate relevant screen locations, but only during the initial exposures to these stimuli (reflected in performance on the earlier blocks). However, this pattern reversed as a function of block: participants eventually became less accurate following a fixation to a relevant screen location, following multiple exposures to the stimuli. For stimuli with inconsistent locations, therefore, attempts to use spatial location as a retrieval cue became increasingly—and perhaps unsurprisingly—error prone.

In the cued-recall trials interspersed in the training task, participants from both groups also exhibited lower error rates for items consistently encoded in fixed locations *and* with fixed contexts. We speculate here that, while participants were still being trained on the novel bindings, availability of *multiple* episodic memory cues supported recall. In the absence of cues, however, or when only one consistent cue was present, recall became more effortful, and thus less accurate.

Taken together, these findings show that *all participants*, *both typical and impaired*, readily leveraged temporal and spatial consistencies to bootstrap audiovisual learning over multiple exposures. Our findings are in line with the regularity principle of statistical learning (Perry et al., 2010; Vlach and Sandhofer, 2011; Twomey et al., 2014), in which the cognitive system structures inherent environmental variability by integrating frequently occurring items by their co-occurrence, or consistency. This enables us to build supraordinate categories for words, and parts of words in the lexicon, and associated semantic webs. In real-world learning contexts, both spatial location and context would presumably be considerably more varied (though perhaps context less so), so the regularity principle would lead beginning readers to average them out as noise. When we increased the consistency of these features, however, readers appear to have incorporated these co-occurrences into their proto-orthographic representations, thus reinforcing our previous claim that even experienced readers track such information as potentially meaningful (Jones et al., 2018).

Differential Stimulus Consistency Effects on Typical and Dyslexic Readers

Typical readers were more accurate than readers with dyslexia in all tasks, as in Jones et al. (2018) cued-recall study. The main recognition task also suggested differences in the effect of stimulus consistencies on typical and dyslexic readers'

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task. Also note that no interactions with "location" approached significance in our response time analyses (see **Supplementary Material**), suggesting that participants were not particularly slower or faster as a function of location consistency.

performance, in the form of a significant 5-way interaction. Such high-order interaction is challenging to interpret, and based on pre-experiment simulations, we did not expect to have power to accurately assess them. As others have noted (e.g., Button et al., 2013), low power increases the likelihood of false positives as well as false negatives in null hypothesis statistical testing. At present, we tentatively suggest this interaction may be understood as suggesting global differences emerging for errors that implicate re-fixations vs. errors that proceed *via* direct access.

In the post-training recognition and cued-recall tests—the two tasks we administered to examine longer-term retention of the bindings—participants from the two reading groups recognized more bindings than they recalled, consistent with the general trend whereby recognition of previously studied items is often successful even when the items cannot be accurately recalled (Tulving, 1982). Overall, typical readers recognized and recalled twice as many bindings as did readers with dyslexia. We suggest that, given dyslexic readers' propensity to benefit less from multiple exposures during training (Ahissar, 2007), there are knock-on effects for later retrieval. Their comparatively worse performance in the two post-training tests is consistent with previous studies showing reduced long-term memory capacity in readers with dyslexia (Menghini et al., 2010; Huestegge et al., 2014).

In the post-training tests, one might reasonably predict that if repeated exposure to bindings is sufficient for participants to build strong representations to support recognition and recall, they may no longer rely on episodic cues to aid memory retrieval. Behavioral data showed that whilst this was indeed the case for the typical reader group, it was not the case for readers with dyslexia: compared to typical readers, they more frequently correctly recalled bindings which had *consistently* been trained with the same distractors. We suggest that dyslexic readers' reliance on episodic cues may be indicative of a more fragile memory representation: bindings that are robustly represented in memory are accessed and retrieved *via* a direct visual-to-auditory route rather than *via* an indirect route that is dependent on seemingly irrelevant episodic cues (Jones et al., 2018). Our findings suggest that readers with dyslexia use context in order to support retrieval, consistent with previous findings, in which dyslexic readers benefited from item presentation in a fixed temporal order (Saffran et al., 1996; Toffalini et al., 2018).

TABLE 3 | Summaries of logistic mixed effects regression analyses of error frequency.

	Coef. (β)	SE (β)	*p*	OR [exp (β)]
Recognition error frequency (training)				
(Intercept)	−2.18	0.12	<0.001	0.11
log (Block)	−1.13	0.08	<0.001	0.32
Group (typical, dyslexic)	1.00	0.22	<0.001	2.72
Context (consistent, inconsistent)	0.30	0.13	0.018	1.35
log (Block) × Location × FixatedAnyROI	0.85	0.36	0.018	2.33
Location × Context × FixatedAnyROI	−0.94	0.48	0.049	0.39
log (Block) × Group × Location × Context × FixatedAnyROI	3.80	1.38	0.006	44.78
Cued-recall error frequency (training)				
(Intercept)	0.33	0.13	0.011	1.39
Group (typical, dyslexic)	0.82	0.19	<0.001	2.28
Location × Context	−1.04	0.39	0.007	0.35
Cued-recall error frequency (post-training)				
(Intercept)	0.44	0.16	0.007	1.56
Group (typical, dyslexic)	1.25	0.28	<0.001	3.50
Group × Context	0.39	0.19	0.047	1.48
Recognition error frequency (post-training)				
(Intercept)	−2.23	0.18	<0.001	0.11
Group (typical, dyslexic)	0.99	0.33	0.003	2.71

Taken together, our findings with respect to group differences show a deficit for readers with dyslexia in both recognizing and recalling audiovisual bindings of novel items, in all tasks. This finding is in line with previous PAL studies (Messbauer and de Jong, 2003; Warmington and Hulme, 2012; Jones et al., 2013b, 2018; Litt and Nation, 2014; Wang et al., 2017; Toffalini et al., 2018, 2019). Even at the behavioral level, then, adult readers with dyslexia required substantially more repetition in order to achieve accuracy comparable to typical readers (see **Figure 2**), a pattern that is remarkably consistent with Saffran et al. (1996) predictions that word learning in individuals with language disorders requires at least twice the exposure. Even these highly compensated adults with dyslexia were therefore relatively impervious to the effects of frequency on learning. Did this mean that they were insensitive to stimulus consistencies, which should, under normal circumstances, help in the statistical learning process? Our findings suggest not. Readers with dyslexia seemed perfectly able to use consistency in spatial location information to improve recall, which was on a par with the effect of location-consistency on their typically reading peers. This finding is at odds with the hypothesis that readers with dyslexia fail to use location information as a cue for cross-modal binding (cf. Jones et al., 2013b; Toffalini et al., 2018), as typical readers are shown to do (Treisman and Gelade, 1980; Treisman and Zhang, 2006). And it shows, moreover, that readers with dyslexia are in fact able to track longer-range statistical probabilities when the cues afforded across trials are highly salient and beneficial for item recognition. However, our findings showed a reader-type discrepancy in the use of context-consistency cues for item recognition: dyslexic readers' error rates decreased disproportionately compared with typical readers' when items were shown in a consistent context (i.e., item A appearing on each exposure with items B and C). Thus, readers with dyslexia showed an increased reliance on context consistency, suggesting that the entire episode (trial) was encoded as a whole. Previous studies have also noted a proclivity for chunking in dyslexia (Ullman and Pullman, 2015), in which memorization of whole word forms is favored over phonological decoding, leading to a disproportionate reliance on declarative memory for reading. We tentatively suggest that readers with dyslexia may use co-occurrences or consistencies to bootstrap their relative insensitivity to frequency: in a cognitive system that fails to efficiently integrate a current instance with previous exposures to that same item (Ahissar, 2007; Altmann, 2017), there may be a tendency to over-rely on episodic traces from within a single trial (as shown in the looks-at-nothing data), but also across trials (shown in an increased dependency on co-occurrences).

An important feature of this study is that testing was conducted *via* remote access to participants' personal webcams to collect eye-tracking data. Despite the rigorous controls and procedures documented in the methods and results sections, such convenience does not come without its possible limitations and challenges. Online data collection generally raises a number of questions, such as the participant's full capacity to understand and follow the instructions, length of task completion relative to similar in-lab studies, and the element of trust in participants' self-reported data (such as dyslexia status, which we nevertheless mitigated to the extent that it is possible *via* objective literacy and cognitive measures). Collection of eye-tracking data *via* webcam-based eye tracking is a new and exciting method that requires highly stringent procedures in order to ensure the best possible data quality (see Bott et al., 2017; Semmelmann and Weigelt, 2018 for empirical validation of web-based eye-tracking as a suitable experimental method). Here, we took careful design considerations such as providing pictorial as well as written instructions, adding frequent attention checks to ensure participants' computers were not left unattended mid-experiment, and enforcing an overall time limit to prevent excessively long breaks between tasks. We also employed a conservative filtering approach to exclude eye tracking estimates with low face detection values to avoid as much as possible fluctuation depending on variables such as lighting conditions and/or participants' sitting conditions. We also calculated participants' viewing distance, and avoided relying on fine-grained eye tracking analyses that would require sophisticated infrared technology.

CONCLUSION

This study aimed to shed further light on audiovisual learning differences in typical and dyslexic readers. Our findings show that all of our participants used consistencies in the input during stimulus exposure in order to improve recognition and recall of items. However, dyslexic readers showed a persistent difficulty in integrating items in memory, and an overreliance on episodic detail in order to assist in the retrieval process. These findings may be of clinical relevance in understanding the challenges facing apparently high functioning adults. Overall, our findings provide novel evidence on dyslexic readers' reduced ability to create abstracted representations in memory, relying instead on instance-based memory.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found on GitHub (https://github.com/simOne3107/BindingExperimentLocationContextWebcamEyetracking).

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Bangor University Ethics Committee. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

SC, MJ, and GO designed the experiment, analyzed the data, and wrote the manuscript. SC programmed and conducted the experiment. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.754610/full#supplementary-material

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Curved vs. Straight-Line Handwriting Effects on Word Recognition in Typical and Dyslexic Readers Across Chinese and English

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Handwriting serves to link auditory and motor routines with visual word processing, which is a hallmark of successful reading. The current study aims to explore the effect of multisensory integration as a pathway to neural specialization for print among typical and dyslexic readers across writing systems. We identified 9–10-year-old dyslexic Chinese children ($n = 24$) and their typically developing counterparts ($n = 24$) on whom we conducted both behavioral and electroencephalogram (EEG) experiments. We designed four learning conditions: Handwriting Chinese (HC), Viewing Chinese (VC), Drawing followed by Character Recognition in Chinese (D-C), and Drawing followed by Word Recognition in English (D-E). In both handwriting and drawing conditions, we also designed curved vs. straight-line stimuli. Both behavioral and EEG results showed that handwriting straight line strokes facilitated visual word recognition in Chinese compared to handwriting curved lines. Handwriting conditions resulted in a lateralization of the N170 in typical readers, but not the dyslexic readers. Interestingly, drawing curved lines facilitate word recognition in English among dyslexic readers. Taken together, the results of the study suggest benefits of handwriting on the neural processing and behavioral performance in response to Chinese character recognition and curved-line drawing effects on English word recognition among dyslexic readers. But the lack of handwriting effects in dyslexic readers suggest that students who have deficits in reading may also be missing the link between multisensory integration and word recognition in the visual word form areas. The current study results have implications for maintaining handwriting practices to promote perception and motor integration for visual word form area development for normal readers and suggest that drawing practices might benefit Chinese dyslexic readers in reading English.

Keywords: handwriting, drawing, visual word recognition, N170, laterality, Chinese, English

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INTRODUCTION

Writing meaningful symbols is a major landmark in the evolution of human culture. Handwriting connects visual word processing, a milestone for successful reading, with motor and auditory routines (Dehaene and Cohen, 2011). Early processing of visual word forms is constrained by the interaction with auditory and motor regions (Sekiyama et al., 2003; Wuerger et al., 2012; Callan et al., 2014), but the movement of handwriting promotes the integration of visual word forms through motor and auditory routines (Longcamp et al., 2006; Guan et al., 2011, 2021; James, 2017). Even though handwriting seems crucial for reading development, 30–50% of children with dyslexia show significant handwriting difficulties (Montgomery, 2008; Di Brina et al., 2018). These difficulties persist in college-age students and could possibly be associated with other sensory-motor integrative skills, like drawing (Sumner et al., 2014). The nature of the effect of handwriting on word recognition in students with dyslexia is still unclear, and most of our knowledge on this topic is based on studies conducted on English orthography. In the present study, we aimed to explore the handwriting effects on word recognition in both Chinese and English followed by word recognition between normal and dyslexic readers.

Chinese dyslexia differ from typical dyslexia in its written orthography, which is different from alphabetic languages, like English. The difference between visual processing of written orthography in Chinese and alphabetic languages has also been exacerbated by the fact that handwriting with Chinese characters differs from alphabetic writing such as that used in English. When handwriting Chinese, the visual-spatial features are extracted first, and then followed by visual-semantic mappings (Guan et al., 2011). In contrast, when an individual writes alphabetic words, phonological processing (i.e., mapping letters to phonemes), appears to be more crucial (Wagner et al., 1997; Ehri, 2014). Learning to read cannot be separated from handwriting in literacy development (James and Engelhardt, 2012; Tan et al., 2013; Ehir and Flugman, 2018). Handwriting practice and instruction are also essential to children's writing skills (Daly et al., 2003; van Reybroeck and Michiels, 2018) and reading development in Chinese (Guan et al., 2011, 2021; Tan et al., 2013) and western languages (James, 2010). Nevertheless, there is a dearth of research in handwriting effects of multisensory integration as a pathway to neural specialization for print in terms of word recognition among typical and dyslexic readers across writing systems.

Handwriting influences symbol learning by activating a neural network incorporating both motor and sensory routines in the human brain (Dehaene and Cohen, 2011). The motor system produces variability (*via* handwriting in this case) that promotes behavioral performance and connects brain systems to functional networks (James, 2017). Moreover, much research with both Chinese beginning readers and native English-speaking adults has demonstrated that handwriting Chinese characters highlights strokes, the basic constituents of the orthographic representation of the Chinese characters, and therefore enhances orthographic recognition, facilitating Chinese learners' reading acquisition (Longcamp et al., 2006; James, 2010; Guan et al., 2011, 2015, 2021). Interestingly, drawing squared shapes or line drawing also seem to enhance cognitive ability in character acquisition among Chinese school-aged children (Tan et al., 2013). We can conclude from these studies that handwriting practice or some stroke-like drawing practices might be an important means to promote students' learning of written and spoken language.

There are some important theoretical merits for investigating the different recognition mechanisms associated with handwriting either curved or straight-line units, considering different orthographic features in Chinese and English. Above all, there are 26 letters in the English alphabet, some of which consist of curved lines (like "O, Q"), and others of which consist of straight lines (like "L, H"). English words consist of letter strings in a sequential order. The word recognition process takes place *via* an interactive scope including single letters at the local level and sight words at the global level, depending on the individual differences in words (including length and frequency) and readers (including language proficiency and familiarity with target words; Guan et al., 2020). Unlike English, Chinese orthography is composed of characters. Each character consists of 1–36 overlapping strokes. Strokes can be further arranged into logographemes and then radicals, some of which can also be stand-alone characters, but most of which are within-character subunits (Yu and Reichle, 2017). These subunits of writing consist of either curved or straight-line features (e.g., "心" in a curved shape or "王" in a straight-line shape), but the whole character occupies a uniformly-sized, two-dimensional square-shaped spatial layout in text. Therefore, the cognitive processes involved in word recognition induced by curved and straight-line handwriting might manifest differently in Chinese than in English. Meanwhile, cursive handwriting is a complex cultural skill (Kersey and James, 2013; Kiefer et al., 2015) that involves many brain systems and the integration of both motor and perceptual skills (Vinci-Booher et al., 2016; Thibon et al., 2019). Writing in a cursive manner is commonly used as a tool for acquiring handwriting skills (Arnold et al., 2017; Ose Askvik et al., 2020). Furthermore, handwriting of strokes helps Chinese learners improve orthographic recognition and orthographic-semantic mapping at both the character and lexical levels (Lyu et al., 2021), but the effect of handwriting single letters in English on word recognition remains unexplored. Thus, handwriting curved and straight-line writing units in either language might affect Chinese and English word recognition differently.

The N170 is an event-related potential (ERP) functioning as a neurophysiological indicator of early visual word recognition. The typography of N170 ERP responses demonstrates visual specialization for reading development (Maurer et al., 2005). Moreover, the N170 might indicate a orthographic processing strategy in visual word recognition, which involves selectivity and modulation of the brain regions (e.g., laterality or delayed latency) relating to recognizing the word form (Simon et al., 2007). In terms of expertise in reading Chinese (Zhao et al., 2012) and Japanese (Maurer et al., 2008), the laterization of the N170 serves as an electrophysiological marker as well. Nevertheless, it is still unknown whether handwriting experience modulates the N170. Although there are other early ERP indicators of visual processing (e.g., P1, N1), they are non-linguistic (Planton et al., 2013; Rothe et al., 2015) and are therefore not examined in the present study. Taken together, based on the previously described studies, it is innovative to examine the N170 modulation and its laterality effect involved with the different operationalization of handwriting and drawing practices in comparison to viewing. Furthermore, in the current study, we also considered the effect of curved vs. straight-line inputs as this feature might be crucial for visual-perceptual categorization in visual recognition (Seyll and Content, 2020). Hence, it is of great interest to reveal the effect on N170 modulation of handwriting followed by Chinese recognition in comparison to drawing followed either by Chinese or English recognition.

In summary, there is theoretical merit to explore to what extent handwriting symbols in comparison to drawing or viewing word-like symbols promotes the perception of word recognition in both Chinese and English. Whether handwriting Chinese might promote early visual perception more than drawing shapes or the control condition of viewing characters is still unexplored. Moreover, it is worthy of further examining the handwriting or drawing effects between typical readers and their counterparts who might have disabilities in reading development.

THE CURRENT STUDY

We investigate both condition and stimuli effects between typically developing and dyslexic readers. First, the current study focuses on the condition effect, i.e., the difference between handwriting Chinese (HC), and viewing Chinese (VC) as a control; and the difference between drawing followed by Chinese recognition (DC) and drawing followed by English recognition (DE). Second, the current study also focuses on the stimuli effect of either curved or straight lines. Specifically, we focus on the early visual ERPs indicator of N170, and aims to explore the effect of four learning conditions on the underlying different neural mechanism word recognition. The following research questions guide the present investigation:

1. Whether and to what extent does the handwriting effect exist in word recognition in typical and dyslexic readers in terms of behavioral and ERP responses;
2. Whether and to what extent does the drawing effect exist in word recognition in typical and dyslexic readers in terms of behavioral and ERP responses;
3. Whether and to what extent does the stimuli effect (curved line vs. straight line strokes) exist in Chinese character recognition in handwriting in terms of behavioral and ERP responses;
4. Whether and to what extent does the stimuli effect (curved vs. straight-line shape) exist in English word recognition in drawing in terms of behavioral and ERP responses;
5. How different is it in the laterality effect of the handwriting and drawing on word recognition across languages (e.g., Chinese character vs. English word recognition) between typical and dyslexic readers?

METHOD

Participants

The University of Science and Technology Beijing (USTB) ethics committee approved the study. The consent forms were signed first, and a background language experience survey were also completed by individual parents of the participants. The survey also included questions about children's developmental disorders and learning disabilities. After screening, 21 children (15 males, $M_{\text{age}} = 9.5$ years, SD = 0.86) in grades three and four, in which handwriting instruction has just been introduced and is thus considered as the critical period of handwriting development, participated in the experiment. Dyslexic readers were also diagnosed from a pool of nearly 450 grade 4, 5, and 6 students from elementary school. After screening, 21 children (17 males, $\mathrm{M}_{\text{age}} = 9.2$ years, $\mathrm{SD}_{\text{age}} = 0.86$) in grades three and four participated in the experiment.

To be diagnosed as having dyslexia, children's checklist composite score and at least three sets of cognitive-linguistic composite performance needed to be at least 1 SD below the means of their respective age groups on the parent-report scale of Dyslexia Checklist for Chinese Children (DCCC; Hou et al., 2018), which included ten constructs based on 57 items, i.e., vocabulary, visual word recognition, auditory word recognition, spelling, written expression, attention, oral language, and bad reading habits, as well as family risk of dyslexia and mathematic ability. The theoretical framework of this checklist is based on the standard definition of developmental dyslexia in ICD-10, DSM-IV, and clinical symptoms defined by Liu and her colleagues (Liu and Perfetti, 2003). The DCCC is a standard and well-established rating scale for Chinese dyslexia with good reliability and validity. Higher DCCC scores correspond to lower reading ability. In the current measure, the difference in reading-related scores based on the DCCC were statistically significant between dyslexic and normal children in our sample ($t < 0.05$). All the participants were right-handed, with normal or corrected-to-normal vision, and no history of neurological disorders based on screening tests. The intelligence quotients of our selected participants were all above 80, as assessed by Wechsler Intelligence Scale for Children (WISC)-IV Chinese Version. There was no variability in participants' English proficiency as they were English beginners. At the point of the experiments, they had been taught all 26 letters at school and were familiar with all of the stimuli. We offered the stipends for both traveling to the from the experimental sites and their accommodation fees. Each individual participants were also paid with 80 yuan (approximately $11 USD) per hour.

Materials

We selected both Chinese characters and English words from children's curriculum details about the selection process can be found in Guan et al. (2020, 2021) and Guan and Fraundorf (2020). The materials included the prompt, target 1, and target 2. Chinese prompt stimuli included six-curved-line characters (心, 乙, 人, 飞, 九, 儿), and six straight-line characters (口, 工, 日, 王, 十, and 田). The total of 32 target1-characters were selected according to the following three criteria: (1) high frequency

(Chen and Shu, 2001); (2) easy to be embedded within in target-2 characters; and (3) contained either curved- or straight-line strokes. Target 2 comprised compound characters that contained the target 1 characters, so the compound target 2 must have more strokes than that of target 1. The curve and straight features of the prompts and the targets were counterbalanced. The sample stimuli are shown in **Supplementary Appendix 1**.

The English materials consist of capital letters and words. The stimuli-to-be learned in the learning condition were six straight-line letters and four curved letters (like H, F, I, T, E, L, O, C, Q, and U). Thirty-two target 1 contained all 26 capital letters. The word length of the 32 target 2 words contained no more than 6 letters in caps. Before training, we made sure that all participants were familiar with the forms of these words. Therefore, the words chosen were known by all participants, which controlled for the effect of familiarity. Because participants were familiar with all of the stimuli, learning should not be affected by priming as all four conditions (three experimental conditions and one control condition of viewing) shared experimental stimuli with similar features and the only differences lied in the learning procedure. Even if a priming effect were present, comparison between conditions should cancel it out. The judgment task was the same for both Chinese and English: to decide whether target 1 was embedded in target 2. The sample stimuli are shown in **Supplementary Appendix 2**.

For two drawing condition, the stimuli containing 4 curved-line drawing images (circle, heart, moon, and approximate equal), and 4 straight-line drawing images (rectangle, cross, rising line, and horizontal line). Pleases refer to **Supplementary Appendices 1**, **2** for details. After drawing the images, the participants were required to make the yes or no judgement task on whether target 1 was embedded in target 2 (embedment judgement task). In the drawing condition, we also designed an equal number of control trials in which no visual image of the prompt is shown before the embedded judgement task. To compare the curved vs. straight stimuli effects on word recognition, blank trials were used as a control. Please see **Figure 1** design flow chart for the procedure of the stimuli presentation.

Procedures

A within-subject design was carried out. Four conditions were treated as independent variable; behavioral performance (accuracy and response time) and the magnitudes of N170 ERP component were treated as the dependent variables for different research questions.

There were four learning conditions. The first learning condition was viewing-Chinese (VC), under which participants viewed Chinese word stimuli and then responded to the judgment target task by making a binary decision on whether target 2 contained target 1. The second condition was handwriting-Chinese (HC), in which participants wrote simple Chinese character stimuli on a writing pad and then responded to the same Chinese judgment target task. The drawing condition followed by Chinese recognition (DC) required the participants to draw the prompt (circle, square, triangle, diamond, rectangle, parallel lines, or wavy lines) on the writing pad first and then respond to the embedment judgment task in Chinese. The drawing followed by English recognition (DE) asked the participants to draw the same prompts as those in the DC condition and the responded to the judgement task in English. The order of the four conditions in this experiment was counterbalanced.

Each participant participated in an electroencephalogram (EEG) test with a total duration of 350 s. The data was collected in the EEG laboratory of the National Institute of Education Science, and all materials appeared in the center of the computer screen. Before the formal experiment, participants participated in a training activity designed to familiarize them with the experimental procedures in all four conditions. See **Figure 1** for the flowchart of the presentation. To start, a fixation asterisk appeared on the screen for 200 ms; following the fixation, a blank black screen appeared for 300 ms. Then there was a 2,000 ms learning phase. In all four conditions, the learning phase began with the stimulus in blue, followed by target 1 in red, and then target 2 in white. In the handwriting condition, participants wrote the blue stimulus. In the viewing condition, participants spent the same length of time viewing the stimuli. After a blank black screen appeared for 1,000–1,500 ms (duration chosen at random), the red target 1 was shown to participants for 500 ms followed by a 500-ms blank black screen. Finally, target 2 in appeared in white, and participants was instructed to press button "y" if target 2 included target 1 or button "n" if it did not. In a word, participants decided whether target 1 was included in target 2. When participants pressed the button, the stimulus disappeared; if no button was pressed, the stimulus remained for 3,500 ms. The program then advanced to the next trial. EEG recording began upon the onset of the fixation and proceeded continuously, during which responses to target 1 and target 2 were all marked in the EEG recording.

ERP Data Acquisition and Pre-processing

Response time and accuracy were recorded during EEG data acquisition. EEG data was collected using NeuroScan's ESI-64 system. Electrode position in this study approximated locations of the international 10–20 system. The study used the left mastoid as the reference electrode. The vertical electrooculogram (VEOG) was recorded by using two electrodes placed above and below the midline of the right eye, and the recording electrodes of the horizontal electrooculogram (HEOG) were placed beside the left and right eyes in horizontal alignment with the eyeball.

All electrodes were placed on the scalp using conductive paste to ensure that the impedance of each electrode was kept below 5 $K\Omega$. The EEG data acquisition software was NEUROSCAN. The amplifier was SYNAMPS2, and AC continuous sampling was adopted. Scalp potentials were recorded with a sampling rate of 1,000 Hz, and the bandpass filter is 0.05∼100 Hz.

Offline analysis of EEG data was performed using Curry 7.0. During the recording, the left mastoid was used; later, the data was referenced offline using a reference averaged across left and right mastoids. First, a constant baseline correction was performed. Second, the data was digitally filtered with a 30-Hz lowpass. Then, the components related to eye movement were removed. In addition, amplitudes exceeding $\pm 100\ \mu V$ were also

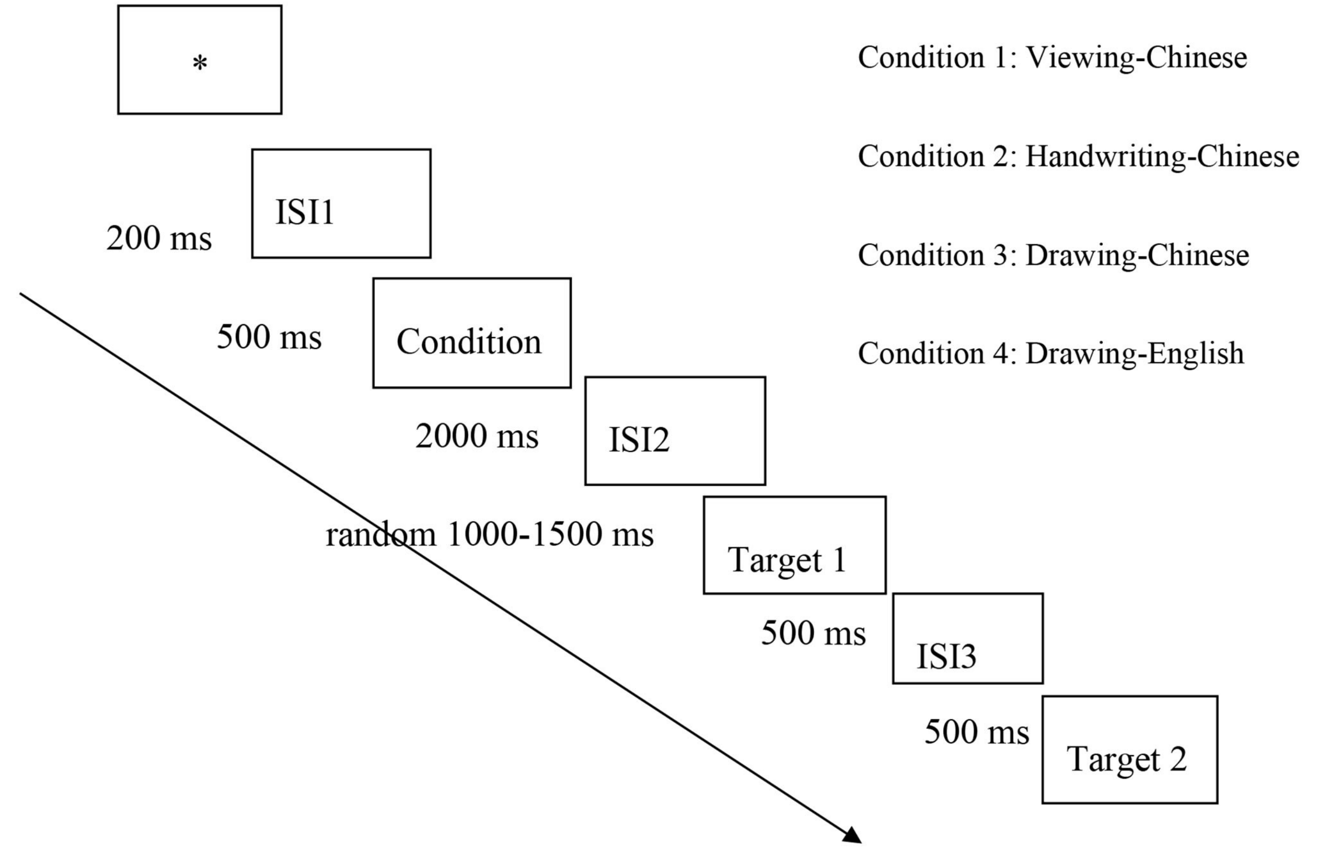

FIGURE 1 | Experimental procedure.

excluded as artifacts. The continuous EEG data was segmented, with the duration of the segmentation starting 200 ms before the onset of target 1 and extending 800 ms after target 1. Finally, the ERP components were superimposed and averaged, and the baseline correction was performed using the baseline of 200 ms before the stimulus.

Behavior and ERP Data Analyses

For behavioral data, we conducted 4 (learning conditions: VC, HC, DC, and DE) × 2 (normal vs. dyslexic readers as between-subject factor) repeated measures ANOVAs on response time and accuracy.

For ERP data, according to prior literature (Maurer et al., 2008), the N170 component elicited by Chinese characters has generally been recorded *via* PO7 and PO8 electrodes, and a lateralization effect has been reported, with the left negative wave larger than the right negative wave (Rossion et al., 2007; Zhang et al., 2011). The stimulus-elicited peak and latency of the N170 at the PO7 and PO8 electrodes of each participant were extracted from the ERP data and analyzed *via* statistical models using SPSS 17.0.4. Four (learning conditions: VC, HC, DC, and DE) × 2 (electrode position: left PO7 and right PO8) repeated measures analyses of variance (ANOVAs) were performed to analyze the amplitude and latency of the N170 of both normal and dyslexic readers. After demonstrating a significant main effect of group and learning condition, as well as their interaction, we broke the analyses down into two groups (normal and dyslexic readers). To answer the first two research questions, we compared three pairs of learning conditions (VC vs. HC, HC vs. D-C, HC vs. DE) in the normal and dyslexic readers groups respectively.

To answer the third and fourth research questions regarding stimuli and laterality effects, we conducted Stimuli (curved vs. straight-line) × Laterality (PO7 vs. PO8) analyses on both behavioral data and hemispheric differences in the N170. A Bonferroni correction was used to correct for multiple comparison as the data violated the assumption of sphericity (Blan and Altman, 1995; Chen et al., 2017). We used 0.05 significance level for all analyses.

RESULTS

Behavioral Results

Differences in the behavioral analyse between the two groups of normal and dyslexic readers could be only related to their cognitive ability (Palmis et al., 2020), as we used the same materials, same training procedures. We did not focus on comparisons between normal and dyslexic readers directly. Instead we investigated the differences in behavioral results in

TABLE 1 | Mean and SD of both ACC and RTs in the four conditions.

Condition	RT			ACC		
	Normal	Dyslexic	Cohen's *d*	Normal	Dyslexic	Cohen's *d*
VC	1,795.05 (76.90)	1,973.15 (46.80)	1.71	0.89 (0.02)	0.67 (0.11)	1.44
HC	1,688.90 (70.20)	1,952.85 (55.66)	1.60	0.98 (0.01)	0.65 (0.11)	3.28
DC	1,742.35 (86.90)	1,931.45 (49.80)	1.63	0.91 (0.03)	0.70 (0.11)	0.36
DE	1,725.70 (70.10)	1,909.95 (52.21)	1.51	0.87 (0.02)	0.83 (0.11)	1.17

RT, response time; VC, viewing character; HC, handwriting character; DC, drawing followed by Chinese recognition; DE, drawing followed by English recognition. Standard deviation of each measure per condition presented in parentheses. We calculated Cohen's d by using the following formula: $[4\eta^2/1\text{-}\eta^2]^{1/2}$. Cohen's d < 0.2 indicates a small effect size, 0.2 < Cohen's d < 0.8 indicates a medium effect size, and Cohen's d > 0.8 indicates a large effect size (Fritz et al., 2012).

the pairs of four learning conditions between the normal and dyslexic readers.

For behavioral data analyses, we collected both accuracy (ACC) and response time (RT) for target 2. Accuracy analyses were based on the aggregated means per subject per condition. We recorded the response time (RTs) at the onset of target 2 button press. The analyses also excluded the outliers in RTs in the extreme 5% on either end of the Z-normalized distribution of RTs (i.e., above and below 1.65 SD of each mean RT per participant). At last, 7.5% of trials being excluded as outliers, following the criteria (from 5 to 10%) suggested by Ratcliff (1993). The descriptive statistics of mean and standard deviation of both ACC and RT for each of four conditions per groups are shown in **Table 1**. The violin plots summarizing the behavioral data for both normal readers and dyslexic readers are present in **Figure 2**.

Four repeated-measures analyses of variance (ANOVAs) were performed using a single factor (learning conditions: VC, HC, DC and DE), by submitting response time and accuracy for each condition across normal and dyslexic readers. The group (normal vs. dyslexic) factor was used as the between-participant factor. Response time and accuracy of normal and dyslexic readers demonstrated significant effects of learning condition. For response time, there was a significant effect of learning condition [$F_{(3,\,57)} = 24.71$, $p = 0.04$, $\eta^2 = 0.029$] and condition × group interaction [$F_{(3,\,57)} = 10.03$, $p = 0.04$, $\eta^2 = 0.01$]; for accuracy, there was a significant effect of learning condition [$F_{(3,\,57)} = 861.88$, $p < 0.01$, $\eta^2 = 0.09$] and a significant condition × group interaction [$F_{(3,\,57)} = 470.49$, $p < 0.01$, $\eta^2 = 0.05$]. Therefore, three sets of *post-hoc* analyses were carried out below in normal and dyslexic readers, respectively.

Handwriting Effects in Comparison to Other Learning Conditions in Normal vs. Dyslexic Readers

Comparing Handwriting vs. Viewing

Among normal readers, the response time in HC (M = 1,688.90 ms, SD = 70.26) was significantly shorter than VC (1,795.05 ms, SD = 76.95), [$F_{(1,\,38)} = 6.46$, $p = 0.02$, $\eta^2 = 0.15$], and the accuracy rate in HC (M = 0.98, SD = 0.01) was significantly higher than in VC (M = 0.89, SD = 0.02), [$F_{(1,38)} = 512.97$, $p < 0.01$, $\eta^2 = 0.93$]. For dyslexic readers, the patterns were the same. Their response time in HC (M = 1,952.85 ms, SD = 55.66) was shorter than VC (M = 1,973.15 ms, SD = 46.80), [$F_{(1,38)} = 1.568$, $p = 0.218$, $\eta^2 = 0.04$], and accuracy of HC (M = 0.65, SD = 0.11) was lower than VC (M = 0.67, SD=0.11), [$F_{(1,38)} = 0.32$, $p = 0.574$, $\eta^2 = 0.01$].

Comparing Handwriting vs. Drawing Followed by Chinese Recognition

For normal readers, the response time in HC (M = 1,688.90 ms, SD = 170.26) was shorter than DC (M = 1742.35 ms, SD = 86.90), [$F_{(1,\,38)} = 1.56$, $p = 0.22$, $\eta^2 = 0.04$], and the accuracy in HC (M = 0.98, SD = 0.01) was significantly higher than DC (M = 0.91, SD = 0.03), [$F_{(1,\,38)} = 72.27$, $p < 0.001$, $\eta^2 = 0.66$]. For dyslexic readers, there was a longer response time of HC (M = 1,952.85 ms, SD = 55.66) compared with DC (M = 1,831.45 ms, SD=49.80), [$F_{(1,\,38)} = 1.64$, $p = 0.21$, $\eta^2 = 0.04$] and accuracy in HC (M = 0.65, SD = 0.11) was lower than DC (M = 0.70, SD = 0.11), [$F_{(1,\,38)} = 2.07$, $p = 0.16$, $\eta^2 = 0.05$].

Comparing Drawing Followed by Chinese Recognition vs. Drawing Followed by English Recognition

For normal readers, the response time of Chinese recognition in the DC condition (M = 1,742.35 ms, SD = 86.90) was not significantly different from English recognition in the DE condition (M = 1,725.70, SD = 270.10), [$F_{(1,\,38)} = 0.069$, $p = 0.79$, $\eta^2 = 0.002$], but the accuracy of DC (M = 0.91, SD = 0.03) was significantly lower than the DE condition (M = 0.97, SD = 0.03), [$F_{(1,\,38)} = 39.97$, $p < 0.001$, $\eta^2 = 0.51$]. This pattern of results might not be affected by the condition effect between DC and DE, but by the fact that the normal readers felt more familiar with the English stimuli than the Chinese stimuli. For dyslexic readers, there was no difference in response time ($p = 0.28$), and no significant difference between accuracy with DE higher than DC either ($p = 0.17$).

Based on the above analysis, the results suggest that there is a significant handwriting effect among normal readers and a significant drawing effect. Thus, we further analyzed the stimuli effect of curved- and straight-line characters in handwriting and drawing.

Comparing Curved-Line vs. Straight-Line Handwriting in Chinese

For normal readers, the response time for curved-line characters (M = 1,700.19 ms, SD = 172.12) was higher than for straight-line

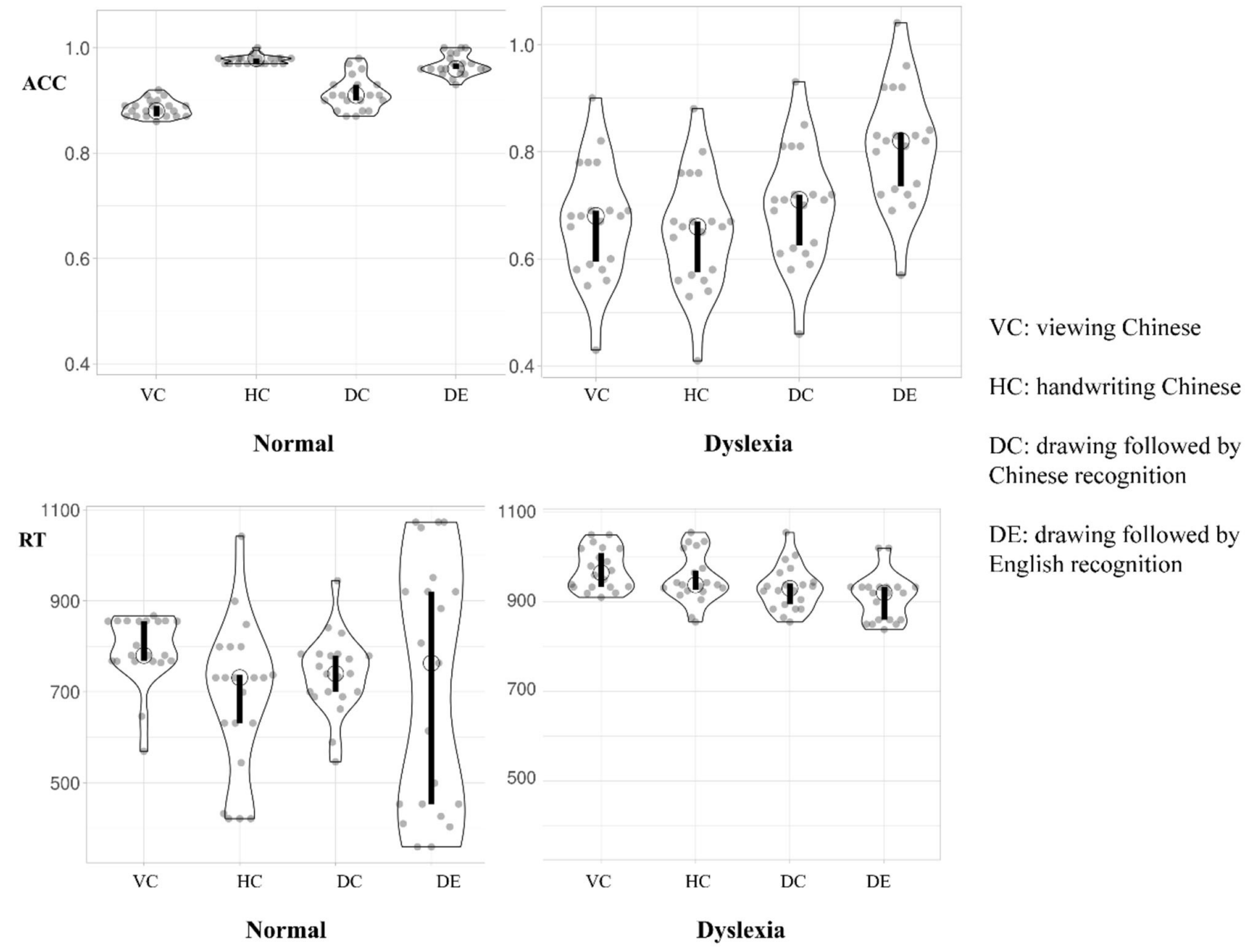

FIGURE 2 | Behavioral data of normal readers and dyslexic children. Open circle indicates the median in each condition. Bar chart indicates the 95% confidence interval for each median determined by bootstrapping.

characters ($M = 1{,}672.10$ ms, $SD = 154.04$), [$F_{(1,\,38)} = 0.28$, $p = 0.60$, $\eta^2 = 0.007$], and the accuracy for curved-line characters ($M = 0.96$, $SE = 0.01$) was lower than straight-line characters ($M = 0.97$, $SE = 0.02$) [$F_{(1,\,38)} = 0.714$, $p = 0.403$, $\eta^2 = 0.02$].

Comparing Curved-Line vs. Straight-Line Drawing Followed by English Recognition

For dyslexic readers, there was a longer response time for curved-line drawing ($M = 1{,}918.55$ ms, $SD = 47.31$) compared with straight-line drawing ($M = 1{,}801.35$ ms, $SD = 61.69$), [$F_{(1,\,38)} = 0.93$, $p = 0.34$, $\eta^2 = 0.02$] and accuracy for curved line drawing ($M = 0.85$, $SD = 0.09$) was significantly higher than straight-line drawing ($M = 0.76$, $SD = 0.12$), [$F_{(1,\,38)} = 6.2$, $p = 0.013$, $\eta^2 = 0.15$].

ERP Results

Figures 3A,B presents the waveforms of ERP modulations that marked target 2 responses at PO7 and PO8 for normal readers, and **Figures 4A,B** for dyslexic readers. A 4 (learning conditions) × 2 (hemisphere: left PO7 and right PO8) × 2 (group: normal vs. dyslexic) × 2 (stimuli: curved vs. straight) repeated measures ANOVA was conducted on the amplitude of N170. The results revealed significant main effects of condition [$F_{(3,\,60)} = 4.72$, $p = 0.005$, $\eta^2 = 0.02$] and hemisphere [$F_{(1,\,20)} = 18.98$, $p < 0.001$, $\eta^2 = 0.076$], and a significant condition × hemisphere × group interaction [$F_{(3,\,60)} = 11.02$, $p < 0.001$, $\eta^2 = 0.04$]. Moreover, we found a significant condition × hemisphere 2-way interaction [$F_{(3,\,60)} = 7.07$, $p < 0.001$, $\eta^2 = 0.019$], and significant group × condition two-way interaction [$F_{(3,\,60)} = 10.21$, $p < 0.001$, $\eta^2 = 0.04$]. This indicates a different pattern across hemispheres between conditions and between the two groups, and also a significant group × hemisphere × stimuli three-way interaction [$F_{(2,\,40)} = 9.34$, $p < 0.001$, $\eta^2 = 0.032$].

Therefore, the ERP analyses on the N170 amplitude were conducted to test comparison between normal and dyslexic groups separately in each of all four conditions. The descriptive statistics of ERP data are shown in **Table 2**. We only reported the amplitude data. Previous studies (Maurer et al., 2008; Yum

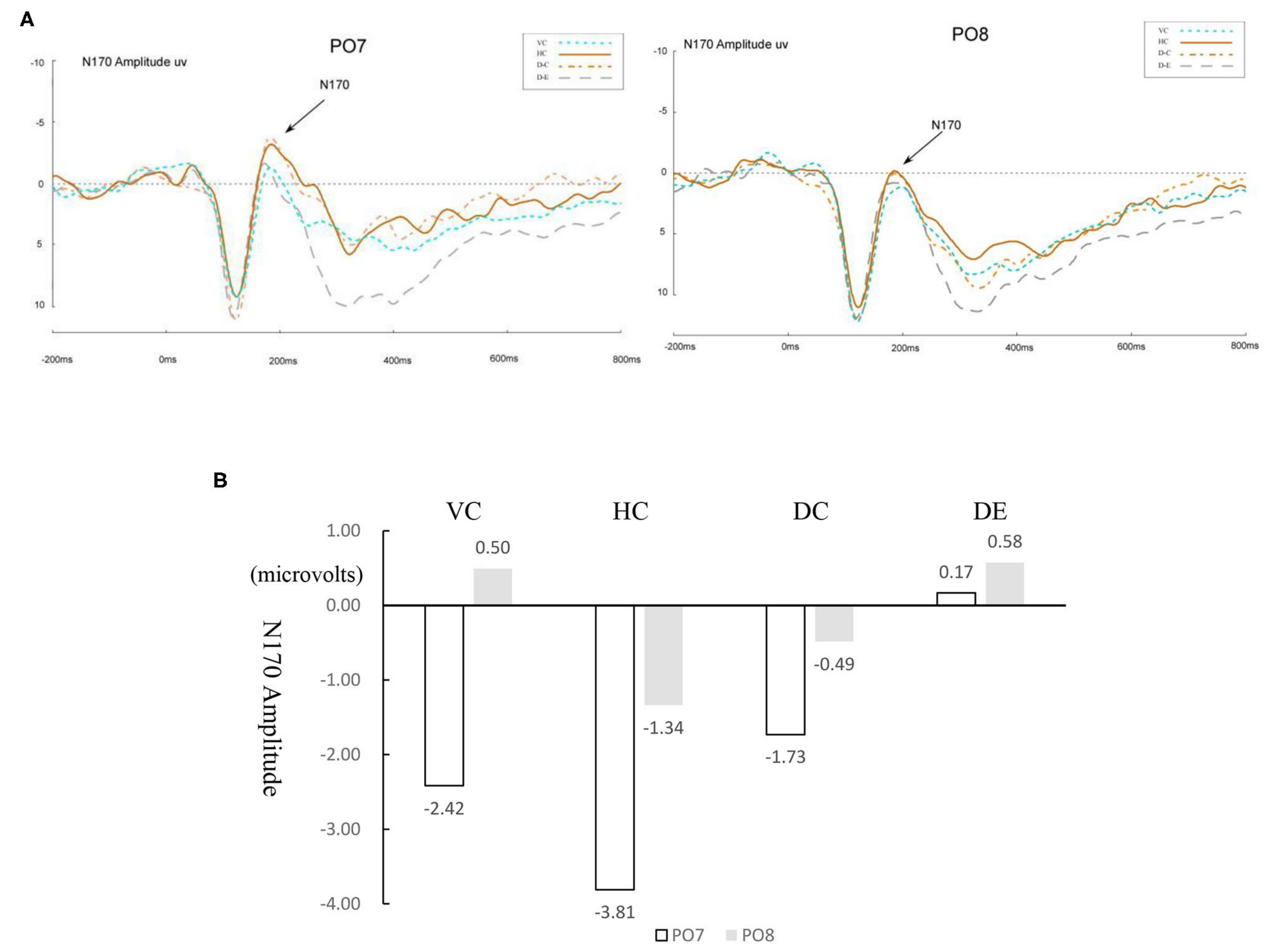

FIGURE 3 | (A) ERP waveforms of the N170 under four conditions for normal readers for the left (PO7) and right (PO8) parietal leads. VC, viewing-Chinese; HC, handwriting-Chinese; DC, drawing followed by Chinese recognition; DE, drawing followed by English recognition. **(B)** Differences between four conditions for normal readers in the amplitude of N170.

et al., 2014; Yum and Law, 2021) did not find the statistical significance on the latency. **Figures 3B**, **4B** show the differences in amplitude voltage between the conditions for normal and dyslexic separately.

Figures 5, **6** present violin plots summarizing the ERP amplitude voltage data for both normal and dyslexic readers.

To better show the handwriting effect, **Figure 7A** presents the original ERP waveforms modulated by stimuli (curved, straight and control) with target 1 responses at PO7 and PO8 marked for normal readers, and **Figure 7B** is the voltage comparison. To better show the drawing effect, **Figure 8A** presents the original ERP waveforms modulated by stimuli (curved, straight and control) with target 1 responses at PO7 and PO8 marked for dyslexic readers, and **Figure 8B** is the voltage comparison.

Comparing Handwriting vs. Viewing

For normal readers, there was a greater N170 amplitude during HC than VC, $F_{(1,\,15)} = 0.72$, $p = 0.035$, $\eta^2 = 0.03$, showing that handwriting facilitates recognition of Chinese characters. For dyslexic readers, this pattern was the same. The amplitude of the N170 was significantly greater for HC than for VC, $F_{(1,\,15)} = 1.879$, $p = 0.03$, $\eta^2 = 0.06$.

Comparing Handwriting vs. Drawing Followed by Chinese Recognition

For both normal and dyslexic readers, there was no difference in N170 amplitude for HC vs. DC, [$F_{(1,\,15)} = 2.191$, $p > 0.05$, $\eta^2 = 0.068$ for normal readers; $F_{(1,\,15)} = 0.473$, $p > 0.05$, $\eta^2 = 0.02$ for dyslexic readers].

Comparing Drawing Followed by Chinese Recognition vs. Drawing Followed by English Recognition

For normal readers, DC elicited a significantly larger N170 response than DE, $F_{(1,\,15)} = 15.07$, $p = 0.02$, $\eta^2 = 0.53$. For dyslexic readers, N170 amplitude was also greater for DC than DE, $F_{(1,\,15)} = 0.527$, $p = 0.04$, $\eta^2 = 0.02$.

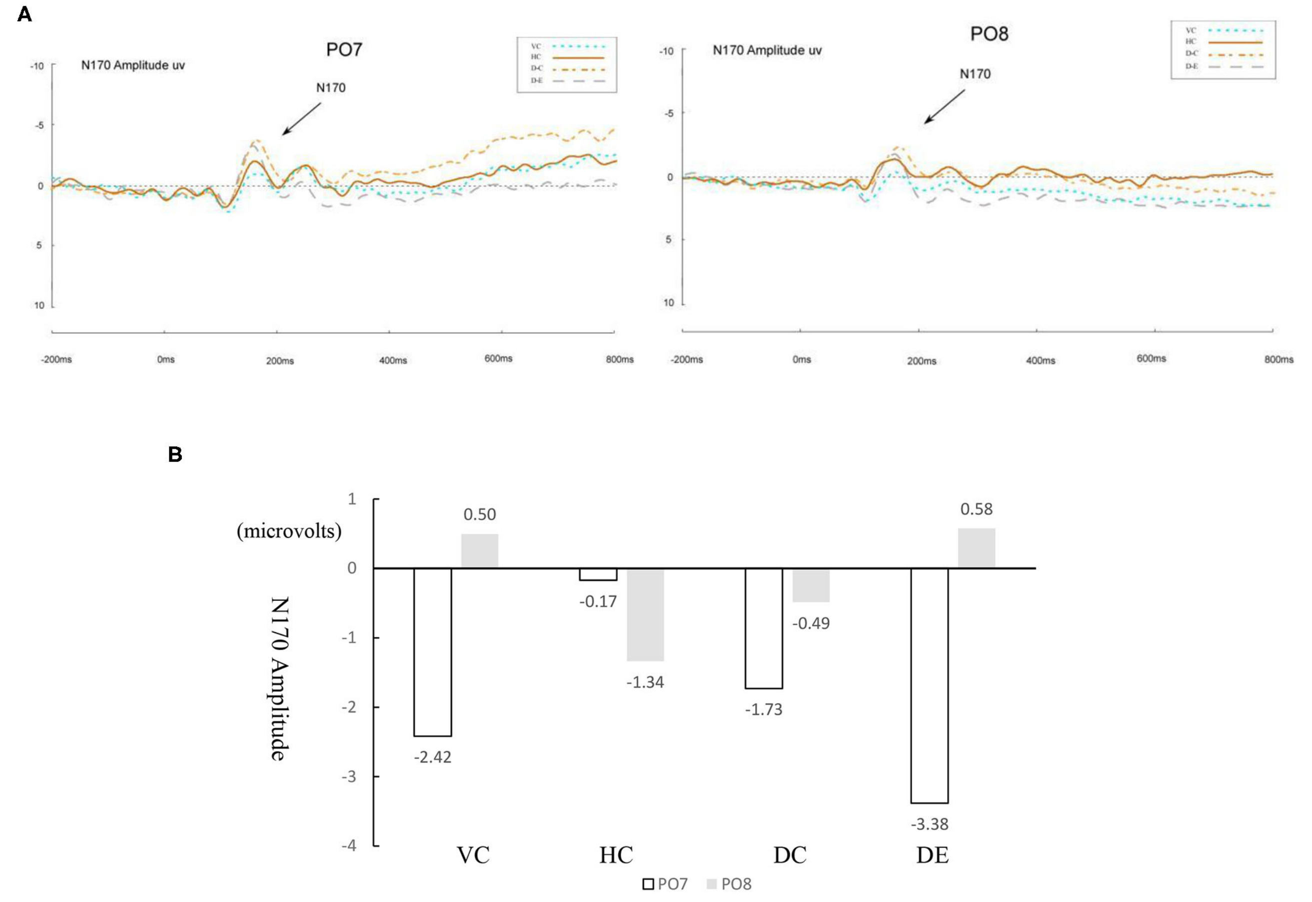

FIGURE 4 | (A) ERP waveforms of N170 under four conditions for dyslexic readers for the left (PO7) and right (PO8) parietal leads. VC, viewing-Chinese; HC, handwriting-Chinese; DC, drawing followed by Chinese recognition; DE, drawing followed by English recognition. **(B)** Differences between four conditions for dyslexic readers in the amplitude of N170.

TABLE 2 | Mean (SD) ERP magnitude at PO7 and PO8 for four conditions.

	Normal Readers		Dyslexic Readers	
	PO7	**PO8**	**PO7**	**PO8**
VC	−2.42 (3.98)	0.50 (2.67)	−2.42 (3.98)	0.50 (2.67)
HC	−3.81 (3.22)	−1.34 (3.10)	−0.17 (2.77)	−1.34 (3.10)
DC	−1.73 (2.88)	−0.49 (3.34)	−1.73 (2.88)	−0.49 (3.34)
DE	0.17 (2.68)	0.58 (2.83)	−3.38 (3.84)	0.58 (2.83)

VC, viewing character; HC, handwriting character; D-C, drawing followed by Chinese recognition; D-E, drawing followed by English recognition. Standard deviation of each measure per condition is presented in parentheses.

Laterality Effect

For normal readers, the peak value of N170 in the left hemisphere (PO7) was significantly higher than that in the right hemisphere (PO8) for HC [$F_{(1, 40)} = 6.43, p = 0.015, \eta^2 = 0.138$], VC [$F_{(1, 40)} = 7.75, p = 0.008, \eta^2 = 0.162$], but laterality effects were not significant in the two drawing conditions [DC: $F_{(1, 40)} = 1.68, p = 0.20, \eta^2 = 0.04$; DE: $F_{(1, 40)} = 0.23, p = 0.64, \eta^2 = 0.006$].

For dyslexic readers, the peak value of N170 in the left hemisphere (PO7) was significantly higher than that in the right hemisphere (PO8) for VC [$F_{(1, 40)} = 7.75, p = 0.008, \eta^2 = 0.16$] and for DE [$F_{(1, 14)} = 14.46, p < 0.001, \eta^2 = 0.27$]. The other two conditions showed no significant laterality effect [HC: $F_{(1, 40)} = 1.64, p = 0.21, \eta^2 = 0.04$; DC: $F_{(1, 40)} = 1.68, p = 0.20, \eta^2 = 0.04$].

Comparing Curved vs. Straight-Line Handwriting on Chinese Word Recognition

For normal readers, the peak value of N170 in the left hemisphere (PO7) was significantly higher than that in the right hemisphere (PO8) for straight-line handwriting [$F_{(1, 40)} = 8.55, p = 0.006, \eta^2 = 0.18$]. Laterality effects were not significant for the curved line condition [$F_{(1, 40)} = 0.04, p = 0.847, \eta^2 = 0.09$] or the control condition [$F_{(1, 40)} = 0.004, p = 0.95, \eta^2 = 0.09$].

Comparing Curved vs. Straight-Line Drawing on English Word Recognition

For dyslexic readers, the peak value of N170 in the left hemisphere (PO7) was significantly higher than that in the right

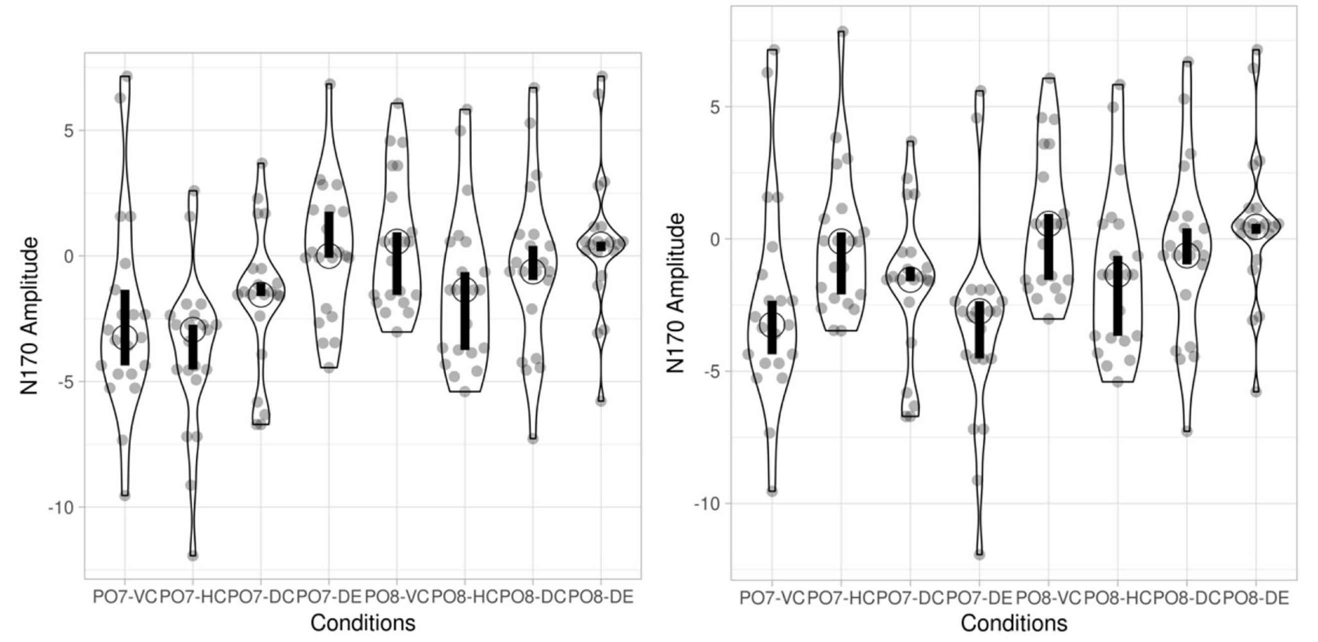

FIGURE 5 | N170 amplitude of normal readers (left) and dyslexic readers (right) in VC, HC, DC and DE condition. Open circle indicates the median of the data. Bar chart indicates the 95% confidence interval for each median determined by bootstrapping. (VC, viewing-Chinese; HC, handwriting-Chinese; DC, drawing followed by Chinese recognition; DE, drawing followed by English recognition).

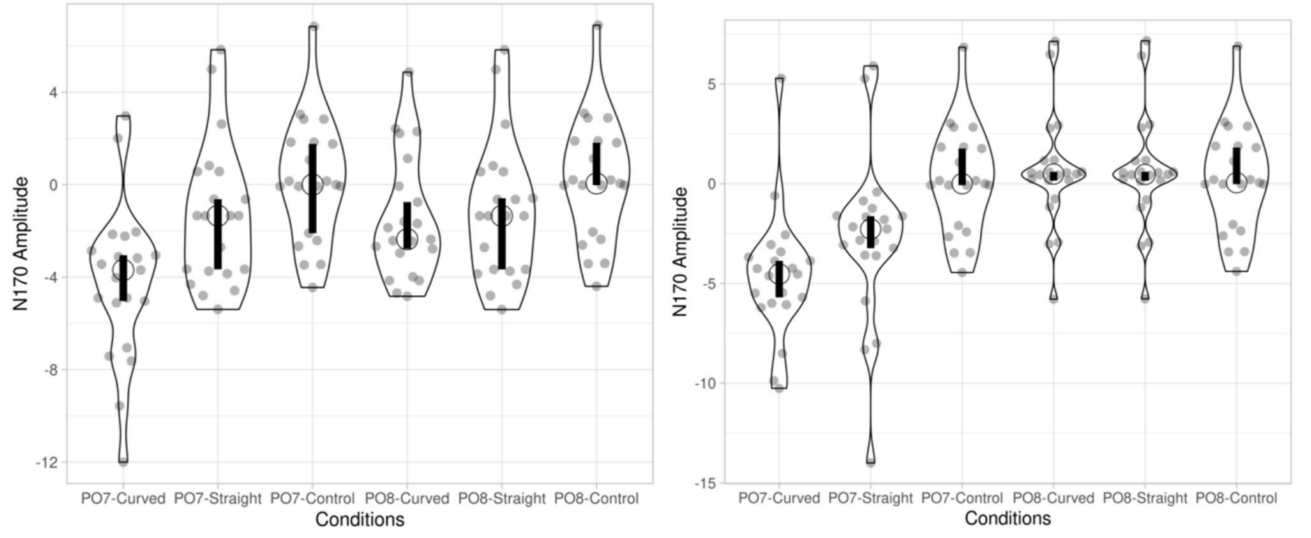

FIGURE 6 | N170 amplitude of normal readers (left) and dyslexic readers (right) in straight, curved and control condition. Open circle indicates the median of the data. Bar chart indicates the 95% confidence interval for each median determined by bootstrapping. (Left: curved: handwriting curved; straight: handwriting straight, control: handwriting control. Right: curved: drawing English curved; straight: drawing English straight; control: drawing English control).

hemisphere (PO8) for curved-line drawing followed by English recognition [$F_{(1,\ 40)} = 30.79$, $p < 0.001$, $\eta^2 = 0.44$], but laterality effects were not significant in the straight-line drawing condition and control condition ($p < 0.01$).

Table 3 presents summaries of both behavioral data and N170 amplitude data for both normal and dyslexic readers.

DISCUSSION

We investigated handwriting in comparison to drawing on word recognition between typical and dyslexic readers. We first compared handwriting-Chinese (HC) with viewing-Chinese (VC) characters and with two other drawing conditions, i.e.,

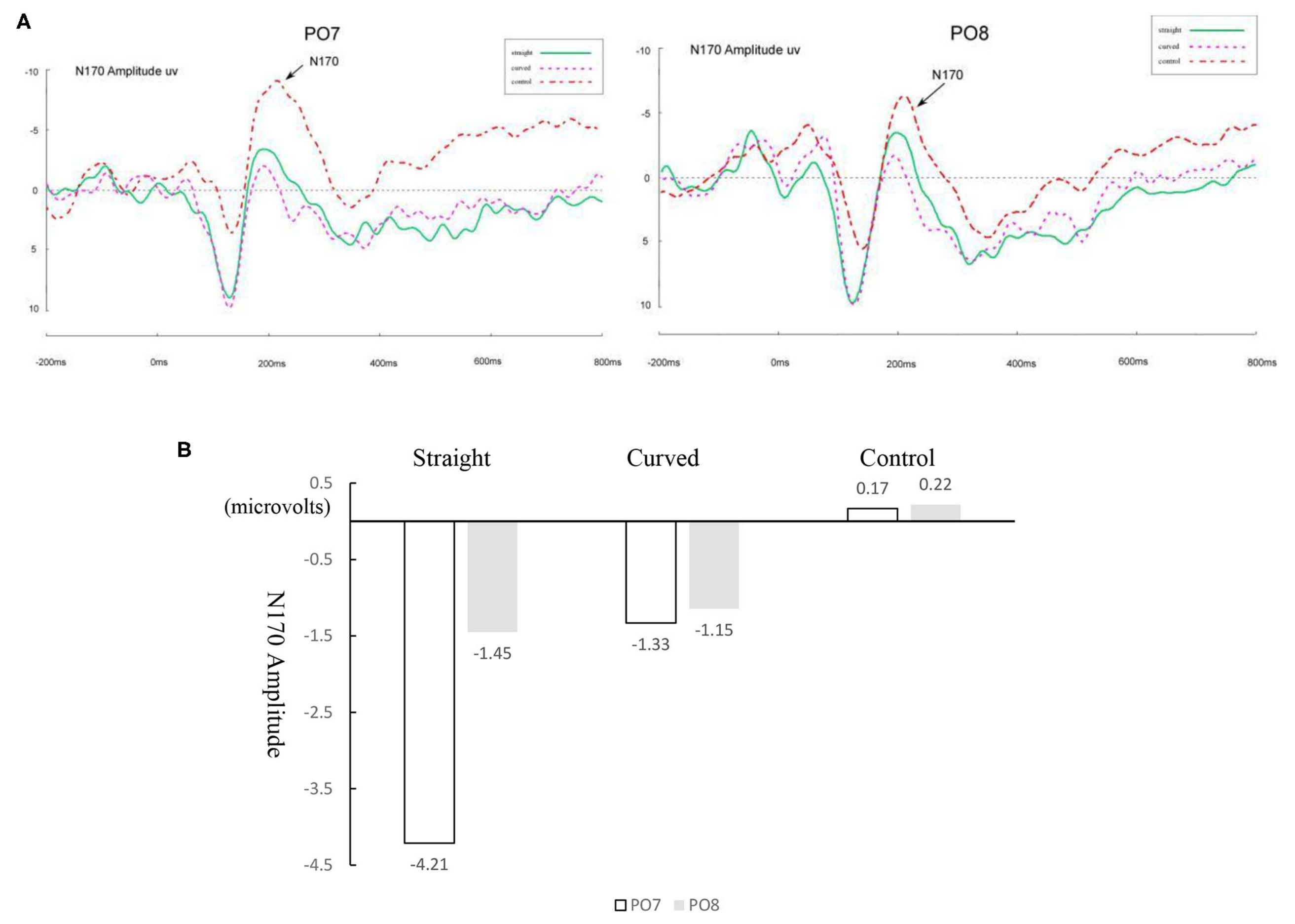

FIGURE 7 | (A) ERP waveforms of N170 under straight, curved control handwriting condition for normal readers for the left (PO7) and right (PO8) parietal leads. **(B)** Differences between three conditions for normal readers in the amplitude of N170.

drawing followed by Chinese recognition (DC) and drawing followed by English recognition (DE). Moreover, stimuli to be handwritten and drawn included both curved-line vs. straight-line strokes and curved-line vs. straight-line shapes. Five main findings were revealed. First, we found a Chinese handwriting facilitating effect in normal readers on behavior and the N170 compared to viewing in Chinese. Second, we found a drawing facilitating effect on English word recognition compared to Chinese character recognition for dyslexic readers, represented by behavioral and N170 indicators. Third, we revealed a laterality effect of handwriting in comparison to viewing Chinese among normal but not dyslexic readers, suggesting greater specialization in reading development in normal readers. Fourth, for normal readers, the left lateralization of the handwriting effects was supported by straight-line stimuli trials only but not for curved-line stroke handwriting. Finally, for dyslexic readers, the drawing effect on English word recognition was supported by curved-line shape drawing but not straight-line shape drawing.

The handwriting-Chinese condition (HC) has a facilitative effect on the Chinese word recognition when compared to the viewing-Chinese condition (VC), with longer reaction time and higher accuracy in VC than in HC. The peak N170 amplitude for HC in microvolts was likewise significantly larger than that of VC. Both the behavioral and ERP results show that HC facilitated the Chinese character processes, and when compared to the results for VC, HC facilitated the Chinese characters processing for typically developing but not dyslexic readers. The fact that the HC condition elicited a greater N170 than the VC condition indicates the N170 reflects efficient orthographic recognition due to handwriting experience, consistent with Liu and Perfetti's (2003) study results for Chinese-English bilinguals as well as other handwriting training (Guan et al., 2011, 2021) and Chinese word recognition research (Guan and Fraundorf, 2020; Guan et al., 2020). Handwriting training is hypothesized to improve recognition of the orthographic representation of the visual inputs in the human brain. Consistently, another study on artificial orthographies revealed that unit size gained during training impacted N170 modulation to word recognition (see Yoncheva et al., 2010). In current study, handwriting learning condition focused more on the smaller units embedded in the

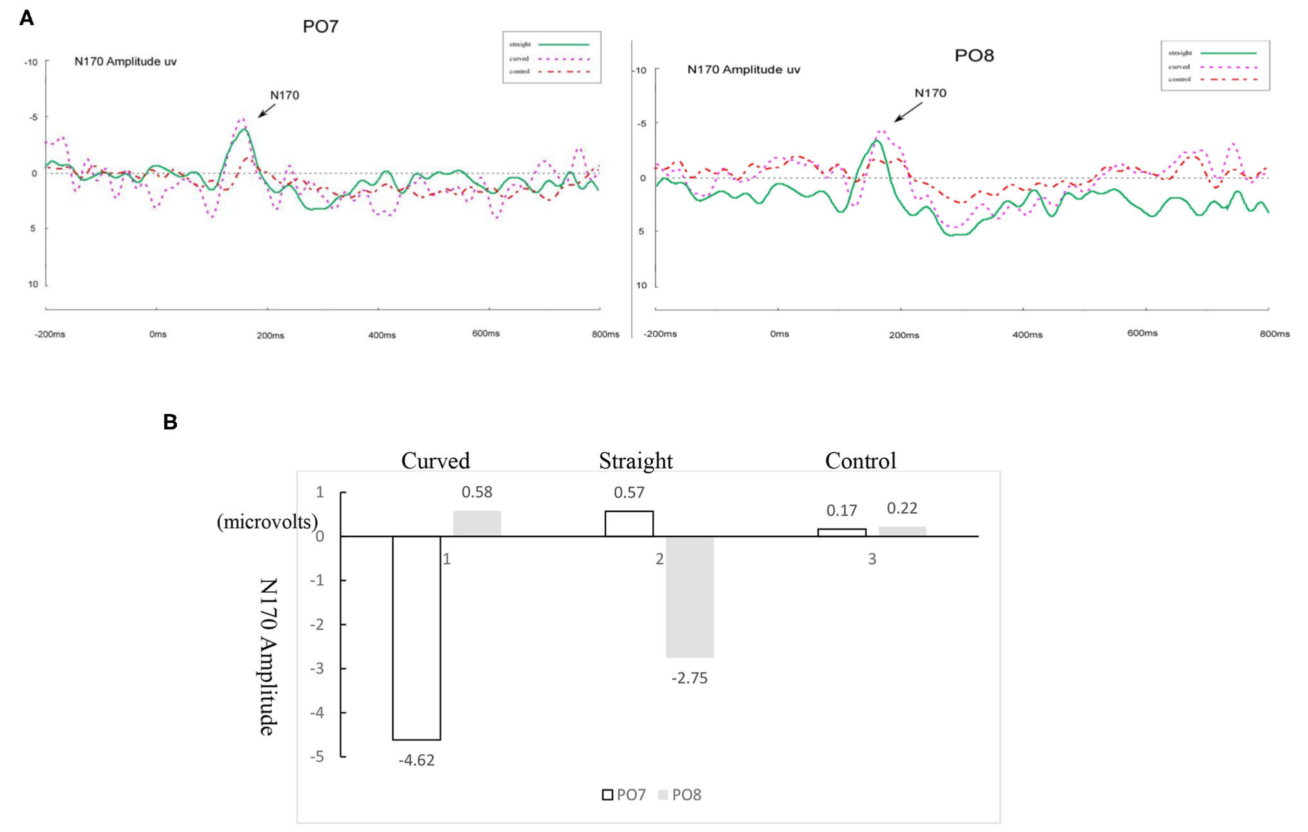

FIGURE 8 | (A) ERP waveforms of N170 under straight, curved control drawing English condition for dyslexic readers for the left (PO7) and right (PO8) parietal leads. **(B)** Differences between three conditions for dyslexic readers in the amplitude of N170.

visual representation of the words. Participants had to evaluate if a single character was included exactly with the same form in a complicated compound character in a binary judgement. They paid attention to local features, which might facilitate early Chinese character processing online, thus causing the N170 modulation.

The handwriting effect, on the other hand, did not persist in the response patterns for the dyslexic readers in our study. For typically developing readers, handwriting practice, which focuses on the intricate visual-orthographic components of stroke construction, is expected to enhance motor-sensory integration to aid visual recognition (Guan et al., 2011, 2021). The lack of handwriting effects in the dyslexic readers might suggest that they could have trouble focusing on the intricate visual-orthographic components of strokes and configurations of the Chinese writing system. Accordingly, other findings have revealed that when past knowledge was controlled for, improvements in handwriting quality predicted advanced performance in reading (Guan et al., 2015). Thus, lacking progress in reading development might be related to the failure in handwriting practices. Handwriting provides a sources for sensory-motor integration in the native language, and then generates a mental representation in alignment with a neural motor memory in a newer and more solid manner, which helps to establish the reading framework in the brains of typically developing readers. Sensorimotor coding plays a facilitating role in language cognition (Guan and Wang, 2017). In other words, it is easier for those who have a better understanding of the visual-motor integration in this language to acquire the written language in a more refined manner of visual-motor coupling, thus producing a more robust visual-orthographic representation in the mental lexicon. Unfortunately, such sensory-motor training in the current study might be difficult for dyslexic readers to master with limited practice.

Moreover, a fMRI study suggested that Chinese dyslexic children showed abnormal brain activation in brain regions associated with motor and visual processing, as well as general executive control, during handwriting (Yang et al., 2021). Consequently, in addition to visual-motor integration processing, it is possible that handwriting recruits attentional resources. However, executive control is integral to the process of handwriting and its deficits. For instance, some studies have attributed the high rate of pauses during handwriting to orthographic spelling difficulties in dyslexia (Sumner et al., 2013, 2014), whereas others have suggested impairment of motor execution during handwriting in developmental dyslexia (DD)

TABLE 3 | Summary table of behavioral and EEG results.

		HC vs.VC	**HC vs. DC**	**DC vs. DE**	
Normal	ACC	> (0.93)	> (0.66)	<(0.51)	
	RT	< (0.15)	< (0.04)	ns	
	N170	> (0.03)	ns	> (0.53)	
		HC	**VC**	**DC**	**DE**
	Laterality	L> R (0.13)	L>R (1.6)	ns	ns
	Stimuli	Straight > curved			
Dyslexic	ACC	< (0.01)	< (0.05)	< (0.22)	
	RT	< (0.04)	> (0.04)	ns	
	N170	> (0.06)	ns	> (0.02)	
		HC	**VC**	**DC**	**DE**
	Laterality	ns	L>R (0.16)	ns	L>R (0.27)
	Stimuli	ns	ns	ns	Curved >straight

Effect sizes represented by Cohen's d for the group comparison are reported in the parentheses. We calculated Cohen's d by using the following formula: $[4\eta^2/1-\eta^2]^{1/2}$*. Cohen's d < 0.2 indicates a small effect size, 0.2 < Cohen's d < 0.8 indicates a medium effect size, and Cohen's d > 0.8 indicates a large effect size (Fritz et al., 2012).*

VC, viewing character; HC, handwriting character; DC, drawing followed by Chinese recognition; DE, drawing followed by English recognition; ACC, accuracy rate for binary decision; RT, response time; L, left hemisphere; R, right hemisphere.

given that children with DD fail to comply with the principles of isochrony and homothety in the motor execution of handwriting (Pagliarini et al., 2015). Moreover, compared to age-matched and spelling-matched controls, people with DD are more impacted by the graphic complexity of words (Gosse and Van Reybroeck, 2020).

The accuracy level for HC was higher than DC, revealing that handwriting Chinese characters resulted in better performance than drawing followed by Chinese recognition, implying that handwriting facilitates in the coordination of the eye, mind and hands in order to establish a more sensible representation of the sub-lexicon forms (Guan et al., 2011). For readers who are typically developing, handwriting may help them perceive Chinese characters faster (Guan et al., 2015). For dyslexic readers only, however, DC reaction times were quicker than HC, and the EEG values for HC and DC were not statistically different. The findings suggested that both drawing could impact the N170, but handwriting might not. As a result, we will continue to investigate the stimuli effect in connection to the handwriting and drawing effect in both normal and dyslexic readers.

For typical readers, the lower accuracy rates for DC than HC suggested handwriting Chinese characters facilitated performance than drawing, and handwriting helped to coordinate the brain, eyes, and fingers to establish a subtle representation for sub-lexical word forms (Guan et al., 2011). Handwriting may accelerate the perception of Chinese characters for typically developing readers (Guan et al., 2015). However, the reaction times for DC were faster than HC for dyslexic readers only, and the ERP comparison between handwriting and drawing did not statistically differ from each other. The results suggest that a modulation in the ERPs indicator of the N170 by handwriting and drawing learning practices. Therefore, we continue examining the stimuli effect in correlation with the handwriting and drawing effect in typical and dyslexic readers.

The drawing followed by English and Chinese recognition differed between the DE and DC conditions. This may possibly reflect differences in the ways readers process Chinese and English. Above all, our results implied the language specificity effect. When processing Chinese, the brain functions the specific categorical perception in the written word unit. Therefore, processing Chinese characters might arouse a higher magnitude in N170 amplitude, and meanwhile the readers might show a more laterality in the left hemisphere in the N170 indicator. Previous study had a consistent findings in showing a more left-lateralized N170 in Chinese recodnition for English-Chinese bilinguals than the native-English readers (Wong et al., 2005). That is to say, the Chinese recognition, like processing faces could trigger a language-specific processing mechanism in the brain. Unfortunately, the laterality effect in the left hemisphere of this N170 to such language-specific stimuli is unclear.

Meanwhile, there was a drawing facilitation effect on the ERP indicator of N170 in the DE condition but not in the DC condition in dyslexic readers. But the results were vice versa for typically developing readers. This also shows a native language specificity effect. Chinese children children start to learn English in the grade 3. The stimuli in Chinese seemed to be more familiar than those in English stimuli to all participants in our study. Therefore, we found that normal students had a greater N170 magnitude on those Chinese stimuli than the English stimuli as English was the second language. This findings is in alignment with Liu and Perfetti's (2003). They found that the N170 effect on a native language in Chinese was larger than that an L2 language like English. Some other studies also showed that the N170 indexed visual-orthographic recognition processes. Stimuli in the orthographic stimuli (such as letter strings, non-words or real words) triggered a larger N170 effect than non-orthographic stimuli (such as shapes or other meaningless symbols) (Bentin et al., 1996; Pylkkanen and Marantz, 2003; Simon et al., 2004). Normal readers in our current study are much more familiar with their native language Chinese, so that there persisted greater N170 modulations by the native language if their reading networks develop well.

Typical readers showed a laterality effect on the N170 in the left hemisphere in the handwriting and viewing conditions. However there were no such laterality effect among the readers with developmental dyslexia. First, typical readers have had more experience with handwriting. They are not born with laterality according to literature, nor does the laterality effect appear in early stages of cognitive processes in children. As years grow, the laterality effect persists with written language when the readers mature (Kim et al., 2004). Consistent with the findings in Maurer et al. (2008), other studies have also reported an N170 facilitation for words in syllabic writing systems compared to the control (Shirahama et al., 2004). Shirahama et al. did not test left laterality effect, but this effect persisted among the experienced readers when they processed the alphabetic scripts (Bentin et al., 1996; Rossion et al., 2003; Maurer et al., 2005, 2008). Our findings echoed the same underlying mechanism of N170 laterality in the Chinese writing system that contained larger features of orthographic units, including syllables.

More importantly, our findings are consistent previous studies that demonstrated laterality effect in Chinese word recognition. Cao et al. (2011) claimed that the specialized mechanism of Chinese word recognition should merge among children turn to 7-year-old. Researchers examined different aged readers (ranging from 7 to adults) and found the left laterality effect on N170 modulation. On the contrary, children with dyslexia ($M_{\mathrm{age}} = 9.5$ years) did not have such an effect.

The absence of handwriting effects in dyslexic readers might be due to the following three reasons. First, the priming strokes of the basic symbols in the handwriting condition included only curved vs. straight-line strokes. These simple straight-line or curved-line handwriting experiences might not elicit dyslexic readers' sensitivity to the positional hierarchy and internal structure of the constituent parts of the Chinese characters (Leong et al., 2000). Second, basic stroke symbols do not facilitate grapheme-phoneme connection among dyslexic readers, who have deficits in grapheme-phoneme connection in reading performance (Aravena et al., 2013, 2017). A recent study showed that grapheme-phoneme learning training failed to significantly contribute to reading outcomes in an unknown orthography in dyslexic readers. This finding suggests that, to conquer the difficulties of dyslexia, readers should target phonological and orthographic knowledge directly mapping onto the grapheme-phoneme-conversion process itself (Law et al., 2018). A third reason might be due to the lack of handwriting practice. We speculate that increasing the number of handwriting practice trials might lead to different patterns of handwriting effects on dyslexic readers' word recognition.

Our findings revealed drawing effects of curved-line shapes on word recognition in English. Drawing curved shapes such as hearts, moons and waves involved studying highly variable instances of a symbol, facilitating symbol categorization relative to grapheme-motor connection of Chinese characters, regardless of visual-motor production (Li and James, 2016). This symbol categorization might not be a basic requirement for word recognition in English and might not a deficit among Chinese dyslexic readers. In fact, in our behavioral measures of English word reading, there were no differences between normal and dyslexic readers, leading us to speculate that that Chinese dyslexic readers might not perform worse in English reading. Xue et al. (2019) found an increased and left-lateralized N170 response for regular characters compared to cursive characters that were less familiar. It is likely that handwriting straight-line regular characters might prompt a quicker word recognition in Chinese. For the dyslexic readers, however, it is possible that the amount of training was not sufficient for increasing the familiarity of the visual characters for the children in our study.

Chinese children who are diagnosed with developmental dyslexia tend to have difficulty in spelling and reading Chinese characters, as well as writing and dictation (Leong et al., 2000). Nevertheless, the previous literature did not indicate that children with developmental dyslexia have trouble in drawing. For children with developmental dyslexia, the drawing skills acquired in free manual practice may improve children's visual mapping ability, thereby improving the visual-recognition patterns of the sequential letter recognition in English (Lam et al., 2011). For example, Seyll and Content (2020) evaluated the effects of graphic motor programs in letter-like shape recognition by interfering with graphic motor activity. The results showed that impaired handwriting was less accurate than normal handwriting, suggesting that handwriting motor skills contribute to the construction of letter representations. It is likely that, for Chinese dyslexic readers, a better way to improve their visual recognition skills could be through drawing practice (Poon et al., 2010) or that cursive pattern recognition skills could be improved through motor training like drawing (Schwellnus et al., 2012), improving English reading ability in which Chinese developmental dyslexics may not necessarily show impairments.

There are some limitations deserving consideration for future research. First, as we used the same stimuli across groups, the difficulty level of our stimuli might not be the same for typical and dyslexic readers. Future research should consider varying stimulus difficulty levels across age among typical and dyslexic readers, as the critical period for handwriting might begin at age of 7 and end at about 10 years old. Second, as the participants only engaged in handwriting or drawing for a few seconds, the modest effects might be due to limited prime duration. If participants are exposed to the learning conditions for a longer time period, there might be more significant effects and larger effect sizes. Third, future research should consider the possible effects of attention mechanisms on visual inputs (such as curved vs. straight shapes) on dyslexic children's handwriting in relation to orthographic features of linguistic writing units. It is speculated that the visual-form areas in the brain might be less activated by curved letters in comparison to straight-line letters in English as the visual-motor integrative processing of curved and smooth shapes requires less cognitive effort than straight but sharp-angled shapes (Ose Askvik et al., 2020). Moreover, the aesthetics of curved and smooth shapes might be more highly valued by dyslexic readers and may be processed at the same speed and with the same visual span as the normal readers (O'Brien et al., 2005). Finally, future research should also examine fine-grained modulation features of ERPs before 170 ms post stimulus onset (Woodman, 2010), which might reveal an effect of handwriting on sensory processing (Pratt, 2011), word recognition (Hillyard et al., 1998), or visual discrimination (Vogel and Luck, 2000).

In conclusion, handwriting straight-line Chinese characters led to a larger N170 laterality effect in the left hemisphere and quicker behavioral responses than viewing Chinese characters and quicker behavioral response than drawing for typically developing readers. Drawing curved-line shapes produced better performance in word recognition in English for dyslexic readers. The visual-motor integration mechanism might be the key underlying mechanism. The word visual representation might be enhanced by the efficient integration between visual and motor areas of the brain. This is the basic requirement for Chinese word recognition. The laterality effect in the left hemisphere was shown in normal but not dyslexic readers. The finding that drawing curved lines/shapes might enhance word recognition in English deserves more detailed future research. Future research should vary in methodologies to examine whether and to what extent handwriting or drawing affects orthographic perception among Chinese and English bilinguals.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by University of Science and Technology Beijing. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

CG and WM designed the study, collected and analyzed the data, and wrote the paper. YL analyzed the data. LM wrote the paper. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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Developmental Trajectories of Letter and Speech Sound Integration During Reading Acquisition

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Reading acquisition in alphabetic languages starts with learning the associations between speech sounds and letters. This learning process is related to crucial developmental changes of brain regions that serve visual, auditory, multisensory integration, and higher cognitive processes. Here, we studied the development of audiovisual processing and integration of letter-speech sound pairs with an audiovisual target detection functional MRI paradigm. Using a longitudinal approach, we tested children with varying reading outcomes before the start of reading acquisition (T1, 6.5 yo), in first grade (T2, 7.5 yo), and in second grade (T3, 8.5 yo). Early audiovisual integration effects were characterized by higher activation for incongruent than congruent letter-speech sound pairs in the inferior frontal gyrus and ventral occipitotemporal cortex. Audiovisual processing in the left superior temporal gyrus significantly increased from the prereading (T1) to early reading stages (T2, T3). Region of interest analyses revealed that activation in left superior temporal gyrus (STG), inferior frontal gyrus and ventral occipitotemporal cortex increased in children with typical reading fluency skills, while poor readers did not show the same development in these regions. The incongruency effect bilaterally in parts of the STG and insular cortex at T1 was significantly associated with reading fluency skills at T3. These findings provide new insights into the development of the brain circuitry involved in audiovisual processing of letters, the building blocks of words, and reveal early markers of audiovisual integration that may be predictive of reading outcomes.

Keywords: audiovisual integration, congruency effect, dyslexia, fMRI, children, superior temporal gyrus, ventral occipitotemporal cortex, inferior frontal gyrus

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INTRODUCTION

Reading is acquired over the course of many years and extensive practice is required to achieve fluent and efficient text reading competence and comprehension skills. Alphabetic writing systems are based on the principle that each speech sound corresponds to one or a combination of printed characters, namely letters. This process of mapping speech sounds to letters is taught at the very beginning of formal reading instruction and is a prerequisite for decoding sublexical units, such as syllables, bigrams, and trigrams, and eventually for the recognition of word forms. However, insights into how children's brains develop during the acquisition of culturally defined character-speech sound associations and how specific areas in the auditory and visual processing system adapt to process letter-speech sound combinations as audiovisual concepts are still sparse.

Parts of the auditory cortex and superior temporal regions have been identified as the main audiovisual integration site for words (McNorgan et al., 2014), as well as for letters and speech sounds (Raij et al., 2000; van Atteveldt et al., 2004). Letter-speech sound integration is a fast, automated process with electrophysiological responses characteristic to audiovisual processing arising as early as 150 ms (mismatch negativity; Froyen et al., 2009) but also extending to later multisensory integration processes at 380–540 ms (superior temporal sulcus (STS) activation, Raij et al., 2000) and around 650 ms after stimulus presentation (late negativity, Žarić et al., 2014). During letter-speech sound processing, expert readers of transparent and semi-transparent alphabetic systems have been found to engage superior temporal brain areas more strongly when speech sounds are paired with congruent letters compared to incongruent letters (Raij et al., 2000; van Atteveldt et al., 2004; Blau et al., 2009). A similar congruency effect was also observed in the Heschl's gyrus of 9-year-old typical readers (Blau et al., 2010), while adolescent readers with typical reading skills showed the opposite pattern, characterized by stronger responses for incongruent than congruent print-speech pairs in the left superior temporal gyrus (STG; Kronschnabel et al., 2014).

Letter-speech sound integration has been shown to rapidly develop at a very early stage of reading acquisition and is related to reading outcomes (Frost et al., 2009; Preston et al., 2016; Chyl et al., 2018). Already prereaders showed effects of audiovisual integration after a short artificial letter-speech sound training, which depended on their learning rate (Karipidis et al., 2017). Fast learners showed stronger congruency effects for trained artificial letter speech sound pairs in the right STG and left inferior temporal cortex. In addition, audiovisual integration in the left planum temporale (PT) of prereading children was significantly related to future reading fluency outcomes (Karipidis et al., 2018). Learning audiovisual correspondences also induced changes in the visual processing of artificial letters in text-selective regions of left ventral occipitotemporal cortex (vOTC), located in the posterior fusiform and occipitotemporal sulcus (OTS), which were dependent on the training performance of the preschoolers (Pleisch et al., 2019a).

Specific portions of vOTC located along the middle and posterior OTS are commonly referred to as the visual word form area(s) (VWFA) and selectively respond to words, letters, and other print stimuli (Cohen et al., 2002; McCandliss et al., 2003; Lerma-Usabiaga et al., 2018; Caffarra et al., 2021a). This visual specialization emerges rapidly when children learn how to read and is refined over the course of reading acquisition. It has been shown that children (Brem et al., 2010; Pleisch et al., 2019a) and adults (Madec et al., 2016) show increased activation in text-selective portions of vOTC after intensive grapho-phonological training. In beginning readers, auditory processing with high phonological awareness demands also engages parts of vOTC, activation of which depends on reading ability (Wang et al., 2018). Audiovisual processing of letters and speech sounds engages left vOTC more than other audiovisual stimuli, such as numerals and number names (Holloway et al., 2015). Activation in vOTC during audiovisual processing of letter-speech sound pairs also depends on reading ability and has been found to be reduced in dyslexia (Richlan, 2019; Romanovska et al., 2021). Effects of audiovisual congruency have been reported less consistently for vOTC. In a sample of adolescent readers, Kronschnabel et al. (2014) reported an incongruency effect for letter-speech sound pairs and short pseudowords in left vOTC for typical readers, while poor readers showed effects toward a congruency effect.

Despite the increasing interest in studying print and speech processing in early stages of development, longitudinal studies covering multiple time points during the course of reading acquisition are still very scarce (Chyl et al., 2021). We recently reported first longitudinal evidence showing a positive association between congruency effects for non-word stimuli in the left STG and improvement in reading skills from first to second grade (Wang et al., 2020). In addition, a recent magnetoencephalography (MEG) study showed in a cross-sectional and longitudinal cohort that an electrophysiological incongruency effect for syllables emerges from prereading to early reading stages, stemming from the left superior temporal cortex (Caffarra et al., 2021b). An earlier MEG study found that beginning readers show an audiovisual processing effect for letters and speech sounds in temporoparietal sources and this effect correlated with literacy skills (Xu et al., 2018).

However, it remains unclear how audiovisual processing of letter-speech sound pairs changes from the prereading to the early reading stages and how it is associated with reading development. Automated retrieval of correspondences between letters and speech sounds is a prerequisite for successful reading acquisition (Ziegler and Goswami, 2005). One of the leading theories of dyslexia postulates that difficulties in crossmodal integration can lead to an impairment in the automatization of grapho-phonological entities (Blomert, 2011). Deficits in print-speech automaticity could also be driven by difficulties in selectively processing linguistic information or poor phonological and language skills, which often characterize young struggling readers (Pennington et al., 2012). Considering audiovisual integration of letters and speech sounds as a sensory process that develops during reading acquisition, presumably by engaging brain regions that are specialized for auditory, visual, and cross-modal processing, understanding its development could help explain neurobiological mechanisms that influence reading acquisition.

The aim of the current study was to investigate developmental trajectories of neural activation to letter-speech sound pairs in a group of children with varying risk for developmental dyslexia and reading outcomes. We focused on analyzing longitudinal fMRI data during an audiovisual target detection task at three crucial stages: (1) before the start of formal reading instruction (at the end of second year of kindergarten), (2) at the middle of first grade, when full letter knowledge is almost attained but reading is still imprecise and sluggish, and (3) at the middle of second grade, when accurate reading is expected but reading fluency is still being practiced intensively. Additionally, we investigate how development of audiovisual letter-speech sound processing relates to children's reading outcomes.

MATERIALS AND METHODS

Participants

A sample of 50 German-speaking children completed the fMRI experiment presented here at least on one of the following three time points: at T1, within 4 months prior to the start of formal reading acquisition (kindergarten), at T2, 5–9 months after the start of formal reading acquisition (grade 1), and at T3, 5–9 months after the start of the second year of formal reading acquisition (grade 2). The data of three participants was excluded due to poor data quality at all available time points. From the remaining 47 participants, $n = 29$ met the stringent data quality criteria for all three time points and eighteen had no available data in at least one of the time points due to the following reasons: one only participated at T1, six discontinued participation or wore braces at T3, for two participants data were excluded due to poor data quality at T1, and additional nine had no available data for T1 because they were enrolled to the study at T2. The subsample of $n = 29$ with complete longitudinal fMRI data served as the core sample for the whole-brain analyses, while the enlarged sample of $n = 47$ ($n_{T1} = 36$; $n_{T2} = 45$; $n_{T3} = 40$) was used for region of interest (ROI) analyses that permitted missing values (**Table 1**).

This sample was drawn from a large longitudinal study focusing on cognitive and brain development of children at varying familial risk for developmental dyslexia over multiple time points during the course of reading acquisition (Karipidis et al., 2017, 2018; Pleisch et al., 2019a,b; Mehringer et al., 2020; Wang et al., 2020; Fraga-González et al., 2021). Familial risk for dyslexia was estimated using the Adult Reading History Questionnaire (ARHQ; Lefly and Pennington, 2000). Two participants of the enlarged sample were treated for attention deficit/hyperactivity disorder and discontinued their medication for 48 h before all neuroimaging sessions and behavioral testing. All participants reported no other neurological or psychiatric disorders, had normal visual and auditory acuity, and had a non-verbal IQ-estimate of above 80. The study was approved by the ethics committee of the Kanton of Zurich and neighboring cantons in Switzerland. All assessments and experiments were undertaken with the understanding and written consent of a legal guardian and oral consent of all children.

Neurocognitive and Reading Assessments

An extensive neurocognitive test battery was performed at all-time points (**Table 1**). Letter sound knowledge was tested for all upper- and lower-case letters of the Latin alphabet, as well as for the umlaut vowels of German (ä, ö, ü). Letter-sound knowledge scores only showed meaningful variability at T1, with children reaching ceiling performance at T2 and T3. Word and pseudoword reading fluency were tested using the Salzburger Lese- und Rechtschreibtest at T2 and T3 (SLRT-II, Moll and Landerl, 2010). For T3, age-adjusted standardized scores for word and pseudoword reading were averaged to compute the reading fluency outcome score. Participants with a mean reading fluency score below the 16th percentile were classified as poor readers ($n = 10$ for the core sample; $n = 17$ for the enlarged sample). Non-verbal IQ was assessed using the CFT1-R (Weiß and Osterland, 2013).

Experimental Paradigm

The participants performed an implicit audiovisual target detection task at all-time points (Kronschnabel et al., 2014; Karipidis et al., 2017). The task was programmed using Presentation® (Version 16.4)[1] and included four conditions: congruent and incongruent pairs of single letter-speech sound correspondences, as well as unimodally presented letters and speech sounds. The current analysis focuses on the fMRI data of the audiovisual conditions (for analyses of the visual condition see Pleisch et al., 2019a; Fraga-González et al., 2021).

The task consisted of 16 blocks (4 blocks/condition) and total task duration was 375 s. Unimodal and bimodal blocks (15 trials/block) alternated pseudorandomly and were separated by fixation periods of 6 or 12 s. Each condition included 54 experimental trials and 6 target trials. The trials within each block were presented pseudorandomly for 613 ms with an interstimulus interval of 331 or 695 ms (**Figure 1**). Visual information was presented over video goggles (VisuaStimDigital, Resonance Technology, Northride, CA) and auditory information over in-ear headphones (MR confon GmbH, Magdeburg). Letters were presented in black in the middle of a gray background (mean visual angle: horizontally 2.8°; vertically 4.8°). Participants were instructed to respond by button press to the target, which was the drawing or sound of a cat, or the audiovisual presentation of both.

Accuracy and reaction times were analyzed using linear mixed models. Accuracy in target detection was high, 93.4 ± 6.2% for the core sample and 94.0 ± 6.5% for the enlarged sample, with a mean reaction time of 677 and 674 ms, respectively. Accuracy did not significantly differ between the three time points [ACC_{core}: $F_{(2,\ 83)} = 1.71$, $p = 0.188$; $ACC_{enlarged}$: $F_{(2,\ 117)} = 0.71$, $p = 0.494$]. As expected, reaction times decreased over time, i.e., children responded significantly faster as they grew older [RT_{core}: $F_{(2,\ 83)} = 13.68$, $p < 0.001$; $RT_{enlarged}$: $F_{(2,\ 117)} = 11.57$, $p < 0.001$]. Responses of one participant at T1 were not logged due to a technical problem and therefore not included in the response analysis.

MRI Data Acquisition and Preprocessing

MRI data was recorded on a Philips Achieva 3 Tesla scanner (Best, The Netherlands) using a 32-element receive head coil. Using a T2*-weighted whole-brain gradient-echo planar image sequence, 189 volumes were acquired during a simultaneous EEG-fMRI recording. The following acquisition parameters were used: slices/volume: 31, repetition time: 1.98 s, echo time: 30 ms, slice thickness: 3.5 mm, slice gap: 0.5 mm, flip angle: 80°, field of view: 240 × 240 mm^2, in-plane resolution: 3 × 3 mm^2,

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[1] www.neurobs.com

TABLE 1 | Participant characteristics.

	Core sample (n = 29)			Enlarged sample (n = 47)		
	Typical	**Poor**	**Group statistics**	**Typical**	**Poor**	**Group statistics**
Sex (f/m)	8/11	6/4	$\chi^2 = 0.84$ $p = 0.359$	14/16	10/7	$\chi^2 = 0.64$ $p = 0.423$
Handedness(R/L)	16/3	10/0	$\chi^2 = 1.76$ $p = 0.184$	26/4	16/1	$\chi^2 = 0.63$ $p = 0.426$
ARHQ[a]	0.49 ± 0.17	0.61 ± 0.10	$t = -2.53$ $p = 0.017$	0.47 ± 0.15	0.56 ± 0.12	$t = -1.99$ $p = 0.053$
IQ	102.68 ± 10.48	101.60 ± 9.42	$t = 0.27$ $p = 0.786$	102.10 ± 10	100.82 ± 8	$t = 0.45$ $p = 0.655$
Age T1	6.68 ± 0.32	6.63 ± 0.32	$t = 0.44$ $p = 0.660$	6.66 ± 0.31	6.62 ± 0.29	$t = 0.32$ $p = 0.748$
Age T2	7.32 ± 0.31	7.31 ± 0.30	$t = 0.09$ $p = 0.925$	7.32 ± 0.30	7.38 ± 0.36	$t = -0.57$ $p = 0.570$
Age T3	8.44 ± 0.32	8.37 ± 0.30	$t = 0.58$ $p = 0.567$	8.40 ± 0.31	8.43 ± 0.33	$t = -0.28$ $p = 0.783$
Letter-speech sound knowledge T1[b]	16.00 ± 11.64	11.60 ± 8.97	$t = 1.04$ $p = 0.307$	16.96 ± 11.88	12.42 ± 8.36	$t = 1.19$ $p = 0.241$
Word and pseudoword reading fluency T3[c]	48.68 ± 19.51	7.60 ± 5.70	$t = 7.54$ $p < 0.001$	48.64 ± 17.56	7.16 ± 5.03	$t = 10.17$ $p < 0.001$

Values are mean ± SD [a]Highest parental ARHQ score: 22 children of the core and 34 children of the enlarged sample exceeded the ARHQ risk score of > 0.4, indicating a considerable familial risk for developmental dyslexia; [b]raw values: n; [c]percentile scores.

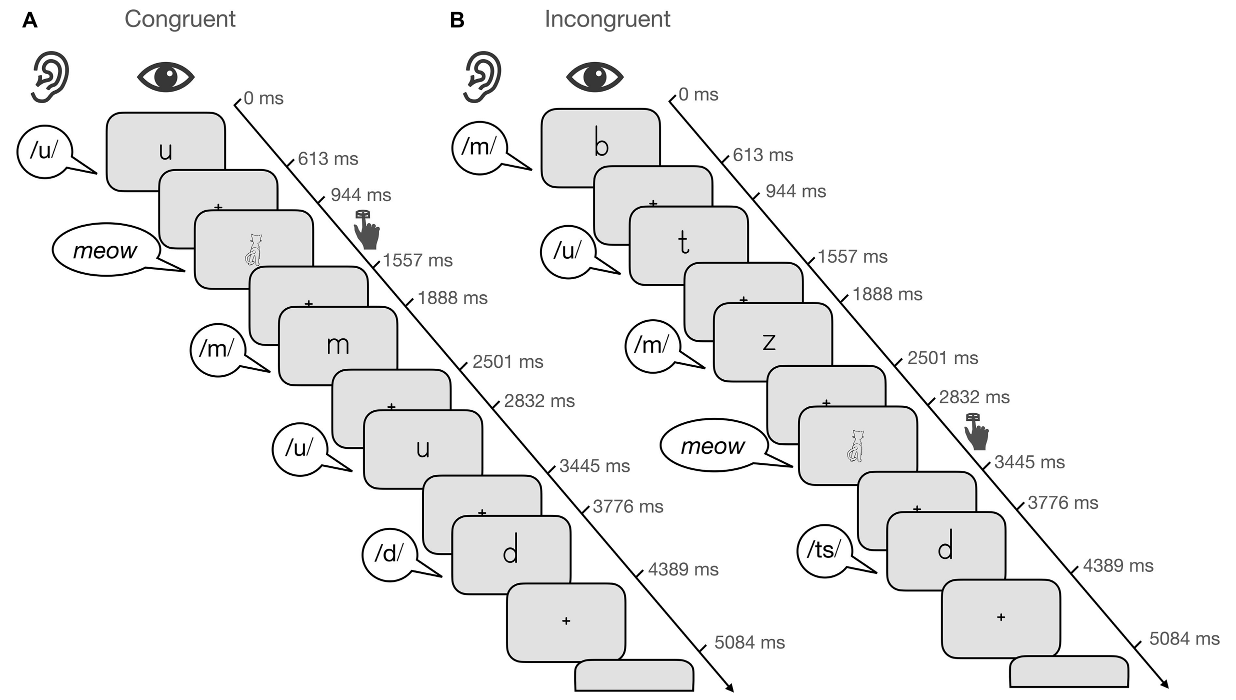

FIGURE 1 | Audiovisual target detection task. Illustration of five trials for **(A)** the audiovisual congruent condition and **(B)** the audiovisual incongruent condition. Each block consisted of 15 trials that were presented pseudorandomly for 613 ms with an interstimulus interval of 331 or 695 ms. Participants were instructed to respond when the target, i.e., the drawing of a cat appeared.

SofTone factor: 3, sensitivity-encoding (SENSE) reduction factor: 2.2. In addition, a field map and a high-resolution T1-weighted anatomical image were acquired.

FMRI data was preprocessed and analyzed using SPM12. Preprocessing included B0 field map correction, realignment and unwarping, slice time correction, coregistration and segmentation, normalization, resampling (3 × 3 × 3 mm^3), smoothing (8 mm FWHM), and normalization to Montreal Neurological Institute (MNI) standard space based on deformations derived from the segmentation and a pediatric anatomical template (age range 5.9–8.5 years) created using the Template-OMatic toolbox (Wilke et al., 2008).

After preprocessing, movement artifact correction was performed as implemented in the ArtRepair toolbox (Mazaika et al., 2007). Motion affected volumes with scan-to-scan movement of more than 1.5 mm were repaired using linear interpolation between the nearest unrepaired scans. If more than 15% of the scans needed to be repaired, the data was excluded from further analysis. In addition, if a scan was preceded and followed by a motion affected scan or if more than two consecutive scans were affected by movement, scrubbing was performed by modeling the affected volumes in a binary regressor of no interest (for details see **Supplementary Material**).

Whole-Brain fMRI Analysis

The whole-brain analysis focused on the development of audiovisual processing of single letters and speech sounds and was performed using the core sample ($n = 29$). We calculated a whole-brain ANOVA with factors time (T1, T2, and T3) and congruency (congruent and incongruent) to test for developmental effects of audiovisual integration. In addition, familial risk for dyslexia, letter-sound knowledge at T1 and individual reading fluency scores at T3 were used to perform multiple regression analyses with whole-brain activation of each condition within each time point. All whole-brain analyses were restricted to a gray matter mask which included all voxels that were classified as gray matter volume with a probability of > 0.5 in the tissue probability map of the pediatric MNI template. We applied a voxel-wise uncorrected threshold of $P < 0.001$ with a cluster size threshold of $k > 15$. We also report cluster-level corrected P-values ($P < 0.05$). Results that are not significant after correction for multiple comparisons should be interpreted with caution and need to be replicated.

Region of Interest Analysis

To investigate the development of letter processing in key regions of reading and audiovisual processing, region of interest (ROI) analyses were performed. ROIs were selected using the meta-analysis tool of NeuroSynth (Yarkoni et al., 2011). The search term “letter” yielded two peaks, one in the vOTC ($x = -44$, $y = -60$, $z = -14$) and one in the IFG ($x = -46$, $y = 2$, $z = 24$; **Figure 2**). In addition, the search term “audiovisual” revealed two peaks in the STG, a mid STG ROI (midSTG: $x = -52$, $y = -22$, $z = 6$) and a posterior ROI in the STG/STS (postSTG: −56, −42, 10; **Figure 3**). The midSTG ROI falls within the primary auditory cortex, while the postSTG ROI includes parts of the STS and represents audiovisual integration regions (Blau et al., 2009; Holloway et al., 2015). Each ROI was defined as a 6mm radius sphere around the peak coordinates, which are provided in MNI space.

For each ROI, we calculated a linear mixed model (LMM) with factors time (T1, T2, T3), reading fluency at T3 (typical, poor), and congruency (congruent, incongruent). The enlarged sample ($n = 47$) was used for these analyses, given that LMM can handle missing data points. Standardized residuals were used to identify and exclude outliers deviating more than 3 standard deviations from the mean. For significant interaction effects, *post hoc t*-tests were computed, and Tukey Kramer corrected P-values are reported. We also tested for associations of audiovisual integration at each time point with familial risk for dyslexia, letter-sound knowledge at T1, and reading fluency outcome at T3. Individual differences in processing incongruent and congruent letter-speech sound pairs in each ROI were used as a measure for audiovisual integration and were correlated with each of the behavioral measures ($P < 0.05$).

LMM with factors time and reading were also computed using the incongruency effect (**Supplementary Figures 4, 5**). In addition, supplementary ROI analyses were performed to replicate the vOTC and STG effects in functionally defined ROIs (**Supplementary Figures 2, 3**).

RESULTS

Whole-Brain Analyses

The ANOVA ($n = 29$) with factors time (T1, T2, T3) and congruency (congruent, incongruent) showed that audiovisual processing of single letter-speech sound pairs elicited strong blood oxygen level dependent (BOLD) responses in large portions of vOTC and STG, as well as in the inferior frontal gyrus (IFG), middle frontal gyrus (MFG), superior parietal lobule (SPL), and angular gyrus (AnG; **Supplementary Figure 1** and **Supplementary Table 1**). We found a significant main effect of congruency that was characterized by stronger BOLD responses for incongruent than congruent pairs in the left IFG and left vOTC across all time points (**Figure 4A**). In addition, brain activation in the left IFG and STG, including parts of the planum temporale (PT) significantly increased from T1 to T2 during audiovisual processing of letter-speech sound pairs (**Figure 4B**). Audiovisual processing of letter-speech sound pairs was also stronger in the left STG at T3 compared to T1 (**Figure 4C** and **Table 2**).

Using multiple regression analysis, we investigated whether audiovisual integration at each time point, reflected by the incongruency effect (incongruent vs. congruent), was associated with familial risk for dyslexia, letter knowledge at T1 and reading outcomes at T3. We found no association between individual risk for dyslexia and the strength of the incongruency effect on a whole brain level. Prereading children with higher letter-sound knowledge at T1 showed a stronger incongruency effect in the left planum polare (PP), the anterior portion of the STG (**Figure 5A**). Particularly children with low letter knowledge showed higher neural responses for congruent than incongruent letter-speech sound pairs in this region. A stronger incongruency effect at T1 bilaterally in a more posterior portion of the STG, extending to parts of the posterior insular cortex, was significantly associated with higher reading fluency scores at T3 (**Figure 5B**). Finally, a stronger incongruency effect in the left angular gyrus (AnG) at T2 was associated with lower reading fluency scores at T3 (**Figure 5C**; **Table 2**), i.e., children with better reading fluency scores at T3 showed stronger responses to congruent than incongruent letter-speech sound pairs in the left AnG.

Region of Interest Analysis

Letter-Speech Sound Processing in Letter-Specific Regions of Interest

Using the meta-analysis tool Neurosynth with the search term “letter,” we identified two ROIs that previously showed letter-specific activation, one in the left vOTC and one in the left IFG (**Figure 2**). The LMM with factors time, congruency, and reading fluency was computed using mean beta values in these ROIs.

For the left vOTC ROI, we found a main effect of time [$F_{(2,\ 176)} = 13.07$, $P < 0.001$; **Figure 2A**]. Activation in left vOTC significantly increased from T1 to T2 [$t(176) = 3.90$, Pcor < 0.001] and decreased from T2 to T3 [$t(176) = 4.65$, Pcor < 0.001]. The significant interaction of time and reading ability [$F_{(2,\ 176)} = 8.27$, $P < 0.001$] indicated that this developmental effect showed distinct developmental trajectories

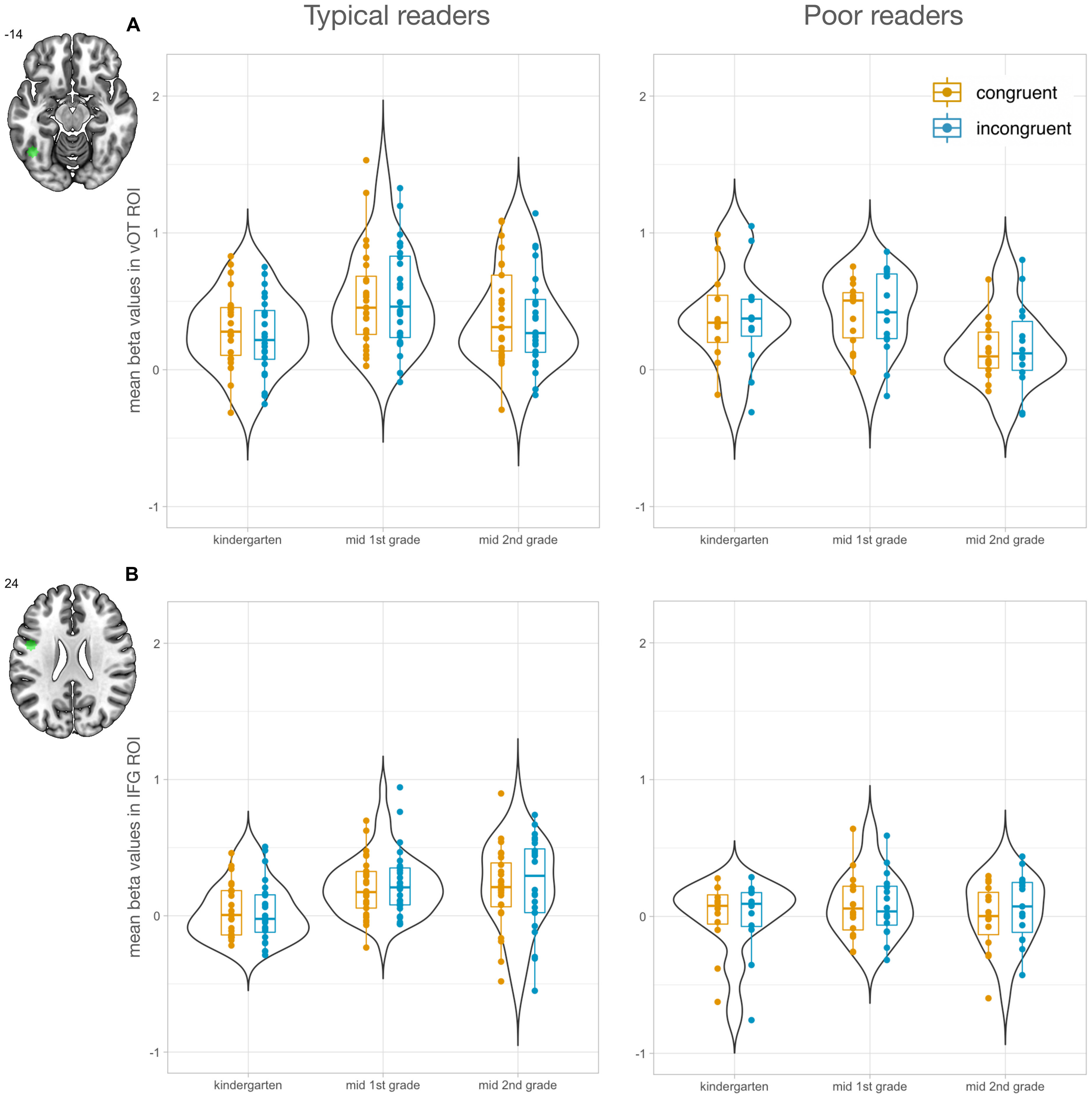

FIGURE 2 | Letter-specific region of interest analyses (*n* = 47). Left panels show values for typical readers and right panels for poor readers. Mean responses to congruent letter-speech sound pairs are shown in orange and to incongruent in blue. **(A)** Mean beta values in left vOTC ROI increased from kindergarten (T1) to 1st grade (T2) and second grade (T3) in the typical reading group, while the poor reading group showed a significant decrease from 1st grade (T2) to second grade (T3). **(B)** Mean beta values in left IFG ROI increased from kindergarten (T1) to 1st grade (T2) and second grade (T3) in the typical reading group. IFG activation was significantly higher for typical readers than poor readers at T3.

based on reading outcome (**Figure 2A**). Activation in left vOTC during audiovisual processing of letters only increased in children with typical reading outcomes from T1 to T2 [$t(176) = 5.15$, Pcor < 0.001], a developmental increase that was still evident in T3 [$t(176) = 2.93$, Pcor = 0.043]. Children with poor reading outcomes did not show a significant increase of activation in left vOT from T1 to T2 [$t(176) = 1.10$, Pcor = 0.879] but a decrease at T3 [T1 > T3: t(176) = 2.90, Pcor = 0.048; T2 > T3: $t(176) = 4.24$, Pcor = 0.001], which probably drove the reduction of activation observed in the main effect for T3. Even though the two groups showed diverging developmental patterns, group differences within time points were not significant (Pcor > 0.121). A supplementary analysis revealed that the incongruency effect in left vOTC increased over time (**Supplementary Figure 4A**). We found no significant correlations between incongruency effects and letter-sound knowledge at T1, reading fluency outcome at T3 or familial risk for dyslexia.

The LMM in the left IFG revealed a significant main effect of time [$F_{(2,\ 183)} = 6.32$, $P = 0.002$; **Figure 2B**]. Audiovisual processing in the left IFG increased after the start of formal

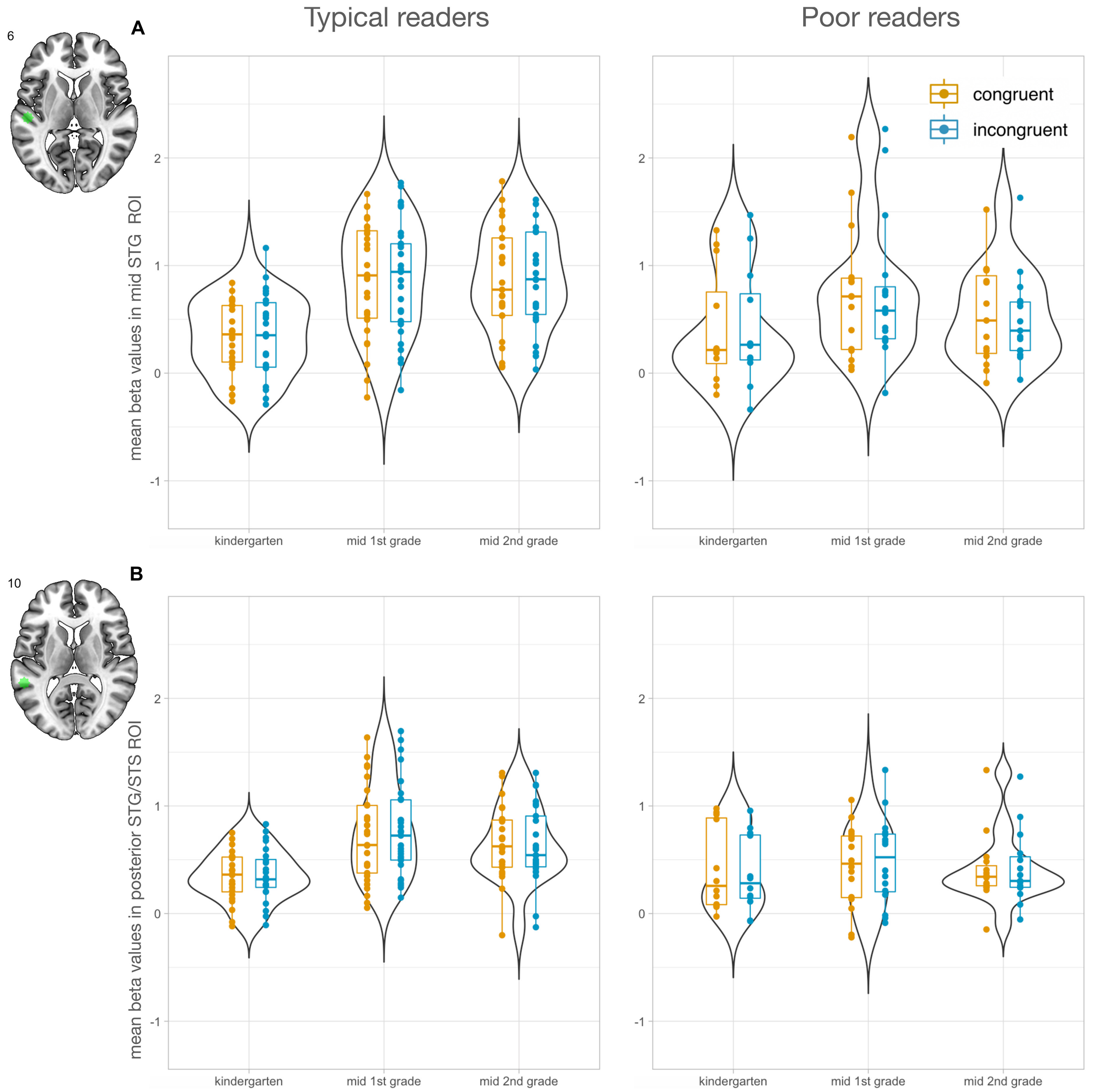

FIGURE 3 | Region of interest analyses in audiovisual processing areas of the STG (*n* = 47). Mean beta values in STG ROIs increased from kindergarten (T1) to 1st grade (T2) and second grade (T3) in the typical reading group. **(A)** Mid STG ROI (midSTG). **(B)** Posterior STG ROI (postSTG). Left panels show values for typical readers and right panels for poor readers. Mean responses to congruent letter-speech sound pairs are shown in orange and to incongruent in blue.

reading instruction and was significantly stronger for T2 > T1 [$t(183) = 3.42$, Pcor = 0.002] and T3 > T1 [$t(183) = 2.73$, Pcor = 0.019]. The interaction between time and reading ability showed that this developmental increase was specifically evident in typical readers [T2 > T1: $t(183) = 3.91$, Pcor = 0.002; T3 > T1: $t(183) = 3.86$, Pcor = 0.002] and not in poor readers ($P > 0.732$). In addition, at T3 the typically reading group showed significantly stronger responses in the left IFG compared to the poorly reading group [$t(183) = 2.93$, Pcor = 0.044]. In line with the whole-brain analysis, supplementary results focusing on the incongruency effect in the IFG showed an increase of incongruent vs. congruent activation over time (**Supplementary Figure 4B**). Incongruency effect in the left IFG ROI was not significantly correlated with familial risk for dyslexia, letter-sound knowledge at T1, and reading fluency outcome at T3.

Letter-Speech Sound Processing in Audiovisual Regions of Interest

The search term "audiovisual" in NeuroSynth resulted in two peaks along the STG/STS. We found a significant main effect of time for both STG ROIs [midSTG: $F_{(2,\ 185)} = 16.51$, $P < 0.001$; postSTG: $F_{(2,\ 185)} = 10.77$, $P < 0.001$]. STG activation increased over time particularly from T1 to T2 [midSTG: $t(185) = 5.71$, Pcor < 0.001; postSTG: t(185) = 4.59, Pcor < 0.001], and from

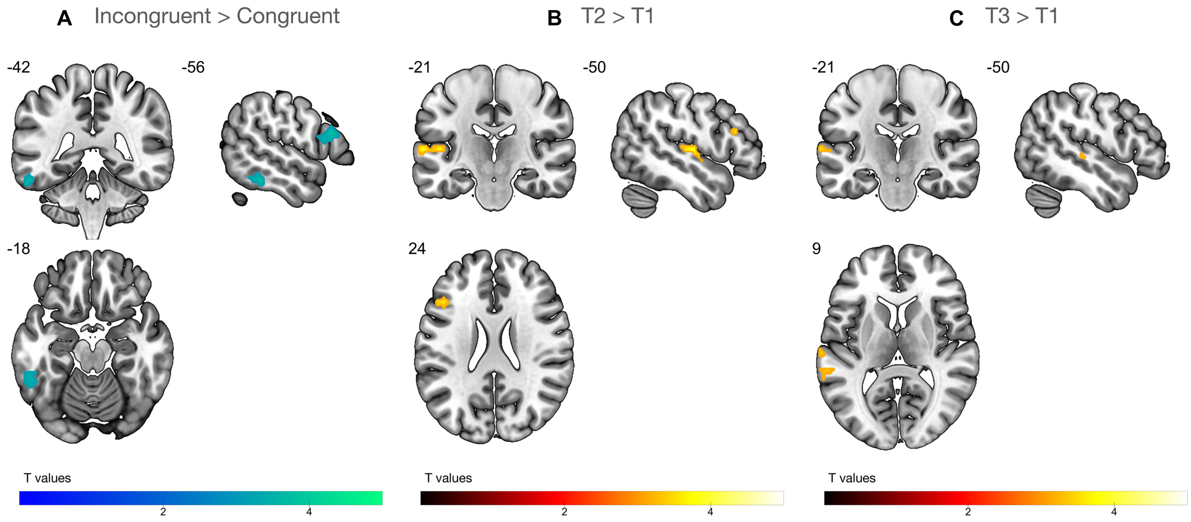

FIGURE 4 | Whole-brain analysis (*n* = 29). **(A)** Incongruency effect: higher activation for incongruent than congruent letter-speech sound pairs in the left inferior frontal gyrus and the left ventral occipitotemporal cortex. **(B)** Effect of time: stronger audiovisual processing at T2 than T1 in the left inferior frontal gyrus and superior temporal gyrus/planum temporale. **(C)** Effect of time: activation increase for audiovisual processing in the left superior temporal gyrus is still evident at T3.

TABLE 2 | Whole-brain analysis (*n* = 29).

Brain area	MNI coordinates			Voxels	*T*-value	Peak-level P uncor	Cluster-level P uncor	Cluster-level P FWEcorr
	x	y	z					
Incongruent > congruent								
IFG left	−56	21	21	41	3.86	<0.0001	0.035	0.273
ITG/vOTC left	−59	−42	−24	36	3.70	0.0001	0.046	0.344
T2 > T1								
STG/PT left	−59	−30	6	85	4.23	<0.0001	0.004	0.038*
IFG left	−47	24	21	22	3.70	0.0001	0.108	0.632
T3 > T1								
STG left	−68	−18	9	20	3.67	0.0002	0.124	0.682
STG left	−65	−39	9	17	3.44	0.0004	0.154	0.758
Incongruent > congruent T1 × letter knowledge T1								
STG/PP left	−47	3	−6	16	4.48	<0.0001	0.160	0.781
Incongruent > congruent T1 × reading ability T3								
STG/insula	40	−3	0	32	4.77	<0.0001	0.050	0.390
	−32	0	12	20	4.34	<0.0001	0.112	0.669
Congruent > incongruent T2 × reading ability T3								
AnG left	−47	−54	48	16	4.06	0.0002	0.120	0.752

Results were masked using a gray matter mask. Voxel-wise uncorrected threshold of P < 0.001, k > 15. Asterisk marks cluster-level FWE corrected P < 0.05.
IFG, inferior frontal gyrus; ITG, inferior temporal gyrus; vOTC, ventral occipitotemporal cortex; PT, planum temporale; STG, superior temporal gyrus; PP, planum polare; AnG, angular gyrus.

T1 to T3 [midSTG: $t(185) = 3.75$, Pcor < 0.001; postSTG: $t(185) = 3.20$ Pcor < 0.005]. No significant main effect of reading was found for midSTG [$F_{(1,\ 185)} = 1.67$, $P = 0.197$], while postSTG showed group differences on a trend level [$F_{(1,\ 185)} = 3.76$, $P = 0.054$]. The interaction of time and reading ability was significant for both STG ROIs [midSTG: $F_{(2,\ 185)} = 4.66$, $P = 0.011$; postSTG $F_{(2,\ 185)} = 5.69$, $P = 0.004$] and revealed that audiovisual processing in the STG particularly increased in the typical reading group [midSTG: T2 > T1 $t(185) = 6.29$, Pcor < 0.001, T3 > T1 $t(185) = 5.75$, Pcor < 0.001; postSTG: T2 > T1 $t(185) = 6.64$, Pcor < 0.001, T3 > T1 $t(185) = 5.00$, Pcor < 0.001] and not in the poor reading group ($P > 0.129$). The typical and poor reading groups showed the strongest difference at T2 for the postSTG ROI [$t(185) = 2.81$, Pcor $= 0.061$] and at T3 for the midSTG ROI [$t(185) = 2.67$, Pcor $= 0.086$].

The supplementary analysis, focusing on the development of the incongruency effect, only revealed a developmental change of incongruent vs. congruent activation in the postSTG ROI (**Supplementary Figure 5**). The strongest incongruency effect in the postSTG ROI was evident at T2 (**Supplementary Figure 5B**).

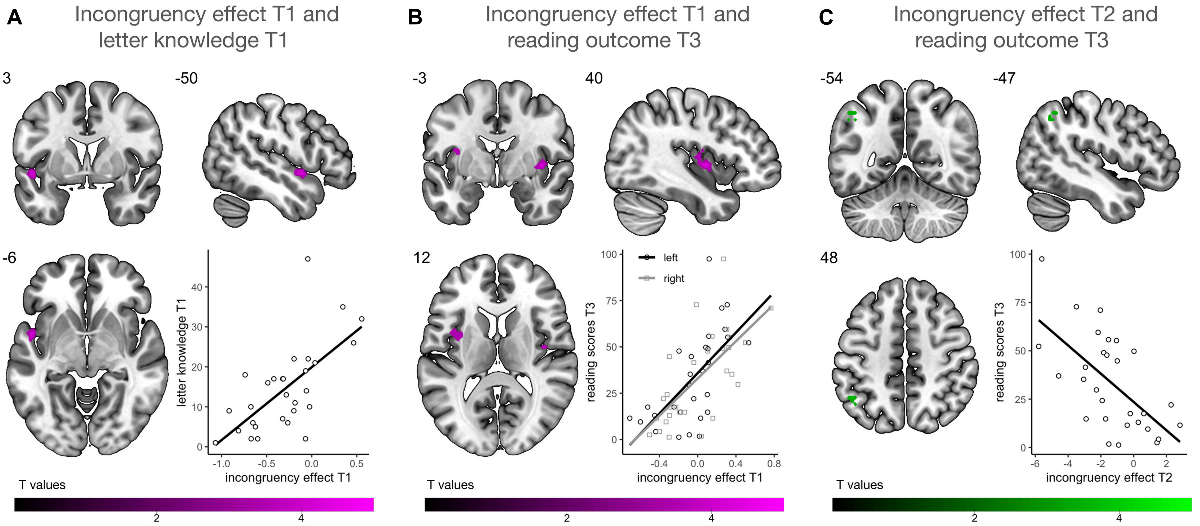

FIGURE 5 | Multiple regression analysis (*n* = 29). **(A)** Higher activation for incongruent than congruent letter-speech sound pairs in the left anterior superior temporal gyrus (STG)/planum polare at T1 was associated with higher letter knowledge at T1. **(B)** Higher activation for incongruent than congruent letter-speech sound pairs bilaterally in the left STG and insula at T1 was associated with higher reading fluency scores at T3. **(C)** Higher activation for incongruent than congruent letter-speech sound pairs in the left angular gyrus at T2 was associated with lower reading fluency scores at T3.

We found no significant correlations between incongruency effects in the two STG ROIs and letter-sound knowledge at T1, reading fluency outcome at T3 and familial risk for dyslexia.

DISCUSSION

Here, we investigated the development of audiovisual letter-speech sound processing and integration from prereading to early reading stages by acquiring longitudinal fMRI data in a group of children before the start of formal reading acquisition (T1), in the middle of first grade (T2) and in the middle of second grade (T3). We found that after the start of reading acquisition at T2, brain activation to audiovisual letter presentations increases in the STG, IFG, and vOTC, a network of regions that is involved in orthographic and phonological processing of written language (Richlan, 2019). This developmental increase was particularly pronounced for children with typical reading abilities in second grade. In addition, effects of audiovisual integration, measured as the incongruency effect between matching and non-matching audiovisual letter presentations, were found in the left vOTC and IFG and appeared to show only marginal changes over time. Interestingly, stronger incongruency effects in bilateral parts of the STG and posterior insula at T1 were associated with higher reading fluency levels at T3. Overall, these results suggest that neural responses to audiovisually presented letters rapidly change in the first 2 years of reading acquisition in line with the behavioral improvements in letter knowledge and the gains in reading skills during this developmental stage. Particularly typical readers showed the strongest developmental increase in audiovisual processing from kindergarten (T1) to first grade (T2) while poor readers showed a different developmental trajectory in the target regions, with hardly any differences, paralleling their reading expertise.

The whole-brain analysis revealed that the strongest developmental effects of letter-speech sound processing from T1 to T2/T3 were located in the left STG. Reading acquisition leads to increased activation in brain regions involved in phonological processing, including the superior temporal cortex (Monzalvo and Dehaene-Lambertz, 2013). Our results suggest that after a few months of reading instruction audiovisual processing in the left STG increases. Examining two ROIs in the STG revealed that this developmental effect was evident in children who eventually had typical reading skills at the middle of second grade (T3). However, children who would develop poor reading skills did not show significant increases in STG activations from T1 to T2/T3. In addition, lower activation was observed in the posterior STG/STS in poor beginning readers, with the strongest group difference evident at T2, when posterior STG/STS activation was higher for typical than poor readers on a trend level. Therefore, the most pronounced group difference of audiovisual processing in the left STG/STS between typical and poor readers was found in the middle of first grade, when letter-speech sound correspondences are intensively trained but are not yet fully automatized.

A previous fMRI study focusing on beginning readers reported that STS activation to speech and print positively correlated with word reading skills (Chyl et al., 2018). Our experimental paradigm allowed us to also investigate how effects of audiovisual integration are related to reading skills. Stronger incongruency effects bilaterally in the STG and parts of the posterior insula at the prereading stage were associated with future reading skills 2 years later (T3). Thus, early markers of audiovisual integration in primary and associative auditory regions may be predictive of individual reading development.

In older children, congruency effects in the auditory cortex have been found to increase as a function of literacy skills (Blau et al., 2010; McNorgan et al., 2014). The direction of the congruency effect shows extensive inconsistencies in the literature that are likely caused by differences in temporal and spatial resolution of the applied neuroimaging methods (fMRI vs. EEG/MEG; Caffarra et al., 2021b), attentional demands of the experimental paradigms [e.g., synchronous vs. asynchronous audiovisual presentation (van Atteveldt et al., 2007); implicit vs. explicit], stimulus material (letters, syllables, pseudowords or words; Kronschnabel et al., 2014), different levels of transparency in the studied alphabetic languages (Holloway et al., 2015; Xu et al., 2019), and the varying age-ranges of the samples (Wang et al., 2020).

We were also interested in whether audiovisual integration effects in our sample were related to individual familial risk for dyslexia. Familial history of dyslexia has been reported to influence phonemic representations in temporal regions and audiovisual integration in the left superior temporal cortex at early reading stages (Plewko et al., 2018; Vandermosten et al., 2020). In an fMRI study, Polish-speaking children with low familial risk showed an incongruency effect for letter speech sound pairs, while children with increased familial risk for dyslexia showed a congruency effect (Plewko et al., 2018). We were not able to replicate this finding in children of a slightly less transparent language i.e., German. However, we also show that in typical reading development an early incongruency effect emerges in superior temporal regions. Plewko et al. (2018) argue that the incongruency effect in the left STC is characteristic for beginning readers and it might reverse into a congruency effect later, when letter-speech sound pairs are automatized. Their study showed that children at a very early reading stage who later developed dyslexia showed higher activation in the STC for congruent letter speech sound pairs than future typical readers (Plewko et al., 2018). This is in line with our findings, given that a higher congruency effect in the STG at T1 was associated with lower reading skills at T3. Larger longitudinal studies are needed to clarify if the initial congruency effect observed in struggling readers diminishes over time or if it eventually reverts into an incongruency effect as seen in typical readers.

As children train the associations of letters and speech sounds, parts of the word-selective visual cortex rapidly begin to specialize in processing written language (Brem et al., 2010; Dehaene-Lambertz et al., 2018). Parts of vOTC, often referred to as the VWFA, have been shown to preferably respond to words over other categories of visual stimuli (Dehaene et al., 2010). Already after a short artificial grapheme-phoneme training, young prereaders (5–6 years old) show increased neural responses to letter-like symbols in parts of vOTC (Pleisch et al., 2019a). This emerging specialization in vOTC to visually and audiovisually presented written characters has been shown to be performance-dependent, with faster grapheme-phoneme correspondence learning being associated with increased vOTC activation (Karipidis et al., 2017; Pleisch et al., 2019a).

Besides activations in superior temporal areas involved in multisensory processing, our longitudinal analysis confirms the rapid increase in vOTC activation when processing letters after the onset of reading acquisition. Activation in the letter-specific vOTC ROI increased from kindergarten to first grade, with this developmental effect being particularly pronounced in the typical reading group. Text-sensitive parts of the vOTC (VWFA) have been consistently found to respond less to text stimuli in children (van der Mark et al., 2009; Olulade et al., 2015; Brem et al., 2020), adolescents (Kronschnabel et al., 2013), and adults (McCandliss et al., 2003) with dyslexia compared to typical readers. Reduced vOTC activation in children with dyslexia has also been reported during audiovisual processing of syllables (Romanovska et al., 2021). Importantly, visual processing of text in vOTC might also facilitate access to phonological representations through connectivity to other regions, such as the auditory cortex. Disruptions in functional and structural connectivity from vOTC to other regions of the reading network are likely to be associated with impairments in fast word recognition in dyslexia (Richlan, 2019). Here, we provide longitudinal evidence of reading-skill dependent development of vOTC activation during audiovisual processing of single letter-speech sound correspondences. In addition, the observed incongruency effect in the left vOTC suggests that visual areas specialized to process letters and words are sensitive to effects of audiovisual integration during critical periods of learning.

Audiovisual integration effects have been predominantly described in auditory and visual regions, and lesions in the above mentioned temporal and occipital regions have been found to be most disruptive of audiovisual integration processes for speech (Hickok et al., 2018). However, there are frontal and parietal regions involved in reading that may also play a crucial role in letter-speech sound processing (Pugh et al., 2000). We found a congruency effect in the left angular gyrus that was present in first grade and positively associated with later reading skills. Parts of the inferior parietal cortex are involved in cross-modal processing and in semantic processing, including componential analysis of letter-sound associations (Taylor et al., 2014). The engagement of parietal regions may support learning a novel orthography (Quinn et al., 2017) and may reflect less automatized audiovisual processing in beginning readers (Xu et al., 2018). Learning new letter-speech sound correspondences also results in changes of activation patterns in the IFG (Hashimoto and Sakai, 2004). Typical readers showed overall higher activation in the IFG which significantly increased after the start of reading acquisition and showed the largest deviation from the poor reading group at T3. Across all participants and time points, we identified a cluster in the left IFG that responded stronger to incongruent than congruent letter-speech sound pairs, suggesting a strong mismatch response in this region. Supplementary analysis in the left IFG ROI suggested that this incongruency effect increased over time. The IFG has been discussed as an integration site for multisensory information and may be specifically involved in category learning (Li et al., 2020).

Recent fMRI studies have shown a strong convergence of spoken and written language networks in perisylvian and frontal brain regions that appears to be universal for skilled readers of different languages (Rueckl et al., 2015) and already present in beginning readers (Marks et al., 2019). The present study extends this knowledge by providing additional longitudinal evidence for the crucial role of integrating audiovisual information in the early stages of reading acquisition. We found evidence for a growing engagement of auditory, visual, and multisensory integration areas in processing letter-speech sound pairs in the first months of reading acquisition. Although the contribution of familial risk for dyslexia to this development remains unclear, we demonstrate different developmental trajectories between typical and poor readers in the STG, IFG, and vOTC. Future research will clarify how well these developmental effects generalize to less transparent alphabetic languages, such as English. Importantly, we also found a predictive association between early sensitivity to audiovisual congruency in prereading stages and later reading fluency skills. This longitudinal study provides evidence that individual developmental trajectories of letter and speech sound processing are related to children's reading achievement and advances current knowledge about the development of brain systems for reading.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, upon reasonable request.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Kantonale Ethikkommission Zürich. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

IK, GP, and SB conceptualized study. IK and GP collected the data. IK, GP, SD, and GF-G analyzed the data. SB acquired funding and provided resources. IK made the figures and wrote the manuscript. All authors contributed to the editing of the manuscript and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.750491/full#supplementary-material

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Graph Analysis of EEG Functional Connectivity Networks During a Letter-Speech Sound Binding Task in Adult Dyslexics

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We performed an EEG graph analysis on data from 31 typical readers (22.27 ± 2.53 y/o) and 24 dyslexics (22.99 ± 2.29 y/o), recorded while they were engaged in an audiovisual task and during resting-state. The task simulates reading acquisition as participants learned new letter-sound mappings via feedback. EEG data was filtered for the delta (0.5–4 Hz), theta (4–8 Hz), alpha (8–13 Hz), and beta (13–30 Hz) bands. We computed the Phase Lag Index (PLI) to provide an estimate of the functional connectivity between all pairs of electrodes per band. Then, networks were constructed using a Minimum Spanning Tree (MST), a unique sub-graph connecting all nodes (electrodes) without loops, aimed at minimizing bias in between groups and conditions comparisons. Both groups showed a comparable accuracy increase during task blocks, indicating that they correctly learned the new associations. The EEG results revealed lower task-specific theta connectivity, and lower theta degree correlation over both rest and task recordings, indicating less network integration in dyslexics compared to typical readers. This pattern suggests a role of theta oscillations in dyslexia and may reflect differences in task engagement between the groups, although robust correlations between MST metrics and performance indices were lacking.

Keywords: EEG, networks, dyslexia, letter-speech sound associations, phase lag index, minimum spanning tree (MST)

INTRODUCTION

Neuroimaging evidence suggests disrupted functioning in several brain systems involved in reading script in individuals with dyslexia (Shaywitz et al., 2002; Kronschnabel et al., 2014; Žarić et al., 2014) as well as connectivity deficits in brain networks (Pugh et al., 2000; Quaglino et al., 2008; van der Mark et al., 2011; Žarić et al., 2017). Functional neuroimaging studies indicated that dyslexia is associated with disruptions in a broad set of brain systems beyond those typically associated with reading (Finn et al., 2014) and resting-state functional magnetic resonance (fMRI) studies reported that dyslexia is associated with dysfunctional brain connectivity in networks related to reading abilities (Hampson et al., 2006; Koyama et al., 2010, 2013). Another stream of evidence pointed at the potential role of large-scale oscillatory activity networks in dyslexia (e.g., Vourkas et al., 2011; Dimitriadis et al., 2013). In general, oscillations at different frequencies are thought to control communication between anatomical networks (Akam and Kullmann, 2014), enabling different functions under shared anatomical pathways (Fries, 2015). In relation to this, a recent resting-state study using magnetoencephalography (MEG) found support for spatially distinct and behaviorally relevant networks at each classical frequency band (Becker and Hervais-Adelman, 2020).

Previously, we used graph analysis of EEG data to assess the topographical configuration of long-range EEG connectivity at different frequency bands between children (Fraga González et al., 2016) and adults (Fraga González et al., 2018) with dyslexia and typical readers. Graph analysis of the EEG consists of computing a measure of connectivity between each pair of sensors or nodes (N) to define an adjacency matrix. The values in this matrix are weights that represent strength of connectivity and they are used to define the network links (m). Subsequently, the network can be represented in a graph that allows to calculate metrics describing its topological properties, i.e., how connectivity is organized in the network (e.g., Bullmore and Sporns, 2009; Stam, 2014). These descriptors can be used to characterize the efficiency and specialization of brain systems (both globally and locally) and can help finding new markers of a wide range of disorders (Stam, 2014).

In our resting-state studies on Dutch speakers (Fraga González et al., 2016, 2018), we took advantage of spanning trees (MSTs), a special type of sub-networks which minimizes biases in comparing network metrics between conditions or groups that may differ in overall strength of connectivity (Tewarie et al., 2015). The MSTs contain the highest weights possible without forming any loop or cycle and, in this regard, they can be considered a "connectivity backbone," which has always the same number of links given a fixed number of nodes ($m = N - 1$), assuming that all weight values are unique. Applying this method to resting-state EEG data, our child study revealed statistically significant group differences in the theta (4–8 Hz) band suggesting reduced network integration and less communication between network nodes in children with dyslexia compared to typical readers (Fraga González et al., 2016). A similar study used the same approach on Chinese-speaking children of similar age and found differences between dyslexic and typical readers in the same direction but in MST metrics in the beta band (Xue et al., 2020). They used shorter epoch length and a smaller montage with less electrodes compared to our previous study, which may have contributed to the differences in addition to the different alphabetic systems. Our MST analysis of resting-state EEG data in adults yielded significant network differences between groups in the alpha band (8–13 Hz) and, in contrast to the results observed for children, suggested a more interconnected network configuration in individuals with dyslexia relative to typical readers (Fraga González et al., 2018). These studies yielded no robust associations between graph metrics and cognitive performance. However, a recent study yielded positive results examining the relation between EEG networks and reading skills on L1 Chinese and L2 English-speaking children from first to fifth grade (Lui et al., 2021). The study found that network modularity (derived from the connectivity measure of phase coherence) correlated with Chinese word reading, phonological and morphological awareness, and reading comprehension, but not with any literacy skills in L2 English. That study supported the need to continue exploring the potential of EEG network metrics as predictors of literacy development.

The focus of the current study is a comparison between dyslexic and typically reading adults in EEG data associated with task performance. To date, there are only a couple of studies examining brain networks in dyslexia using a graph theoretic approach to analyze brain activity during task performance. Vourkas and co-workers reported reduced global and local network efficiency in poor readers in the alpha band during a pseudoword reading task and letter-sound naming task (Vourkas et al., 2011). In those tasks participants were asked to read the visually presented pseudowords or to pronounce the sound corresponding to the presented letter, respectively. It should be noted, however, that significant correlations between word reading and graph measures associated with the EEG alpha band were reported only in the more simple letter-sound naming task. In another study, Smith et al. (2018) performed a longitudinal fMRI study examining networks during a rhyming judgment task in young readers over a 2.5 year-span. They reported an association, albeit weak, between a shift in functional segregation (increase in the proportion of functional clusters) and changes in reading skill. A recent study examined fMRI during an auditory rhyming task and a visual spelling task in Chinese children (Mao et al., 2021). The study found differences between poor readers and age-and reading-matched controls in network metrics related to hub properties of frontal and temporal regions relevant for reading, but no relation with behavioral performance was reported. Collectively, the results available to date present little support for a relation between network measures and cognitive skills and/or performance in specific tasks. The current study was designed to investigate just such a relation. More specifically, we examined task-based network organization in dyslexics and typical readers by using an artificial orthography learning task.

The artificial orthography learning task required participants to learn novel letter-speech sound associations by using feedback provided on the screen. The idea behind this task is learning the artificial orthography mimics the initial stages of reading instruction in which correspondences between arbitrary symbols (letters) and speech sounds are established. This specific type of audiovisual integration is considered a key step in fluent reading acquisition by supporting the specialization of visual areas to print, which would ultimately make possible the development of (fluent) sight word reading (Ehri, 2005). Although dyslexic readers seem to be capable of accurately learning letter-speech sound associations, they struggle to automate and sufficiently integrate these associations at the neural level (e.g., Blomert, 2011; Žarić et al., 2014). Our task is inspired by a series of previous studies in which we had children with dyslexia performing a videogame-like task presenting an artificial orthography

(Aravena et al., 2013, 2016, 2017). This approach allowed us to obtain an association between task performance and reading skills (Aravena et al., 2017) and responsiveness to reading intervention (Aravena et al., 2016). These findings underline the importance of incidental category (letter-speech sound) learning in developmental dyslexia. Thus, in a another study we developed a feedback learning task in which new symbols are associated with speech sounds (Fraga González et al., 2019). The study found differences on heart-rate changes associated with feedback anticipation, a physiological response previously studied in the context of probabilistic learning (Crone et al., 2004; Kastner et al., 2017). The task design was motivated by the theoretical framework of Holroyd and Coles (2002) for studying error and feedback processing in adapting behavior (Holroyd and Coles, 2002). Their focus was on midbrain dopamine neurons and the of corticostriatal systems in performance adaptation based on prediction error. A set of previous EEG and fMRI studies suggested that dyslexics may process feedback differently compared to typical readers (Horowitz-Kraus and Breznitz, 2011, 2013; Kraus and Horowitz-Kraus, 2014; Horowitz-Kraus and Holland, 2015; Horowitz-Kraus, 2016). The studies, together with some evidence for atypical activations of frontostrital circuits in dyslexia (Krishnan et al., 2016; Hancock et al., 2017b) and reports of potential probabilistic learning impairments (Howard et al., 2006; Gabay et al., 2015; Singh et al., 2018) motivated the examination of this task. The current focus on EEG data associated with the learning of an artificial orthography would provide a window on the alleged dysfunctional neural networks in dyslexia.

To sum up, the main goal of the current study is to compare EEG power, functional connectivity strength and connectivity organization in typical and dyslexic readers during a letter-speech sound binding task. Additionally, we include a resting-state baseline as an additional condition that will allow us to directly compare changes between conditions in the EEG measures, and to test whether group differences are specific to each condition. We then investigate associations between the different EEG measures during task and baseline, and individual differences in task performance and reading skills.

MATERIALS AND METHODS

Participants

Twenty-four dyslexic adults (22.99 ± 2.29 years old) were recruited via a nation-wide center in the Netherlands offering services for individuals with dyslexia. The sample characteristics are summarized in **Table 1**.[1] A group of 31 typical readers (22.27 ± 2.53 years old) were recruited via ads at the University and through social networks. Participants with diagnosis of ADHD or other neurological or cognitive impairments were excluded from the sample. Participants were required to have normal or corrected-to-normal vision and Dutch as their primary language. Inclusion criteria for participants with dyslexia were first, persistent reading problems manifested and documented since primary school and with poor response to special support at school for at least 6 months. Second, a diagnosis of dyslexia after assessment at the clinic based on the criteria of DSM-5 (American Psychiatric Association, 2013) and third, a score in a standard word reading fluency test of at least 1 SD below the average of a national normative sample of 16-year-olds. The majority of the participants with dyslexia did not report receiving any specialized treatment for reading disability (a few participants received a 3 months training course for study skills). Ethics approval was obtained from the Ethics Committee of the Faculty of Social and Behavioral Sciences of the University. All participants gave signed consent to their participation in the study.

TABLE 1 | Sample characteristics and descriptive statistics showing reading scores.

	Typical readers ***M*** **(*SD*)**	**Dyslexics** ***M*** **(*SD*)**	***F***	***p*-value**	η^2
N	31	24			
Sex ratio (m:f)	9:22	12:12			
Handedness (L:R)	1:30	3:21			
Age	22.27 (2.53)	22.99 (2.29)	1.15	0.289	0.02
RAVEN—IQ test[a]	52.52 (4.72)	52.96 (4.71)	0.12	0.732	0.00
1-Min Test –*fluency*[b]	107.32 (8.87)	82.46 (14.14)	63.69	0.000	0.55
Rapid automatized naming[c]					
Letters	16.88 (3.67)	20.88 (4.63)	12.84	0.001	0.19
Numbers	18.45 (4.16)	21.12 (3.95)	5.83	0.019	0.10
Colors	25.42 (4.64)	30.68 (4.58)	17.53	0.000	0.25
Images	28.11 (5.55)	34.81 (6.12)	17.98	0.000	0.25
Total	22.21 (3.27)	26.87 (4.02)	22.45	0.000	0.30

All raw scores.
[a] *20 min. time-limited version of RAVEN.*
[b] *Raw score = number of correctly read words within 1 min.*
[c] *Raw score = mean reaction time in sec.*

Behavioral Measurements

The following tests were taken at the beginning of the session and before attaching the electrodes. Test scores are presented in **Table 1**. Word reading skills were assessed using a Dutch version of the 1-Min Test (Een-Minuut-Test, EMT; Brus and Voeten, 2010), a time-limited test consisting of a list of 116 unrelated words of increasing difficulty. The number of correctly read words within 1-min serves as reading fluency score (r = 0.82, reliability calculated in a normative sample of 16 years old). In addition, participants completed the Rapid Automatized Naming (RAN; van den Bos and Lutje Spelberg, 2010) task that consists of four subtasks: letters, digits, colors, and objects. A sheet containing five items repeated 10 times (arranged in a pseudo-random order) is presented per subtask. Participants are instructed to name the items as quickly as possible, and the time taken to name all items of a sheet provides the subtask's score (r = 0.79–0.86, split-half reliability). Finally, the RAVEN Advanced Progressive Matrices was used to obtain an estimate of fluid IQ (RAVEN APM; Raven and Court, 1998). A 20-min timed version of this test was used as it was

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[1] The initial sample was 64 participants. 6 typical readers and 3 dyslexics were excluded due to poor task performance (chance levels suggesting they did not engage in the task) or problems during EEG data recording.

previously shown to be a good predictor of the untimed APM (Hamel and Schmittmann, 2006).

EEG Measurements

Recording and Equipment

The EEG recording took place in a dimly lit and sound-proof room. Participants were video-monitored by the lab assistants from an adjacent room to ensure they complied to the instructions and that they did not show behavioral indications of drowsiness or sleep onset during the recording. Participants were seated at approximately 80 cm distance from the computer screen. Their chair was equipped with response buttons at both arms. The EEG session started with preparation and placement of electrodes (lasting around 30 min) and continued with the eyes-open baseline recording and two experimental tasks, which took around 2 h. The order of the experimental tasks was counterbalanced across participants. Following the second experimental task, an additional eyes-open baseline recording was performed to explore reliability and stability of EEG measures within resting state recordings, which falls out of the scope of the current experiment. The current analysis is performed on the data from the initial baseline recording and the main experimental task, i.e., the letter-speech sound binding task (see section " Experimental Task Performance"). The additional experimental task that was part of the recording session, i.e., an audiovisual-binding task, was not used in the present analysis as it is intended for event-related analyses.

The EEG was recorded DC (low-pass: 5th order sync digital filter) with a 2048 Hz sample rate. We used a 64-channel Biosemi ActiveTwo system (Biosemi, Amsterdam, Netherlands). The Biosemi system uses two additional electrodes [Common Mode Sense (CMS) and Driven Right Leg (DRL)] located to the left and right of POz, respectively, which replace the conventional ground electrode. All electrode offsets relative to CMS/DRL were brought within 20 μV in accordance with the manufacturer guidelines. The 64 electrodes were distributed across the scalp according to the extended 10–20 International system (see electrode locations in **Supplementary Figure A1**) and applied using an elastic electrode cap (Electro-cap International Inc.). Ten external Flat-Type Active electrodes were used. Four were used to record vertical and horizontal electro-oculogram (EOG). They were placed below both eyes aligned with the pupils approximately 3 cm outside both outer canthi of the eyes. Two electrodes were placed at mastoids and two were attached to the earlobes to be used as offline reference signals. Finally, two electrodes were used to record the electrocardiogram (ECG) and were placed at the sternum and between the lower two ribs. The ECG data were not used in the current study. Baseline and experimental task.

During the baseline recording subjects were required to look at the center of the screen during 4 min after making a button-press indicating the start of the period. A gray background was used to minimize glare on the screen and a gray fixation circle with shadowing was placed at the center of the screen to assist participants to fixate their eyes while preventing eye fatigue.

The letter-speech sound binding task is a probabilistic learning task in which subjects learned new visual-sound associations via feedback. We used the current format in a previous study examining differences in overt feedback processing between dyslexics and typical readers (Fraga González et al., 2019). In the trials, participants had to learn whether the letter-like unfamiliar symbol was matched with the simultaneously presented speech sound by pressing Yes or No and receiving feedback after their response. However, feedback was only response-related in half of the trials (consistent trials) while in the other half the feedback was random (inconsistent trials; see below in this section). The visual stimuli consisted of 16 symbols from the Georgian alphabet and the auditory stimuli were 16 Dutch phonemes. The complete list of visual symbols and phonemes used in the task is presented in **Supplementary Appendix A**. The phonemes were spoken by A native Dutch male speaker. There were three groups of phonemes with different durations; one group of four phonemes had a mean (SD) duration of 172.66 (22.28) ms and another group of four phonemes had a mean (SD) duration of 380.50 (19.47) ms. The third group consisted of eight phonemes with a mean duration of 451.97 (27.69) ms. The visual stimuli were presented using an ASUS VG236H (resolution 1,920 × 1,080) 60 Hz monitor with a Dell Optiplex 760 dual-core 3.0 GHz computer and an ATI HD 6570, 2Gb graphic card. The symbols were presented using "Arial Unicode MS" font (lower case, bold font and font size 60). The software used to present the stimuli was Presentation (Version 18.2[2]). The sound stimuli were presented through padded earphones.

A schematic of the trial structure is presented in **Figure 1**. On each trial, a visual symbol and a phoneme were presented simultaneously. The trials were terminated by the response. The symbols were presented in white on a black background at the center of the computer screen. Participants had to decide whether the symbol and phoneme presented belong with each other by pressing the buttons located at the right and left arms of the chair. The mapping of YES and NO responses to the right and left hand was consistent across blocks for each participant but was counterbalanced across participants. Green and red stickers were placed on the buttons to indicate whether they were YES or NO buttons, respectively. The button-press was followed by blank screen with 1,000 ms duration. The blank screen was followed by feedback "GOED" (correct; presented in white upper case "Times New Roman" font with size 48), "FOUT" (incorrect; presented in red font), or "TE LANGZAAM" (too slow; presented in upper case "Times New Roman" font with size 48). After the feedback screen, a fixation cross was presented during the inter-trial intervals (ITI) with equiprobable durations of 500, 750, or 1,000 ms.

There were 4 blocks of 200 trials. For each block, two visual-sound pairs were consistently matched, and feedback depended upon the response of the participant. The two other visual-sound mappings were inconsistent and followed by random feedback (50% positive and 50% negative feedback). This feedback probability manipulation was included to analyze differential feedback-responses for informative (consistent trials) vs. uninformative (inconsistent trials) responses in a previous study (Fraga González et al., 2019). Note that the current analysis

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[2] www.neurobs.com

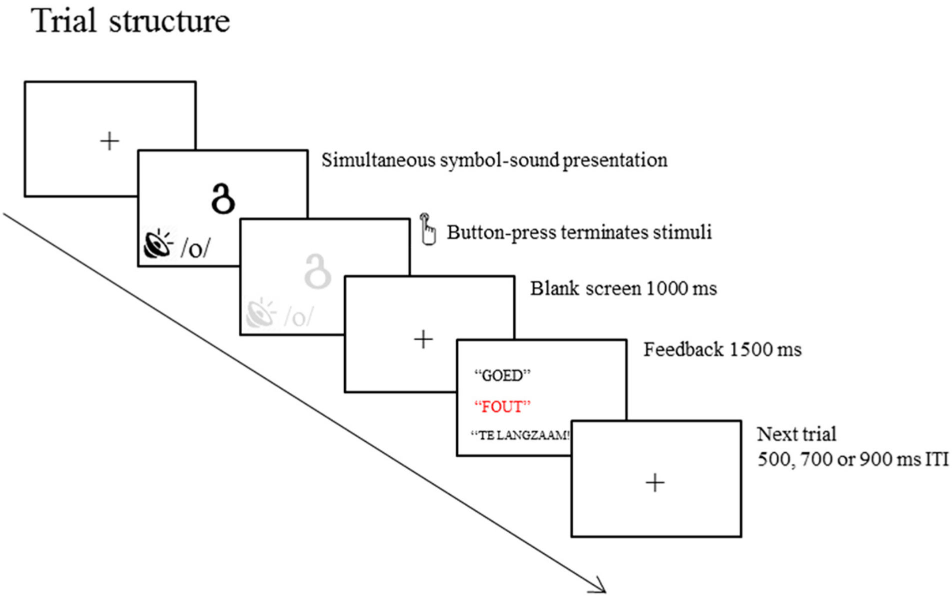

FIGURE 1 | Schematic of a trial in the letter-speech sound binding task. A visual symbol and a phoneme are simultaneously presented and response terminated (only limited by a maximum duration equal to the average reaction time during the practice block + 500 ms). Feedback is presented 1,000 ms after responses to indicate whether the response is correct, incorrect or missed.

of task performance only uses consistent trials and the EEG analysis is based on a segment during performance that includes both type of trials. Each trial block contained 100 consistent and 100 inconsistent mapping trials presented in random order (50 replications of each individual trial). The duration of a trial block was approximately 14 min. The task began with a practice block of 30 consistent mapping trials. The average reaction time (RT) on correct responses during practice + 500 ms was used to determine the response window. The feedback "too slow" was provided when responses were executed after this window. Participants were told that they should infer the visual-sound associations from the feedback provided to them and that each trial block contained a new set of associations. In addition, they were told that some associations would be more difficult to learn than others.

The whole experimental session took around 3 h and 15 min including the initial behavioral measurements and the montage of electrodes. There were short rests between blocks and between tasks and resting-baselines depending on the needs of the participant. The participants were debriefed at the end of the experiment and received a monetary reward for their services.

EEG Preprocessing

The graph analysis followed similar pipeline steps as in our previous study (Fraga González et al., 2016). The sequence of steps of this pipeline are shown in **Figure 2**. The continuous EEG data were imported in EEGLAB v.12.5.4b, a Matlab-based open toolbox (Delorme and Makeig, 2004). The averaged earlobes were used as off-line reference when importing the data. In the baseline analysis a segment with a duration of 4 min was selected, time-locked to the button press indicating the start of the eyes-open resting-state recording. In the task analysis we took the initial 4 min from the beginning of the task, after the practice period. The data were high-pass filtered at 0.5 Hz using a zero-phase FIR filter and channels containing excessive artifacts were removed from the data to be interpolated later on in the pipeline (see below in this paragraph). The data were then segmented into 60 epochs with a duration of 4 s each. The epochs were visually inspected and those containing artifacts such as head or electrode cable movement and jaw clinching were removed. Subsequently, we performed an Independent Component Analysis (ICA) decomposition (Makeig et al., 1996) in order to remove blinks, eye-movements and other stereotyped artifacts from the data. We used the "runica" algorithm available in EEGlab for ICA decomposition (Lee et al., 1999) and the automatic algorithm ADJUST to identify independent components associated with artifacts (Mognon et al., 2011). The algorithm uses artifact-specific spatial and temporal features to detect artifactual components and has been previously validated (Mognon et al., 2011). After removing the independent components selected by the algorithm, data for typical readers and dyslexics were reconstructed based on a mean (SD) of 52.67 (7.82) and 49.37 (14.02) components in the task and 52.23 (4.58) and 51.29 (5.90) components in the baseline, respectively. Afterward, the data from previously removed channels were interpolated using a spherical spline interpolation method (Perrin et al., 1989). Finally, for each condition (baseline and task) a total of 30 epochs, each with a duration of 4 s, were selected per participant,[3]

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[3] As the present analysis requires equal number of epochs across participants, we chose to include 30 epochs to avoid excluding additional participants having an insufficient number of artifact-free epochs.

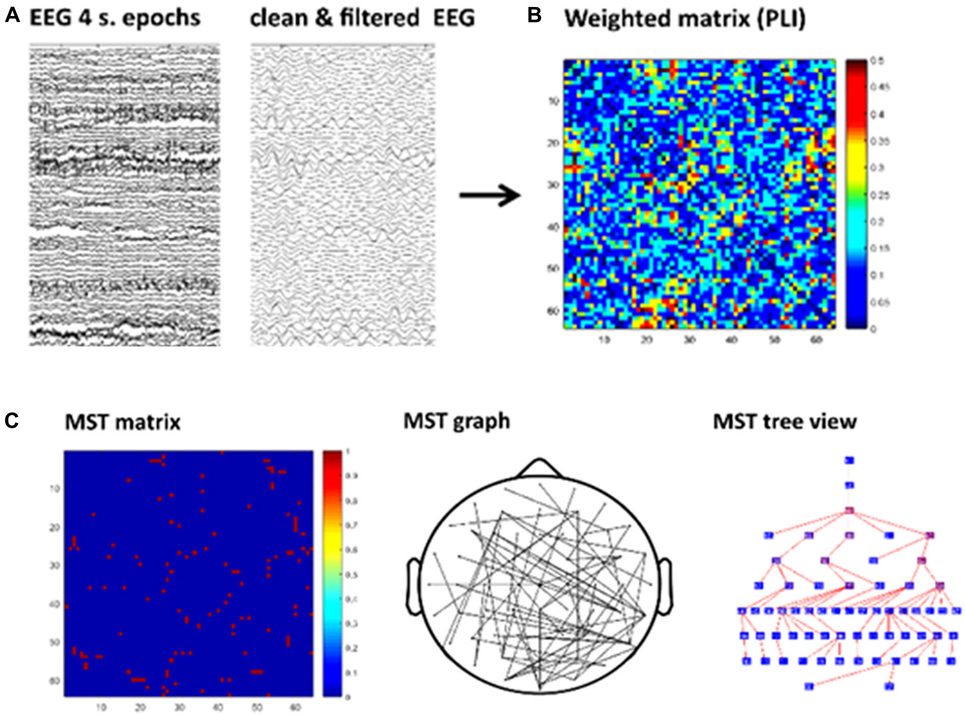

FIGURE 2 | Schematic of the graph analysis. First, visual inspection and Independent Component Analysis (ICA) were applied to remove artifacts. Then data were filtered for each frequency band **(A)**. Second, the functional connectivity matrix based on phase lag index (PLI) is calculated for each frequency band and epoch **(B)**. Kruskal's algorithm is applied to obtain a minimum spanning tree (MST) matrix (**C**-left) which can be displayed on a scalp projection (**C**-middle). The tree view shows the hierarchical structure of the graph starting from an arbitrary root node. The nodes color map from blue to red represents lower to higher betweenness centrality (**BC**; **C**-right). For illustrative purpose this figure shows the MST obtained from a single epoch in one participant.

down-sampled to 1024 Hz and exported to ASCII files for the subsequent EEG analyses.

The ASCII files were imported in Brainwave v0.9.152.4.1 (developed by C.S.; freely available at http://home.kpn.nl/stam7883/brainwave.html) where data were re-referenced to the average of all scalp channels and filtered for each frequency band (see section "Spectral Power") before performing subsequent analyses.

Spectral Power

We calculated spectral power in each epoch using Fast Fourier Transformation (FFT) with a frequency resolution of 1 / 4 s = 0.25 Hz. The power spectra were averaged across segments and all the groups of electrodes described in section "EEG Preprocessing." The "area under the curve" values were calculated for the following frequency bands: delta (0.5–4 Hz), theta (4–8 Hz), alpha (8–13 Hz),[4] and beta (13–30 Hz). Relative power was computed as the ratio of the power of the corresponding band and the total power.

Functional Connectivity

We used the Phase Lag Index (PLI) to calculate functional connectivity between all pairs of electrodes for each frequency band and epoch. In contrasts to other connectivity measures like phase coherence, the PLI reduces the effect of volume conduction by ignoring zero and π phase differences (Stam et al., 2007). It captures the asymmetry of the distribution of instantaneous phase differences, which are determined using the Hilbert transformation (Stam et al., 2007). A symmetric distribution centered around zero may indicate spurious connectivity and a flat distribution indicates a lack of connectivity. A deviancy from a symmetric distribution indicates dependency between sources. The PLI is obtained from time series of phase differences $\Delta\phi\,(t_k)$, $k = 1\ldots N$ by means of:

$$\mathrm{PLI} = |< \mathrm{sign}[\sin(\Delta\phi(t_k))] >|$$

Here "sign" is the signum function. The PLI ranges between 0 and 1. A value of 0 means no coupling or coupling with a phase difference centered around 0 (mod π). A value of 1 indicates perfect phase locking at a value of $\Delta\phi$ different from 0 (mod π). Thus, PLI values closer to 1 indicate stronger nonzero phase locking. In the current analysis we use the term mean total PLI when referring to the average of the PLI between all pairs of electrodes.

Minimum Spanning Tree Analysis

For our network analysis, we calculated a Minimum Spanning Tree (MST) for each connectivity matrix (see **Figure 2**). We used the MST as it allows for direct group or condition comparisons

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[4] A broad alpha range was chosen instead of the lower alpha (8–10 Hz) and upper alpha (10–13 Hz) to account for individual variability observed in alpha peak frequencies.

minimizing the bias caused by differences in connectivity strength (e.g., Stam et al., 2014). The MST is a unique sub-graph based on a weighted matrix that connects all nodes of the network without circles or loops. Importantly, the MST always contains $m = N-1$ links, where N is the number of nodes. The MST was constructed by applying Kruskal's algorithm (Kruskal, 1956) which iteratively selects the links with the lowest distance (i.e., lowest weights) and adds the link to the tree only if no loops are created. The result is a graph without cycles or loops in which all nodes are connected. In our MST computation, we define a link weight as 1-PLI. Thus, the MST represents the sub-network with maximum connectivity.

There are a various MST metrics that are used to describe the topological properties of the tree (Stam et al., 2014). We examined the following metrics: degree, leaf fraction, diameter, eccentricity, betweenness centrality (*BC*), tree hierarchy (*Th*), degree correlation (*R*), kappa and mean. The degree of a node refers to its number of links, and the leaf fraction represents the number of nodes (*N*) on the tree with degree = 1. The leaf number has a lower bound of 2 and an upper bound of $N-1$. It presents an upper bound to the diameter of the MST, which is the largest distance between any two nodes of the tree. The upper limit of the diameter is $d = m - L + 2$, where m refers to the number of links on the tree. This formula implies that the largest possible diameter will decrease with the increasing leaf number. Eccentricity of a node is defined as the longest distance between that node and any other node and is low if this node is central in the tree. The *BC* of a given node u is the number of shortest paths between any pair of nodes i and j that are running through u, divided by the total number of paths between i and j. The *BC* value ranges between 0 and 1 and relates to the importance of a node within the network. The nodes with the highest *BC* have the highest load, i.e., the highest number of shortest paths between any two nodes run through these high *BC* nodes. For example, a central node with a *BC* of 1 could be easily overloaded. Degree, eccentricity and *BC* are different measures for relative nodal importance and may indicate the critical nodes in a tree. The measure of tree hierarchy T_h reflects a balance between efficient communication and prevention of overload of hub nodes, reflected, respectively, by small diameter and a maximal *BC*. This balance is proposed to be important for optimal network performance (Boersma et al., 2013) and is defined as:

$$T_H = \frac{L}{2mBC_{max}}$$

Where L is leaf fraction and m the number of links. Further, the degree correlation R is an index of whether the degree of a node is correlated with the degree of its neighboring edges to which it is connected. The R is quantified by computing the Pearson correlation coefficient of the degrees of pairs of connected nodes (Newman, 2003). If $R > 0$ the graph is considered assortative, and if $R < 0$ disassortative. Kappa is the width of the degree distribution and relates to spread of information across the tree (Stam et al., 2014). High kappa indicates the presence of high-degree nodes, which facilitate synchronization of the tree but also increase the network's vulnerability if a hub is damaged (Otte et al., 2015). Finally, we computed the MST mean, that is the mean of the PLI weights of the tree.

Statistical Analysis

Experimental task performance was evaluated by calculating accuracy and speed on consistent-mapping trials across four bins of 25 trials for each trial block. These data were also averaged across 4 experimental blocks. Mixed-model ANOVAs were used to compare groups in accuracy and reaction times across blocks with the within-subjects factor *bin* (1–4). As behavioral, performance summary measures to correlate with EEG measures we computed the total accuracy average as well as the average RT of correct responses. A more detailed analysis of performance in this task, together with an additional control audiovisual binding task can be seen in Fraga González et al. (2019).

Our main EEG analysis consisted of a mixed ANOVA comparing the groups in task data. Additionally, we performed the same comparisons in the resting-state baseline data. A third analysis explored interactions between group and difference in task vs. resting state with mixed ANOVAs with the within-subjects factor *condition* (2 levels; baseline and task) and the between-subjects factor *dyslexia*. Moreover, regression analysis was performed between PLI and relative power. Greenhouse-Geisser correction of degrees of freedom was used to calculate *p*-values when the assumption of sphericity was violated (Greenhouse and Geisser, 1959). To account for the multiple comparisons performed in network metrics we used False Discovery Rate (FDR; Benjamini and Hochberg, 1995). Given the correlation between network metrics we accepted a 10% of false discoveries ($q = 0.10$), we also report a more stringent FDR correction at $q = 0.05$ (see footnotes in the corresponding tables).

Finally, we used stepwise multiple linear regression in the two groups separately to explore whether EEG power, connectivity and graph metrics could predict task performance, cognitive skills and age. The inclusion criteria for the EEG variables to be included in the regression models were $p < 0.05$ and the exclusion criteria was $p > 0.10$.

RESULTS

Cognitive Measures

The scores for reading accuracy and speed measures are shown in **Table 1**. The dyslexic group performed significantly worse than typical readers on both reading tests and the deficit was more pronounced on the word identification task. The two groups were comparable in non-verbal IQ and age.

Experimental Task Performance

The descriptive statistics of the performance data (accuracy and RTs averaged across blocks) are presented in **Table 2** and **Supplementary Figure A2** and **Supplementary Table A2** shows the extended descriptives per block for the consistent trials). The ANOVA performed on accuracy revealed a significant main effect of Bin, $F(3, 159) = 106.89$, $p < 0.001$, $\eta^2 = 0.67$, indicating that accuracy increased with time-on-task, illustrating

TABLE 2 | Task performance in letter-speech sound task for the consistent trials.

		Typical readers (*N* = 31)		Dyslexics (*N* = 24)	
		Accuracy *M* (*SD*)	**Reaction time** *M* (*SD*)	**Accuracy** *M* (*SD*)	**Reaction time** *M* (*SD*)
Letter-speech sound binding task					
Mean over 4 blocks	Bin1	76.81 (9.90)	886.63 (124.73)	74.71 (9.53)	928.32 (131.80)
	Bin2	86.71 (8.65)	861.42 (138.27)	85.88 (10.27)	934.45 (134.80)
	Bin3	87.68 (9.80)	868.31 (144.24)	87.58 (8.27)	932.66 (118.45)
	Bin4	87.39 (9.92)	861.05 (131.42)	89.08 (9.22)	945.84 (112.73)

Bin 1 = trials 1–25; Bin2 = trials 26–50; Bin3 = trials 51–75; Bin4 = trials 76–100.
Reaction times to correct responses in milliseconds. Accuracy = percentage of correct responses.

probability learning. There were no significant group differences or interactions with the factor dyslexia, *p*s > 0.124. The follow-up pairwise comparisons between bins across groups showed significantly increased accuracy from bin 1 to bin 2 (mean difference 10.53, $p < 0.001$), but not between bin 2 and 3 or bin 3 and 4 (*p*s > 367). The mean accuracy per bin and group are presented in **Table 2** and the **Supplementary Figure A2**. The ANOVA performed on RTs yielded a trend for slower responses in dyslexics relative to typical readers across all four bins, $F(1, 53) = 3.85$, $p = 0.055$, $\eta^2 = 0.07$, all other *p*s > 0.121. The RTs are shown in **Table 2** (see also **Supplementary Figure A2**).

Group Differences in EEG

We performed a mixed ANOVA with the factor condition (task, baseline) to examine group differences during task and resting state, and the interaction between these factors.

Relative Power

The FFT power spectra per condition and group are presented in **Figure 3**. As expected, there were significant differences between the task and baseline recordings in theta [$F(1, 53) = 41.83$, $p < 0.001$, $\eta^2 = 0.44$], alpha [$F(1, 53) = 109.88$, $p < 0.001$, $\eta^2 = 0.68$] and beta relative power, $F(1, 53) = 32.10$, $p < 0.001$, $\eta^2 = 0.38$. Relative power was significantly larger in the baseline compared to the task (see **Figure 4**). There was no evidence for significant interactions or main effect of group in these analyses, *p*s < 0.258.

Phase Lag Index Connectivity

The main analysis on PLI is presented on **Table 3** (see **Supplementary Table A3** for all tests that were performed). There was a significant main effect of condition in the alpha band indicating larger PLI in the baseline compared to task [$F(1, 53) = 29.02$, $p < 0.001$, $\eta^2 = 0.35$], but no interactions or main effect of group in that band, *p*s > 0.119. A significant effect in the same direction was detected in the beta band [$F(1, 53) = 24.64$, $p < 0.001$, $\eta^2 = 0.32$], together with a trend for lower values over both conditions in dyslexics compared to typical readers, $F(1, 53) = 3.1$, $p = 0.084$, $\eta^2 = 0.06$. In the theta band there was no main effect of group or condition (*p*s > 0.151) but, there was a significant interaction between condition and group [$F(1, 53) = 4.45$, $p = 0.040$, $\eta^2 = 0.08$], indicating lower PLI in dyslexics vs. typical readers during the task but not in the baseline. The task vs. baseline in dyslexics but not in typical readers (see **Figure 5** and **Table 3**).

The condition and group interactions were followed by group comparisons in task and baseline data separately (see **Table 4** and **Supplementary Table A4**). In the task, PLI theta was significantly lower in dyslexics compared to typical readers, $F(1, 53) = 7.63$, $p = 0.008$, $\eta^2 = 0.13$ (see left panel in **Figure 5**). The mean (SD) total PLI theta was 0.167 (0.005) and 0.170 (0.005) for dyslexics and typical readers, respectively. The mean total PLI beta was lower in dyslexics compared to typical readers, $F(1, 53) = 5.88$, $p = 0.019$, $\eta^2 = 0.10$. The mean (SD) total PLI beta was 0.090 (0.005) and 0.093 (0.006) for dyslexics and typical readers, respectively. The analysis of the baseline data showed no evidence for significant group differences in PLI, although there was trend for stronger alpha connectivity in dyslexics vs. typical readers at $p = 0.091$, all other *p*s > 0.388.

Minimum Spanning Tree Network Metrics

The results of the main ANOVA on MST metrics revealed significant group differences across conditions (see **Table 3** and **Supplementary Table A3**). Dyslexics showed lower theta degree correlation, i.e., lower network integration, over both task and baseline recordings, $F(1, 54) = 6.36$, $p < 0.015$. In addition, there were significant main effects of condition for all MST metrics except for betweenness centrality in theta and MST mean in beta. The largest effect sizes for the change across conditions were found on degree (alpha) leaf fraction (theta, alpha and beta), kappa (alpha), tree hierarchy (theta and alpha) and degree correlation (theta and alpha) with partial eta-squared > 40. The direction of these differences suggests a less integrated network configuration in task compared to the pre-task baseline. There were significant interactions between condition and dyslexia for theta tree hierarchy, alpha kappa and beta MST mean and theta MST mean (see **Table 3**). The follow-up analyses on these interactions are presented in **Table 4** (and **Supplementary Table A4**). These analyses showed a trend for lower the tree hierarchy in dyslexics compared to typical readers during task [$F(1, 53) = 3.92$, $p = 0.053$] but not in the baseline $p = 0.544$. For alpha kappa, dyslexics showed a trend for larger kappa than typical readers in

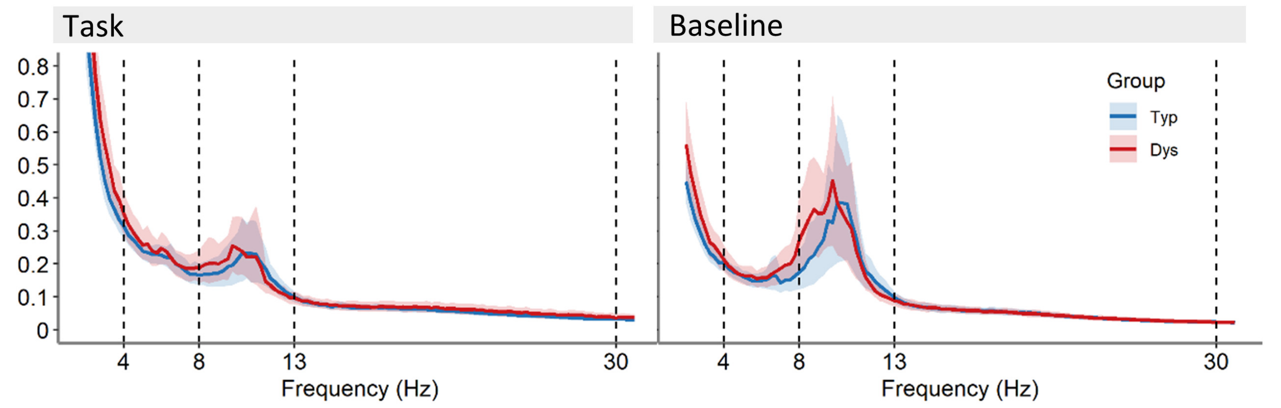

FIGURE 3 | Power spectra averaged across 64 EEG scalp channels with 95% CI for the recording during task and the baseline recording for dyslexics (red) and typical readers (blue). Vertical dotted lines indicate the boundaries for the frequency bands at 4, 8, 13, and 30 Hz.

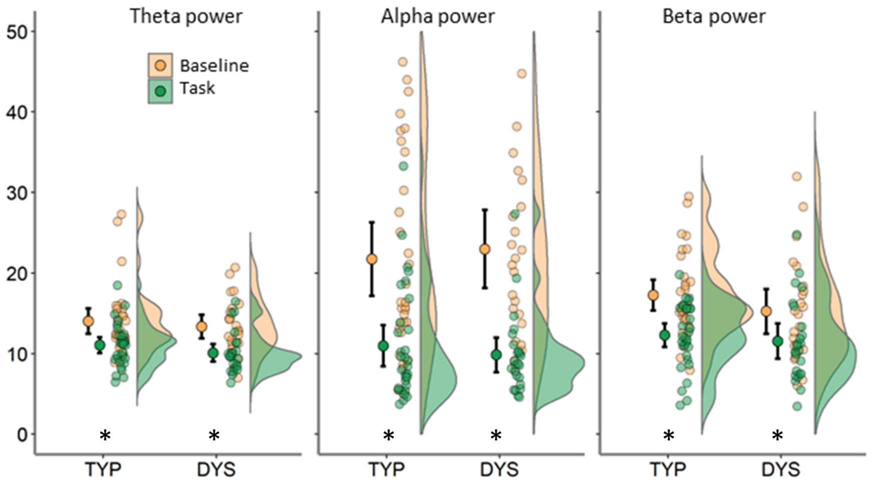

FIGURE 4 | Relative power averaged across 64 scalp electrodes for each condition (indicated by color) and frequency band. Each plot shows data for typical readers at the left side and for dyslexics at the right side. Error bars represent 95% CI. Asterisks indicate significant differences between conditions at $p < 0.01$.

baseline, $p = 0.060$, that was absent in the task 0.948 (see **Table 4**).

Relation Between EEG Measures and Cognitive Performance

Stepwise regressions examined whether EEG power, connectivity and graph metrics could predict task performance, cognitive skills and age in the two groups ($p < 0.05$ for inclusion of EEG variable in the model, $p > 0.10$ for exclusion). The results are presented in **Table 5**.

In typical readers there were significant regression models including different combinations of EEG measures for task RT and accuracy (maximum adjusted $R^2 = 0.596$ in model 4 for mean accuracy) and the RAN subtasks of numbers, colors and images (maximum adjusted $R^2 = 0.577$ in model 6 for RAN images). In the dyslexic group, age was predicted by alpha degree during task (adjusted $R^2 = 0.432$ in model 1), IQ by baseline alpha tree hierarchy (adjusted $R^2 = 0.251$ in model 1) and RAN total, numbers and colors were predicted by several EEG variables combined (maximum adjusted $R^2 = 0.661$ in model 4 for RAN numbers). To sum up, we did not a find a consistent pattern of associations between a specific set of EEG measures and individual performance and cognitive characteristics. Multiple combinations of EEG power, connectivity and graph metrics from all three frequency bands contributed to predict several individual characteristics, which differed between the groups. A similar result was found when using the data of both groups in the analysis, this is presented in **Supplementary Table A5**.

Association Between Phase Lag Index and Spectral Power

Since there were significant differences in power, connectivity and MST measures between baseline and task, we also examined the relation between PLI and relative power for each band and condition. The regression analysis for the theta band revealed a

TABLE 3 | Group (dyslexics, typical readers) and condition (baseline, task) comparisons for PLI and MST metrics.

		Within-subjects						Between-subjects	
		Condition				Condition × Dyslexia		Group	
		ΔTask	***F***	***p***	**η^2**	***F***	***p***	***F***	***p***
Theta	PLI		2.12	0.151	0.04	**4.45**	**0.040**	1.04	0.313
	Degree	↓	**18.06**	**0.000****	**0.26**	*3.45*	*0.069*	1.60	0.211
	Leaf	↓	**59.98**	**0.000****	**0.53**	*3.60*	*0.064*	1.10	0.163
	T_H	↓	**49.70**	**0.000*****	**0.48**	**2.09**	**0.038**	2.47	0.122
	R	↓	**42.86**	**0.000****	**0.44**	*3.20*	*0.080*	**6.36**	**0.015**
	MST mean	↑	**22.29**	**0.000****	**0.30**	**5.70**	**0.021**	0.90	0.766
Alpha	PLI	↑	**29.02**	**0.000****	**0.35**	2.25	0.140	2.50	0.119
	Degree	↓	**74.02**	**0.000****	**0.58**	**4.09**	**0.048**	1.29	0.261
	Kappa	↓	**98.80**	**0.000****	**0.65**	**5.68**	**0.021**	1.47	0.230
	MST mean[a]	↓	**15.21**	**0.000****	**0.22**	2.63	0.111	*3.30*	*0.075*
Beta	PLI	↓	**24.64**	**0.000****	**0.32**	2.66	0.109	*3.10*	*0.084*
	MST mean	.	*3.42*	*0.070*	*0.06*	**5.27**	**0.026**	1.04	0.312

*PLI, phase lag index; Ecc, Eccentricity; BC, betweenness centrality; T_H, tree hierarchy; R, degree correlation; ↑ indicates increase in task vs. baselines; ↓ indicates decrease in task vs. baselines. [a]Direction of effect differs between frequency bands. **Significant effects after FDR correction at q = 0.05; bold text represents significant effects at uncorrected $p < 0.05$; italic text represents trends.*

significant relation between PLI and relative power for baseline theta ($R = 0.55$, $R^2 = 0.31$, $p < 0.001$) and task theta ($R = 0.39$, $R^2 = 0.15$, $p = 0.003$). The same pattern was observed for the alpha band; baseline ($R = 0.73$, $R^2 = 0.54$, $p < 0.001$) and task ($R = 0.86$, $R^2 = 0.47$, $p < 0.001$). It can be observed that the strength of the correlation between PLI and power differed between the groups. In theta band, the strength of this relation was moderate in dyslexics and in typical readers the relation was weak or negligible (these results are plotted in the **Supplementary Figure A3**). In the alpha band, typical readers show moderate to strong correlations between PLI and power, while in dyslexics these values were lower. This result is plotted in **Figure 6**, which also shows the regression lines and coefficients per group. There was no significant relation between PLI and relative power for the beta band.

DISCUSSION

The aim of the current study was to examine whether letter-speech sound binding task-based EEG network measures could discriminate dyslexics from typical readers and/or relate to reading abilities or task performance. In addition, task vs. resting-state differences in functional connectivity and graph measures were explored. The latter examination allows us to extend our discussion on reliability and dependency on FFT power issues that can affect interpretation.

Group Differences in Theta and Beta Connectivity During Task

We found task-specific group differences in theta connectivity. Dyslexics showed lower mean connectivity in theta compared to typical readers. In general terms, oscillatory activity in lower frequency bands such as theta is proposed to reflect long distance synchronization while in higher frequencies it would relate to shorter distances or smaller networks (Buzsáki and Draguhn, 2004). Here, due to our focus on large scale networks, we used the PLI measure which is shown to be more robust against group differences in volume conduction than other measures, albeit at the expense of a higher risk of missing meaningful phase differences at short distances (Stam et al., 2007). Our results regarding PLI theta suggest decreased overall long-range connectivity in dyslexics during the current task simulating reading acquisition. The available literature on functional connectivity has revealed mixed alterations in dyslexia, showing evidence for both increased and decreased connectivity depending on region and task (Marosi et al., 1995; Nagarajan et al., 1999; Shiota et al., 2000; Arns et al., 2007; Dhar et al., 2010). Our finding would be in agreement with previous findings of impaired functional connectivity in dyslexics compared to typical readers across major pathways (e.g., Finn et al., 2014) and the hypothesis that general oscillatory mechanisms may play a role in dyslexia (Hancock et al., 2017a).

Another result in the theta band that emerged from the task data refers to the lower degree correlation in dyslexics compared to typical readers. The graph metric of degree correlation reflects the extent to which connected nodes have similar degrees. A previous EEG study found lower degree correlation (R) in alpha between patients with Alzheimer and controls (de Haan et al., 2009). That finding was interpreted as indicating loss of network structure in the patient group. In addition, an MEG study found an association between lower R and decreased neurocognitive performance in glioma patients (Bosma et al., 2009). In that study higher R in delta was associated with better attentional functioning and R in lower alpha was associated with verbal memory performance. The R of a randomly organized network is close to 0, thus the authors interpreted that result as reflecting deviation from optimal organization of a network.

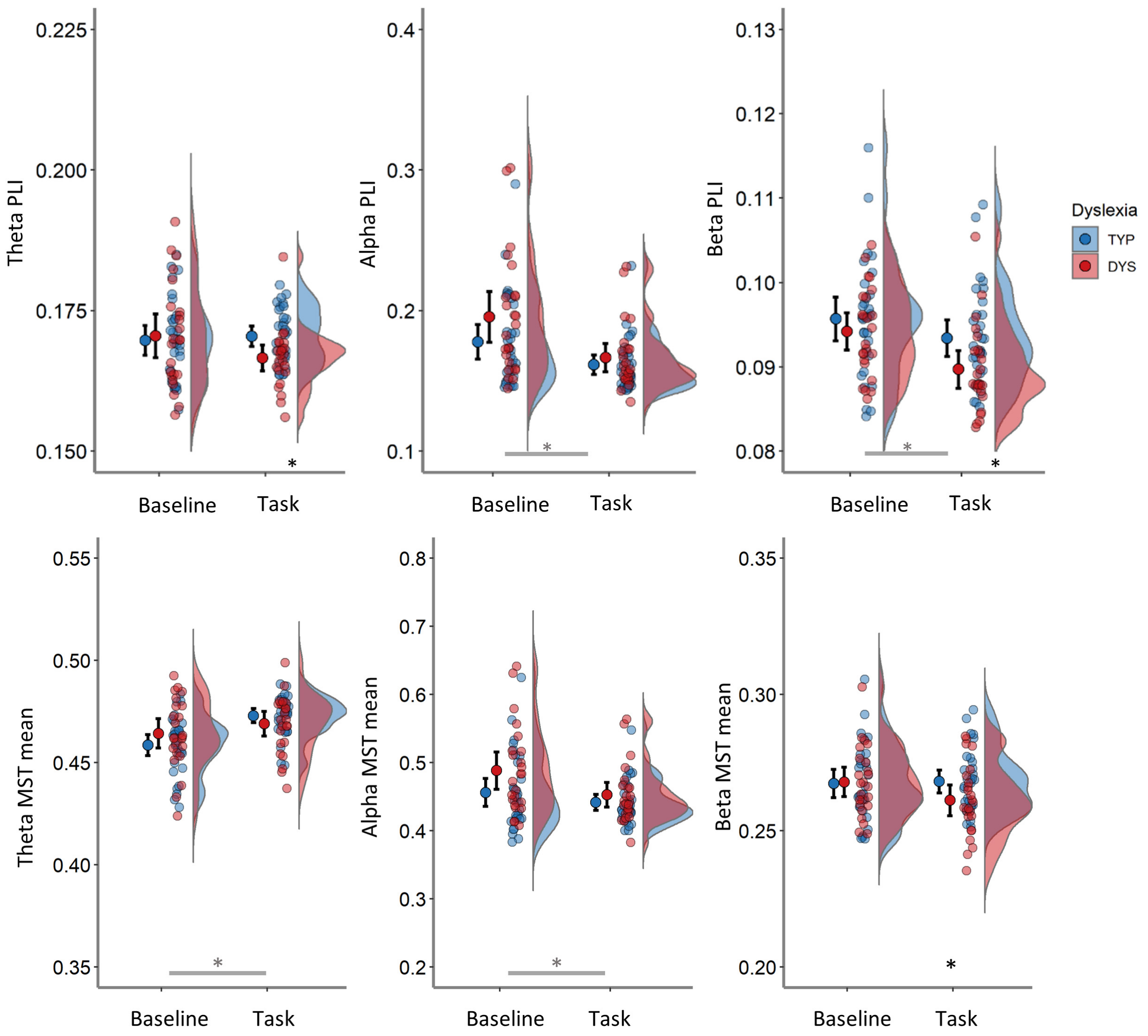

FIGURE 5 | Averaged PLI (top row) and mean MST (bottom row) in the theta (left panels), alpha (middle panels) and beta band (right panels) per condition. Red color indicates data from dyslexics and blue those from typical readers. Error bars represent 95% CI. Black asterisks indicate comparisons between groups significant at $p < 0.05$. Gray asterisk indicates main effect of condition at $p < 0.05$. TYP, typical readers; DYS, dyslexics.

The current group differences in *R* theta might therefore indicate a suboptimal network structure in dyslexics during task performance. However, we did not find a reliable association between *R* and performance measures in the current task. Moreover, the groups did not show significant differences in task performance, although the current trend for longer RTs in dyslexic readers reached statistical significance in our previous work using this task in a sample largely overlapping the present (Fraga González et al., 2019). It is possible that our performance analysis did not capture differences in specific components of learning that impose different attentional and cognitive demands in dyslexics and typical readers and can thus be related to theta networks (this is further discussed in the section "Limitations"). Theta oscillatory activity has been previously associated with working memory and attentional functioning (Klimesch, 1999; von Stein and Sarnthein, 2000; Gootjes et al., 2006). More relevant to the present results, theta activity has been linked to dyslexia and reading difficulties in other studies (Arns et al., 2007; Spironelli et al., 2008; Goswami, 2011; Fraga González et al., 2016). In our previous work using resting-state data showed that several MST metrics in theta related to network integration could discriminate between typical readers and dyslexics in children (Fraga González et al., 2016) but not in adults (Fraga González et al., 2018). The current findings expand previous results and support the involvement of theta oscillations in cognitive performance and dyslexia.

Further, the analysis in the beta band revealed group differences in PLI, suggesting that in dyslexics connectivity was lower during task compared to typical readers. Although the role of beta band activity is less clear, Engel et al. (2001) suggested

TABLE 5 | Significant stepwise regressions of performance, age and cognitive skills to EEG metrics.

			SE	Adj. R^2	ΔR^2	*F change*
Typical readers						
Mean RT	*Model 1*	Task theta power	118.47	0.139	0.168	5.84*
Mean accuracy	*Model 1*	Baseline Beta BC	8.31	0.124	0.153	5.23*
	Model 2	+ Baseline Alpha BC	7.62	0.264	0.160	6.51*
	Model 3	+ Task Alpha BC	6.90	0.396	0.144	7.15*
	Model 4	+ Task beta Th	5.64	0.596	0.194	14.42***
RAN numbers	*Model 1*	Task theta Mean	3.93	0.105	0.135	4.51*
RAN colors	*Model 1*	Baseline Theta PLI	4.22	0.172	0.199	7.21*
	Model 2	+ Baseline Beta BC	3.92	0.288	0.136	5.73*
RAN images	*Model 1*	Task alpha Th	5.14	0.143	0.171	5.99*
	Model 2	+ Task beta Kappa	4.84	0.240	0.120	4.73*
	Model 3	+ Baseline Beta BC	4.58	0.320	0.097	4.30*
	Model 4	+ Baseline Theta PLI	4.30	0.402	0.094	4.71*
	Model 5	+ Baseline Alpha R	3.97	0.488	0.092	5.37*
	Model 6	+ Task theta R	3.61	0.577	0.088	6.25*
Dyslexics						
Age	*Model 1*	Task alpha degree	1.73	0.432	0.456	18.48***
IQ	*Model 1*	Baseline Alpha Th	4.08	2.51	0.284	8.72**
RAN total	*Model 1*	Task theta BC	3.45	0.261	0.293	9.13**
	Model 2	+ Baseline Theta Diameter	3.11	0.401	0.160	6.16*
	Model 3	+ Baseline Theta PLI	2.80	0.513	0.123	5.83*
	Model 4	+ Task alpha power	2.49	0.584	0.080	4.40*
RAN numbers	*Model 1*	Task theta BC	3.47	0.226	0.260	7.72*
	Model 2	+ Baseline Beta R	3.01	0.469	0.210	8.30**
	Model 3	+ Task Beta Leaf	2.75	0.579	0.110	5.21*
	Model 4	+ Task Alpha R	2.53	0.661	0.081	4.56*
RAN colors	*Model 1*	Baseline Beta BC	4.13	0.187	0.223	6.30*

*SE, standard error of the estimate; Adj. R^2, adjusted R squared; ΔR^2, change in R squared; + indicates variable is added to those of preceding models. BC, betweenness centrality; PLI, phase lag index; Th, tree hierarchy; R = degree correlation. *p < 0.05; **p < 0.01; ***p < 0.001.*

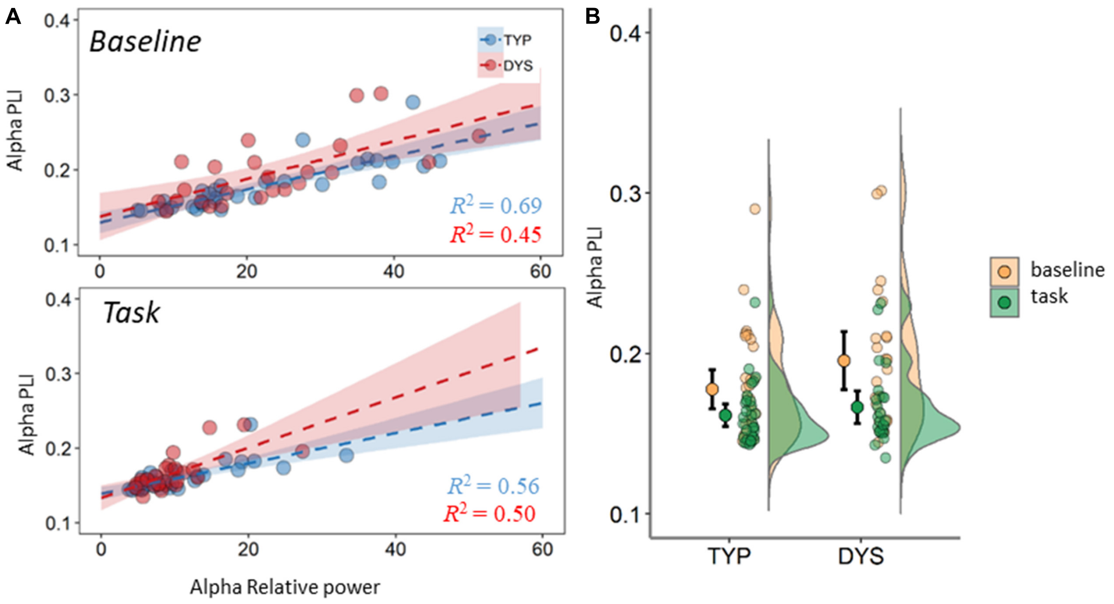

FIGURE 6 | Averaged PLI in the alpha band **(A)** mean PLI plotted against mean relative power. Dashed lines are regression lines for typical readers (blue) and dyslexics (red). **(B)** Mean PLI for task and baseline recordings. DYS, dyslexics; TYP, typical readers. Error bars indicate 95% CI.

TABLE 4 | Group comparisons per condition for PLI and network metrics.

		Task			*Baseline*		
		F	***p***	***Dys* vs. *Typ***	***F***	***p***	***Dys* vs. *Typ***
Theta	PLI	**7.63**	**0.008**	<	0.14	0.715	
	T_H	*3.91*	*0.053*		0.37	0.544	
	R	**7.33**	**0.009***	<	1.23	0.272	
Alpha	PLI	0.78	0.383		*2.97*	*0.091*	
	Degree	0.77	0.383		*3.10*	*0.084*	
	Kappa	0.00	0.948		*3.71*	*0.060*	
Beta	PLI	**5.89**	**0.019**	<	0.76	0.388	
	MST mean	**4.27**	**0.044**	<	0.23	0.879	

PLI, phase lag index; Dys, dyslexics; Typ, typical readers; T_H, tree hierarchy; R, degree correlation.

**Significant effects after FDR correction at q = 0.10; italic text represents trends; bold text represents significant effects at uncorrected $p < 0.05$.*

that beta activity might be associated to maintenance of motor actions and cognition. Specifically, that report indicated a role of beta synchronization in top-down prediction. It is thus possible that our finding in the beta band relates to differences in task engagement between the groups, although we did not find correlational evidence to further support this interpretation. The following discussion on task vs. resting-state comparisons and limitations to our analytic approach to task recording is also relevant to this interpretation.

Network Configuration Differences in Task and Resting-State

The comparisons across conditions revealed a less integrated network configuration and reduced mean connectivity during task performance compared to baseline in all frequency bands and for both groups. This overall pattern may reflect more specialized processing, i.e., recruitment of specific networks, which would be expected during performance of a specific task. In a previous study, surface EEG signals were compared between rest and during a mental arithmetic task in adults vs. children using both static and time-varying networks (Dimitriadis et al., 2015). In that study, inconsistent with our findings, the static network measures of local and global efficiency did not show sensitivity in the task vs. resting-state comparisons, although such difference was found in dynamic measures related to transitivity between network "microstates." A potential reason for the apparent discrepancy in the results is the network construction approach (weighted graph derived directly from the connectivity measures vs. MST graph in the current study). Another issue complicating a direct comparison refers to the task nature (arithmetic vs. association learning) and difficulty: ceiling levels of performance are reported in their study while our behavioral analysis suggests that our task was, to some extent, more challenging to participants. Additional aspects of task design, like trial and feedback structure might have contributed also to these differences. Interestingly, the impact of task difficulty in several MST metrics has been previously studied in another experiment using an arithmetic task (Vourkas et al., 2014). That study suggested more distributed networks in theta and more integrated configuration in alpha with increasing task difficulty, as well as significant, albeit weak, correlations between graph measures and task performance. Unfortunately, our current design did not include a difficulty manipulation. We did find statistically significant association between theta power during task and performance RT in typical readers that would point at the same direction in that group. However, the low strength of this association does not warrant further interpretation.

Another relevant issue when interpreting task vs. baseline network changes relates to FFT power. Our regression analysis (see **Figure 6**) shows that there is a moderate influence of power in the estimation of functional connectivity. This seems especially relevant in alpha where a large drop in power is expected during task- vs. resting-state. This is evident in the mean FFT plots in **Figure 3** as well as in the density plots in **Figure 4**, showing large individual variability in relative alpha power for baselines compared to a narrower distribution with lower values for task data. This result is in agreement with the proposed inhibitory role of alpha activity (Jensen and Mazaheri, 2010; Mathewson et al., 2011). Despite this association and in support of the additional value of mean connectivity measures, there were no significant group differences were found in spectral power. However, such group differences in alpha power were reported during a visuospatial orientation task (Van der Lubbe et al., 2019) and in numerous resting-state studies, although with inconsistent findings (see summary table in Lui et al., 2021). An important consideration derived from the above studies and our regression analysis is the necessity for examining spectral power, often underreported in network studies. This was further brought into attention in a short communication (Demuru et al., 2019).

Limitations

There are some limitations to note for the present this study. A first limitation relates to EEG montage and sensor-level analysis. But as mentioned in our previous work, our choice of PLI as connectivity measure aims at minimizing the impact of volume conduction and it seems to allow reliable network topology estimates (Lai et al., 2018). A second, more specific limitation, is the analysis of task-related activity using measures which have been primarily applied to resting-state data. Here we used a rather "coarse" approach, analyzing epochs derived from a broad segment of the task recording matched in duration to our 4 min baseline period. This approach, used in previous work (Vourkas et al., 2014) ignores the structure of events or task trials and assumes that in order to perform the task, participants must sustain a cognitive and attentional state that is relatively constant during the block. However, it is obvious that levels of concentration, alertness, processing speed and fatigue among other factors, may vary at different levels from each block to the whole experimental session. Other studies used a more event-related approach segmenting a time window preceding and following the event (Vourkas et al., 2011; Wang et al., 2016) which has another set of problems, i.e., related to the amount of data points per segment and network stability (Fraschini et al., 2016). Direct comparisons between these two methods would require a more constrained design beyond the scope of the present work. Finally, using more advanced models for analyzing task performance may yield behavioral indices of the trial-by-trial learning process that can be better associated with large-scale oscillatory activity. The contribution of model-based cognitive neuroscience in the context of networks and dyslexia remains underexplored.

CONCLUSION

We found reduced theta connectivity strength during task in dyslexics compared to typical readers and trends for group differences in both task and resting state in several network metrics. These differences were not detected when examining EEG power and support that overall connectivity in theta activity during task performance may be implicated in dyslexia. This is also suggested by the differences between task and resting-state in theta connectivity that also seem to diverge between the groups. However, it remains unclear whether these group differences in EEG connectivity reflect atypical activations of specific hub regions, recruitment of different networks, or they involve more widespread oscillatory mechanisms. More spatially resolved techniques might clarify some of these questions. In addition, the EEG group differences were not reflected in learning differences during the task and a robust association between functional network metrics and cognitive performance remained elusive. Model-based analyses and tasks that can capture variability in reading skills will be important to further develop a cognitive interpretation of these EEG measures. In this direction, other network metrics that can be derived across frequencies and tasks may offer more promising neural correlates of literacy (Lui et al., 2021). Further, our findings emphasize the need to consider the unique contribution of each set of measures (i.e., overall strength of functional connectivity and graph-derived metrics), their intercorrelation across recordings, as well as the influence of spectral power. This would benefit the interpretability of network findings in future studies.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the local ethics committee of the University of Amsterdam. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

MaV and EG conceived and designed the experiments. GF-G performed the experiments. GF-G, JT, MaV, DS, and EG analyzed the data. JT, MeV, and CS contributed materials and analysis tools. GF-G and MaV wrote the article. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.767839/full#supplementary-material

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CORRECTION
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Corrigendum: Graph Analysis of EEG Functional Connectivity Networks During a Letter-Speech Sound Binding Task in Adult Dyslexics

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A Corrigendum on

Graph Analysis of EEG Functional Connectivity Networks During a Letter-Speech Sound Binding Task in Adult Dyslexics
by Fraga-González, G., Smit, D. J. A., Van der Molen, M. J. W., Tijms, J., Stam, C. J., de Geus, E. J. C., and Van der Molen, M. W. (2021). Front. Psychol. 12:767839. doi: 10.3389/fpsyg.2021.767839

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In the original article the email address of the corresponding author was incorrect. The correct email address is gorka.fragagonzalez@uzh.ch.

The authors apologize for this error and state that this does not change the scientific conclusions of the article in any way. The original article has been updated.

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Protracted Neural Development of Dorsal Motor Systems During Handwriting and the Relation to Early Literacy Skills

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Handwriting is a complex visual-motor skill that affects early reading development. A large body of work has demonstrated that handwriting is supported by a widespread neural system comprising ventral-temporal, parietal, and frontal motor regions in adults. Recent work has demonstrated that this neural system is largely established by 8 years of age, suggesting that the development of this system occurs in young children who are still learning to read and write. We made use of a novel MRI-compatible writing tablet that allowed us to measure brain activation in 5–8-year-old children during handwriting. We compared activation during handwriting in children and adults to provide information concerning the developmental trajectory of the neural system that supports handwriting. We found that parietal and frontal motor involvement during handwriting in children is different from adults, suggesting that the neural system that supports handwriting changes over the course of development. Furthermore, we found that parietal and frontal motor activation correlated with a literacy composite score in our child sample, suggesting that the individual differences in the dorsal response during handwriting are related to individual differences in emerging literacy skills. Our results suggest that components of the widespread neural system supporting handwriting develop at different rates and provide insight into the mechanisms underlying the contributions of handwriting to early literacy development.

Keywords: handwriting, fMRI, dorsal visual stream, literacy, development

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INTRODUCTION

Handwriting is an important sensorimotor skill that takes years to develop. Most children begin their experience with handwriting by producing individual letters of the alphabet by kindergarten, yet the fluid and efficient production of letter-forms in the creation of words and complex sentences continues to develop throughout middle school (Feder et al., 2000; Treiman and Kessler, 2014; Coker and Ritchey, 2015; Mangen and Balsvik, 2016; Fears and Lockman, 2018). Thus, the earliest and most fundamental element of handwriting is the coordination of sensory and motor systems to produce a written form, a task not discernible from drawing. Indeed, neural responses found during handwriting in literate adults are extremely similar to those found during drawing, with only minor differences found in the parietal cortex (Yuan and Brown, 2014, 2015; Ose Askvik et al., 2020). Understanding the development of the sensorimotor system supporting handwriting – how it differs between adults and young children at the earliest stages of learning to write – can provide valuable insights into the role of sensorimotor systems in learning.

Much of what we know about how this neural system supports handwriting comes from studies on adult populations. The adult literature on handwriting suggests that handwriting is supported by a largely left-lateralized neural system comprised of ventral-temporal, parietal, and frontal motor regions (Katanoda et al., 2001; Beeson et al., 2003; James and Gauthier, 2006; Purcell et al., 2011; Rapp and Dufor, 2011; Dufor and Rapp, 2013; Planton et al., 2013, 2017; Yuan and Brown, 2014, 2015; Longcamp et al., 2014; Vinci-Booher et al., 2019; Vinci-Booher and James, 2020b). The involvement of brain regions in this broad neural system has been related to different aspects of the handwriting experience. For example, studies have been conducted to determine which brain regions were related to the sensorimotor action of handwriting and which regions were related to other processes that are commonly engaged during handwriting tasks, such as spelling (Planton et al., 2017). A recent meta-analysis of such studies found that the sensorimotor element of handwriting was primarily supported by the left parietal and frontal cortices (Purcell et al., 2011). The authors noted that additional cortical regions may also be related to the sensorimotor element that were not identified in their meta-analysis, because many of the studies included in their meta-analysis explicitly controlled for the sensorimotor element.

Our prior work in adults evaluated the degree to which the brain regions associated with the sensorimotor element of handwriting could be separated into sensorimotor components, namely, motor and visual components (Vinci-Booher et al., 2019). The motor component was isolated by comparing activation during handwriting to activation while participants passively watched a letter unfold as if being written. The visual component was isolated by comparing activation during handwriting to activation during handwriting using a pen that had no ink. We found that a largely left-lateralized neural system comprised of ventral-temporal, parietal, and frontal motor regions was recruited during handwriting and that the response in frontal motor and parietal regions was related to the motor component of handwriting (i.e., producing the letter), similar to the results of the meta-analysis (Purcell et al., 2011). Our results added, however, that a ventral response was also apparent during handwriting and that this ventral response was related to the visual component of handwriting (i.e., perceiving the letter as it is produced). Of note was an area of motor-visual overlap where activation appeared to be equally related to the motor and visual component of handwriting: the left intraparietal sulcus (Vinci-Booher et al., 2019).

Prior work on the development of the neural system supporting handwriting is limited but generally indicates that the adult neural system is largely in place by the middle school years (i.e., by approximately 11–13 years of age) and perhaps a few years earlier. Work with typically developing middle school children using EEG found that handwriting, drawing, and typing produced reliable differences in brain oscillations in adults that were also observed in middle school children, suggesting that neural processing during handwriting was already adult-like in middle school children (Ose Askvik et al., 2020). Work in clinical populations using fMRI has demonstrated that neural responses during handwriting in middle school children that deviated from the adult-like response were associated with dysgraphia and/or dyslexia, suggesting that the onset of an adult-like neural response during handwriting by the middle school years is associated with typical development (Richards et al., 2011, 2015, 2017). Additionally, one recent study suggested that the neural system that supports handwriting might even be in place prior to middle school (Palmis et al., 2021). In this study, children ages 8–11 years of age and adults were asked to write on a touchscreen tablet during fMRI scanning (Tam et al., 2011; Longcamp et al., 2014). Results demonstrated no significant differences between children and adults in whole brain activation patterns, suggesting that the spatial topography of regions involved in handwriting may be adult-like by as early as 8 years of age.

The development of the neural system supporting handwriting in elementary school children younger than 8 years old is currently unknown; however, hypotheses concerning its development can be made from considering general developmental trends. At least three lines of research suggest that processing in the dorsal cortex, namely, parietal cortex, undergoes a protracted developmental trajectory relative to the ventral-temporal cortex when investigated past 2 years of age (Dekker et al., 2011; Stiles et al., 2013; Freud et al., 2016, 2019; Vinci-Booher and James, 2020a; Vinci-Booher et al., in press). First, behaviors that are often associated with neural processing in the posterior parietal cortex were not yet adult-like by 4.5–6.5 years of age while behaviors associated with processing in the ventral-temporal cortex were adult-like (Freud et al., 2019). Second, the tissue properties of major white matter tracts that connect parietal and frontal motor cortices were not yet adult-like in 5–8-year-old children while white matter tracts predominantly contained within the ventral-temporal cortex were adult-like (Lebel et al., 2008; Stiles et al., 2013; Vinci-Booher et al., in press). Finally, studies using children of approximately the same age ranges have found that object selectivity develops later in the parietal cortex than in ventral-temporal cortex for tools and animals (Dekker et al., 2011) and letters (Vinci-Booher and James, 2020a). Together, these three lines of work suggest that young children rely on different neural systems than adults. More specifically, they suggest that parietal involvement during handwriting may still be developing in elementary school children younger than 8 years of age.

We hypothesized that the responses of brain regions within the neural system supporting handwriting in children younger than 8 years of age would be different from its response in adults. Given the substantial evidence in support of a protracted development of the parietal cortex in young children (e.g., Stiles et al., 2013; Freud et al., 2016; Vinci-Booher et al., in press), we expected that parietal function during handwriting would still be developing in typically developing children younger than 8 years of age. We also expected that the response in the handwriting neural system would be related to early reading development. Studies of handwriting development in children younger than 8 years old have demonstrated that handwriting experience increases activation in several regions that come to support the perception of letters of the alphabet (James, 2010; James and Engelhardt, 2012; Kersey and James, 2013; Vinci-Booher et al., 2016), suggesting that handwriting is influential in neural changes associated with learning to read.

Investigating the development of brain regions supporting handwriting in children younger than 8 years of age comes with several challenges. First, young children are prone to movement and movement presents difficulty for MRI data. Our lab specializes in collecting MRI data from young children even while performing an in-scanner task (e.g., James and Kersey, 2018), including procedures for reducing motion during the scan and for properly addressing motion when it does occur. Second, young children experience extreme difficulty writing letters using the MRI-compatible writing tablets that are currently available because they are unable to see their hand when they are writing (Mraz et al., 2004; Rektor et al., 2006; Tam et al., 2011; Reitz et al., 2013; Karimpoor et al., 2015; Ko et al., 2018). The inability to see their hand during writing makes it very difficult for young children to write letters because they have not yet developed the competence seen in adults and older children who have substantially more practice writing letters of the alphabet (unpublished data). We, therefore, developed an MR-compatible writing tablet, the MRItab (Vinci-Booher et al., 2018). The MRItab is a touchscreen tablet with a video display that provides the user with an experience similar to the common smartphone or tablet. Importantly, the MRItab makes it feasible for young children to write during fMRI scanning because participants can see their hand when they are writing.

To better understand the developmental trajectory of the neural system supporting handwriting and its relationship to early reading development, we assessed neural activation using fMRI imaging in adults and 5–8-year-old children while they wrote letters to dictation. We focused on activation in regions of the ventral-temporal, parietal, and frontal motor cortices that have been identified as being involved with handwriting in adults (Katanoda et al., 2001; Beeson et al., 2003; James and Gauthier, 2006; Purcell et al., 2011; Planton et al., 2013, 2017; Longcamp et al., 2014; Yuan and Brown, 2014, 2015; Vinci-Booher et al., 2019). All participants wrote letters to dictation on the MRItab with a writing utensil. In one condition, they saw what they wrote as they were writing (Write Ink), in a second condition, they wrote with a pen that had "no ink" (Write No Ink), and in a third condition, they observed a letter unfolding as if being written to dictation (Watch Ink). The latter two conditions were designed to allow us to observe activations during two components of handwriting: the motor component during the Write No Ink condition, that is the hand movements required to create the letter, and the visual component during the Watch Ink condition, that is seeing the letter-form unfold as if being written. We also evaluated the relationships between the neural responses in each ROI and a literacy composite score to determine the relationship between the development of the neural system supporting handwriting and emerging literacy.

MATERIALS AND METHODS

Participants

All participants were recruited through word of mouth or an in-house database of community members. Adult participants provided written informed consent and were compensated monetarily for their time. Parents of all children provided written informed consent and children who were 7 years and older provided written informed assent. Participating families were compensated for their time with gift cards as well as small toys for the children. All participants were right-handed, expressed English as their native language, and were free of neurological trauma, developmental disorders, and MRI contraindications.

We obtained usable data from 14 adults and 27 children after excluding five children due to difficulty following instructions and/or technical difficulties as well as nine children and three adults due to an unacceptable amount of motion during conditions of interest. The 13 youngest children were assigned to the younger age group (M = 5.5 years, SD = 0.5 years; seven females, six males) and the 14 oldest children were assigned to the older age group (M = 7.6 years, SD = 0.5 years; eight females, six males). The children were separated into younger and older age groups for consistency with prior work that incorporated data from these same participants (Dekker et al., 2011; Stiles et al., 2013; Freud et al., 2016, 2019; Vinci-Booher and James, 2020a; Vinci-Booher et al., in press). The adult sample included 14 adults (M = 20.31, SD = 1.02; nine females, five males). Sample sizes were selected in line with prior work (Dekker et al., 2011; Vinci-Booher and James, 2020a); *post hoc* power is reported at alpha equal to 0.05.

Materials and Stimuli

Apparatus

Participants used the MRItab for all conditions (Vinci-Booher et al., 2018; **Figure 1**). The MRItab is an MR-compatible digital tablet with touchscreen and display capabilities that provides a user experience similar to writing on a common smartphone or tablet. The MRItab was affixed above each participate through a mounting system. To reduce motion, all participants wore a Wheaton® elastic shoulder immobilizer and inflatable padding was used for padding between participants' heads and the head coil. Verbal instructions were delivered through MRI-compatible headphones. An in-house Matlab program using the Psychophysics Toolbox extensions interfaced with the headphones, projector, and either tablet to record and present all stimuli (Brainard, 1997; Pelli, 1997).

Stimuli

Twelve letters from the Roman alphabet were selected: A, B, C, D, G, H, J, L, Q, R, U, and Y. Based on pilot testing, we expected our youngest children to know and be able to write the 12 letters to dictation within a 4 s time frame. This set of 12 letters also reduces the use of easily confusable letter names (e.g., c and e). All letters were written in white on a black background with a pen width of 7 points within a box that subtended 10 by 10 degrees of visual angle.

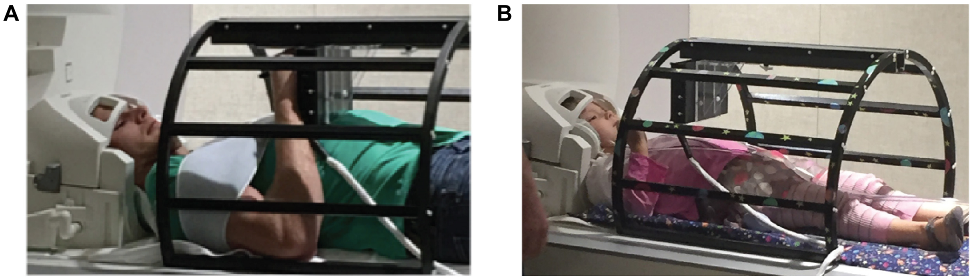

FIGURE 1 | Experimental set up. Adult and child participants (**A,B**, respectively) completed all tasks using a novel MR-compatible writing tablet, the MRItab. The MRItab was mounted to a holding apparatus and positioned at a location that allowed the participant to see and interact with the tablet easily.

Procedure

MRI Procedure

All children underwent training in a mock MRI scanner before entering the MRI environment; adults did not undergo training in a mock MRI scanner. The training was necessary to ensure the ability of each child participant to perform the handwriting task and to ensure that they understood and were able to stay still during the experiment. Only children who produced letter-like forms during the mock training session and appeared comfortable in the mock MRI environment continued in the study. A trained research assistant always remained in the MRI room with the child to provide support and help the child stay on-task. A second trained research assistant ran the experimental protocol from the MRI operator room while watching the child on a camera to ensure that they were on-task during all conditions. Except for the mock MRI training session and the presence of an additional research assistant, the procedures for the children and adults were the same.

All participants underwent a high-resolution anatomical scan followed by up to four fMRI experimental runs, depending upon the comfort and compliance of the participant. During the anatomical scan, participants watched a movie, listen to an audiobook, or simply rested. Each functional run contained one complete set of experimental conditions and lasted 344 s (5:44 min) [see Figure 2 in Vinci-Booher and James (2020a)]. Block orders were pseudo-randomized and counter-balanced across participants.

Each block of the functional runs contained six 4-s trials; one stimulus was presented in each of the six trials. Blocks were separated by 14-s inter-block intervals. During the inter-block interval, only the fixation cross was visible in the mirror. The last 2 s of each inter-block interval contained auditory instructions for the following block: "draw" or "watch."

Each trial began with an auditory prompt that indicated the letter for that trial (e.g., "A" or "B"). During Write Ink and Write No Ink trials, the participant wrote this letter using an MR-compatible pen. In the Write Ink condition, they saw their letter being produced as they wrote it. In the Write No Ink condition, no trace was left from their pen as if their pen had "no ink." During Watch Ink trials, participants passively watched a video of their own letter production unfold as if it were being written. The pen trajectory that they watched was a pen trajectory of their own letter production that had been recorded. In all conditions, the screen became blank at the end of each 4 s trial, and a new letter was prompted.

Behavioral Procedure

All participants that successfully completed the MRI scanning session were asked to return for a one-hour behavioral session with the requirement that the behavioral session must occur within 3 weeks of the neuroimaging session. The behavioral session consisted of a battery of standard assessments designed to assess visual-motor integration, fine motor skill, and literacy level. Only literacy assessments were of interest in the current study. Literacy assessments included four subtests from the Woodcock Johnson IV Tests of Achievement: Letter-Word Identification, Spelling, Word Attack, Spelling of Sounds (Schrank and Wendling, 2018). These four literacy assessments were averaged to create a composite literacy score. All participants completed the assessments; however, only the scores from the children were of interest in the current study. Group means and standard errors for each literacy assessment and the composite literacy score are reported in **Table 1**.

MRI Scanning Parameters

Neuroimaging was performed at the Indiana University Imaging Research Facility, housed within the Department of Psychological and Brain Sciences with a Siemens Prisma 3-T whole-body MRI system. High-resolution T1-weighted anatomical volumes were acquired using an MPRAGE sequence: TI = 900 ms, TE = 2.98 ms, TR = 2300 ms, flip angle = 9°, with 176 sagittal slices of 1.0 mm thickness, a field of view of 256 × 248 mm, and an isometric voxel size of 1.0 mm^3. For functional images, the field of view was 220 × 220 mm, with an in-plane resolution of 110 × 110 pixels and 72 axial slices of 2.0 mm thickness per volume with 0% slice gap, producing an isometric voxel size of 2.0 mm^3. Functional images were acquired using a gradient-echo EPI sequence with interleaved slice order: TE = 30 ms, TR = 1000 ms, flip angle = 52° for blood-oxygen-level-dependent (BOLD) imaging.

MRI Data Processing

Preprocessing

All MRI data preprocessing was performed using BrainVoyager QX, Version 2.8 (Brain Innovation) and was performed as

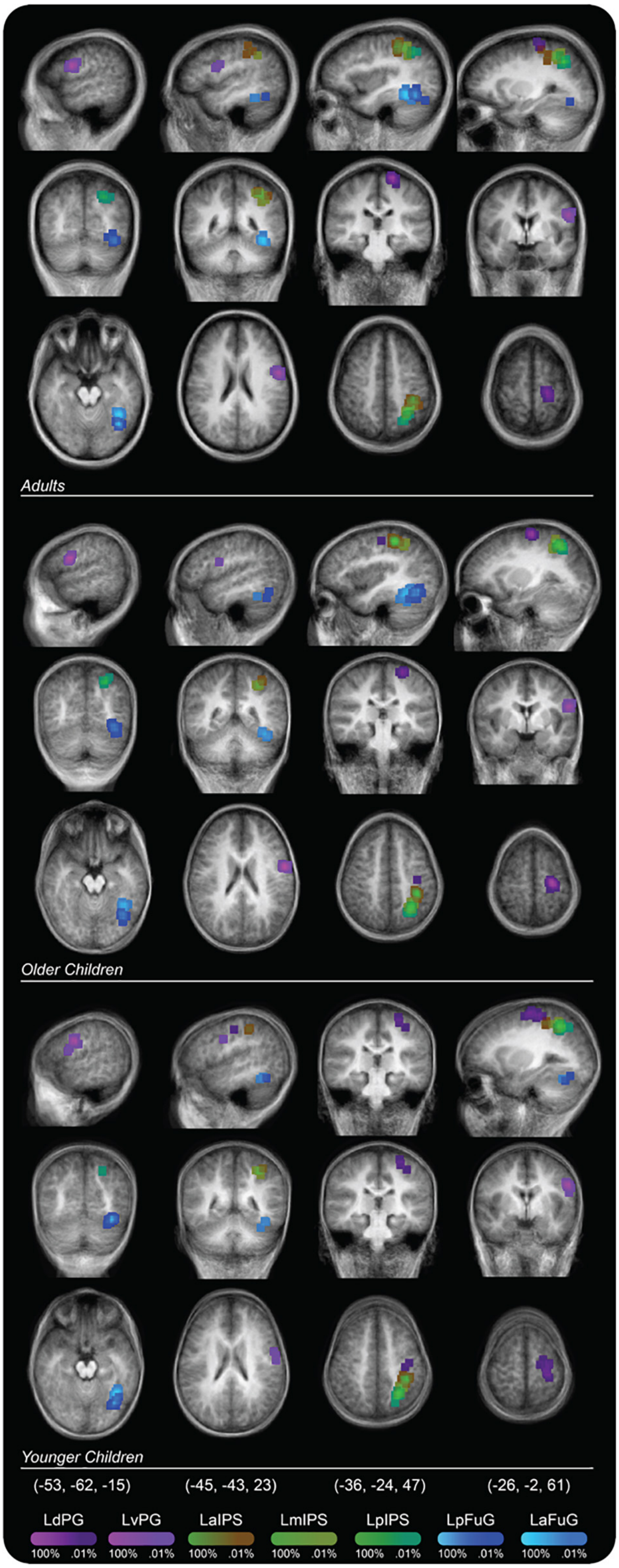

FIGURE 2 | Probability map for regions of interest (ROIs) displayed on a group averaged anatomical image. Percent values correspond to the percentage of participants in a particular group whose ROI placement included that voxel.

TABLE 1 | Mean and standard deviation of behavioral assessments.

	Younger Children (n = 13)	**Older Children (n = 14)**	**Children (n = 27)**
	M (SD)	**M (SD)**	**M (SD)**
Age (years)	5.5 (0.6)	7.7 (0.5)	6.6 (1.2)
Woodcock Johnson IV			
Letter Word Identification	22.4 (14.2)	50.5 (16.3)	37.0 (20.8)
Spelling	9.7 (2.5)	23.3 (8.9)	16.7 (9.5)
Word Attack	9.7 (4.9)	21.4 (5.0)	15.7 (7.7)
Spelling of Sounds	6.4 (2.9)	15.2 (4.4)	11.0 (5.8)
Literacy Composite Score	12.0 (5.7)	27.6 (8.0)	20.1 (10.5)

previously reported in Vinci-Booher and James (2020a). The preprocessing steps will be reiterated here: Preprocessing of functional data included slice scan time correction, 3-D motion correction using trilinear/sinc interpolation, and 3D Gaussian spatial blurring with a full-width at half-maximum of 6 mm. Temporal high-pass filtering was performed using a voxel-wise GLM with predictors that included a Fourier basis set with a cut-off value of 2 sine/cosine pairs and a linear trend predictor. To account for head motion, we calculated the relative root mean squared (RMS) time course for each run using the rigid transformation parameters and counted the number of timepoints within a functional run with RMS > 2.0 mm (Van Dijk et al., 2012; Satterthwaite et al., 2013). If this number was greater than or equal to seven, the entire run was removed from the analysis. Additionally, if visual inspection of the rigid body motion parameters indicated a large amount of non-spiking motion in at least one parameter, the entire run was removed from the analysis. This procedure resulted in a final dataset of 13 younger children, 14 older children, and 14 adults, from sample sizes of 17, 19, and 18, respectively. Individual anatomical volumes were normalized to Talairach space (Talairach and Tournoux, 1988). Coregistration of functional volumes to anatomical volumes was performed using a rigid body transformation. Region of interest (ROI) analyses were performed using the peak percent BOLD signal change from anatomically localized 10 mm^3 ROIs during the Write Ink, Write No Ink, and Watch No Ink conditions.

Anatomical ROI Placement

Individual participant ROIs were placed based on their anatomical image in Talairach space. Anatomical locations were determined by, first, referencing the Talairach Daemon and, second, confirming the location by referencing the human brain atlas to verify. Two ROIs were placed in the ventral temporal cortex: the left anterior fusiform gyrus (LaFuG) and the left posterior fusiform gyrus (LpFuG). Three ROIs were placed along the intraparietal sulcus in parietal cortex: the left anterior intraparietal sulcus (LaIPS), the left middle intraparietal sulcus (LmIPS), and the left posterior intraparietal sulcus (LpIPS). Two ROIs were placed in the frontal motor cortex: the left dorsal precentral gyrus (LdPG) and the left ventral precentral gyrus (LvPG).

Statistical Analyses

ROI Analyses

We were primarily interested in understanding if the neural responses in specific regions of the ventral-temporal, parietal, and frontal motor cortices during handwriting changed with age. While a whole brain analysis might increase the likelihood of finding brain regions to be active during handwriting that were outside of our cortical areas of interest [e.g., the cerebellum (Purcell et al., 2011; Planton et al., 2013)], we chose to restrict our analyses to anatomically specific ROIs that we selected based on *a priori* hypotheses concerning their involvement in handwriting. Additionally, ROI analyses are more powerful and more robust against motion-related artifacts than other statistical analyses (e.g., functional connectivity; Poldrack, 2007).

The ROIs within each region were selected based on prior works that indicated potential involvement of these regions with handwriting (Katanoda et al., 2001; Beeson et al., 2003; James and Gauthier, 2006; Purcell et al., 2011; Planton et al., 2013, 2017; Longcamp et al., 2014; Yuan and Brown, 2014, 2015; Vinci-Booher et al., 2019). For the ventral-temporal cortex, ROIs included the left anterior fusiform gyrus (LaFuG) and the left posterior fusiform gyrus (LpFuG). For the parietal cortex, the ROIs included the left anterior intraparietal sulcus (LaIPS), left middle intraparietal sulcus (LmIPS), and left posterior intraparietal sulcus (LpIPS). For the frontal motor cortex, the ROIs included the left dorsal precentral gyrus (LdPG) and the left ventral precentral gyrus (LvPG). Probability maps for each ROI are shown in **Figure 2** and the mean and standard deviation of the Talairach coordinates for each ROI are reported in **Table 2**.

For each ROI, we performed a Two-way Repeated Measures ANOVA, with age group and writing condition as factors. The age group factor had three levels: younger children, older children, and adults. The writing condition factor had three levels: Write with Ink, Write No Ink, and Watch Ink. The dependent variable for all ANOVAs was peak percent BOLD signal change. Values that were greater or less than 3 standard deviations of the within-ROI, within-group mean were removed. As these comparisons were considered *a priori* comparisons, the results of the ANOVA analyses were considered significant based on uncorrected *p*-values. We note, however, that several comparisons would have passed Bonferroni correction for 7 comparisons, i.e., 7 ROIs, at a threshold of $p_{bonferroni} = 0.05/7 = 0.007$. Simple effects analyses (One-way Repeated Measures ANOVAs) were performed following significant two-way interactions to compare activation among writing conditions within each age group and were followed with three *a priori* paired samples *t*-tests within each age group: Write Ink vs. Write No Ink, Write Ink vs. Watch Ink, and Write No Ink vs. Watch Ink. All *p*-values are reported as uncorrected *p*-values.

Correlations With Behavior

We were also interested in understanding if activation in any of our ROIs was related to literacy and/or age within the child groups. Only the child data were used for the correlation analysis, and we only performed correlations for ROIs for which the prior ANOVA analyses indicated were not yet adult-like: LmIPS, LvPG. Peak percent BOLD signal change and the literacy score were z-scored. We performed Pearson correlations analyses to assess the relationship between activation in each ROI and literacy as well as age. We note that the literacy composite score and the four independent assessments that comprise it were highly correlated with age: WJ-IV Letter-Word Identification ($r = 0.793$), WJ-IV Spelling ($r = 0.816$), WJ-IV Word Attack ($r = 0.854$), WJ-IV Spelling of Sounds ($r = 0.870$), literacy composite score ($r = 0.857$), all $ps > 0.05$. We, therefore, performed partial correlations analyses to assess the relationship between activation in each ROI and literacy, controlling for age. All *p*-values are reported as uncorrected *p*-values; however, all correlation analyses survived Bonferroni correction, i.e., for the 2 ROI-literacy composite score correlations at a threshold of $p_{bonferroni} = 0.05/2 = 0.0025$ and for the 4 ROI-assessment score correlations at a threshold of $p_{bonferroni} = 0.05/4 = 0.0125$.

TABLE 2 | Mean and standard deviation of Talairach coordinates for ROIs.

Participant Group	ROI	Mean			Standard Deviation		
		x	y	z	x	y	z
Adults	LdPG	−18.4	−24.3	64.8	2.6	5.2	3.2
	LvPG	−52.2	0.5	25.3	3.0	2.9	2.2
	LaIPS	−36.1	−35.4	46.6	4.3	2.7	5.1
	LmIPS	−31.6	−47.5	45.86	4.5	4.0	4.5
	LpIPS	−28.6	−57.1	41.1	3.9	3.4	3.2
	LpFuG	−36.1	−58.9	−13.2	2.7	4.4	3.4
	LaFuG	−37.3	−46.3	−13.2	1.9	3.9	3.4
Older Children	LdPG	−23.8	−18.4	60.3	4.0	3.2	3.2
	LvPG	−53.6	1.6	22.3	2.5	1.7	2.9
	LaIPS	−33.4	−34.6	49.9	2.2	2.9	2.6
	LmIPS	−27.4	−49.4	48.2	2.8	2.9	3.3
	LpIPS	−25.9	−56.0	45.8	2.5	3.1	2.8
	LpFuG	−35.6	−61.5	−15.5	2.6	4.1	4.3
	LaFuG	−36.9	−49.0	−16.1	2.4	4.4	4.7
Younger Children	LdPG	−28.6	−18.8	58.4	5.6	6.3	5.5
	LvPG	−52.7	−2.4	28.7	2.2	3.3	4.5
	LaIPS	−35.2	−35.6	49.1	3.3	2.8	2.7
	LmIPS	−29.4	−49.5	48.0	2.2	3.8	2.7
	LpIPS	−25.4	−55.8	44.6	2.3	4.2	2.7
	LpFuG	−36.2	−50.6	−17.2	3.4	3.2	3.2
	LaFuG	−34.5	−61.7	−17.0	3.5	3.8	3.0

Units are in 1 mm isometric voxels. LdPG, left dorsal precentral gyrus; LvPG, left ventral precentral gyrus; LaIPS, left anterior intraparietal sulcus; LmIPS, left middle intraparietal sulcus; LpIPS, left posterior intraparietal sulcus; LpFuG, left posterior fusiform gyrus; LaFuG, left anterior fusiform gyrus.

All statistical analyses were performed using IBM SPSS Statistics for Mac OSX, version 26.

RESULTS

ROI Analyses

Ventral Temporal Cortex

Left Anterior Fusiform Gyrus

The 3 × 3 ANOVA in this region revealed a main effect of condition [$F(2,76) = 4.194$, $p = 0.019$, *post hoc* power 0.721;

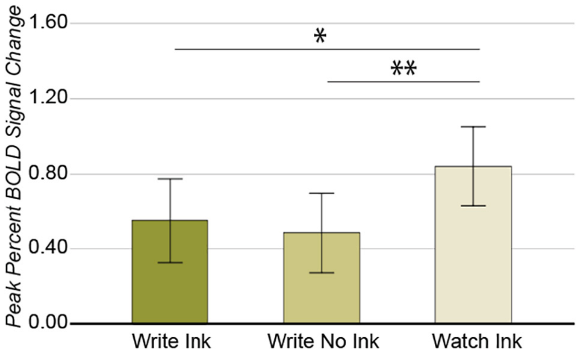

FIGURE 3 | Left anterior fusiform gyrus. Main effect of CONDITION. Error bars represent 95% confidence intervals. $^{**}p < 0.01$; $^{*}p < 0.05$.

Figure 3]. The LaFuG response was greater during the Watch Ink (M = 0.834, SD = 0.713) condition than during the Write Ink (M = 0.553, SD = 0.705) and Write No Ink (M = 0.481, SD = 0.668) conditions [$t(40) = 2.024$, $p = 0.050$ and $t(40) = 2.822$, $p = 0.007$, respectively]. There was no difference between the Write Ink and Write No Ink conditions [$t(40) = 0.534$, $p = 0.596$]. The main effect of age group was not significant [$F(2,38) = 1.713$, $p = 0.194$, *post hoc* power 0.337], nor was the two-way interaction [$F(4,76) = 1.698$, $p = 0.159$, *post hoc* power 0.497].

Left Posterior Fusiform Gyrus

Again, we observed a significant main effect of condition in this region [$F(2,74) = 5.052$, $p = 0.009$, *post hoc* power 0.803; **Figure 4**], with greater response during the Watch Ink (M = 0.876, SD = 0.700) condition than Write No Ink (M = 0.426, SD = 0.641) condition [$t(40) = 3.246$, $p = 0.002$]. There was no difference between the Watch Ink and Write Ink (M = 0.677, SD = 0.641) conditions [$t(39) = 1.548$, $p = 0.130$] or the Write Ink and Write No Ink conditions [$t(39) = 0.1.671$, $p = 0.103$]. The main effect of age group was not significant [$F(2,37) = 0.715$, $p = 0.496$, *post hoc* power 0.162], nor was the two-way interaction [$F(4,74) = 2.050$, $p = 0.096$, *post hoc* power 0.586].

Parietal Cortex

Left Anterior Intraparietal Sulcus

As with the ventral temporal cortex, the main effect of condition was significant [$F(2,74) = 11.851$, $p = 0.00003$, *post hoc* power 0.993; **Figure 5**]. The LaIPS response was greater during the Write Ink (M = 1.14, SD = 0.556) and Write No Ink (M = 1.12, SD = 0.541) conditions than during the Watch Ink (M = 0.506, SD = 0.441) condition [$t(40) = 4.622$, $p = 0.00004$ and $t(39) = 4.411$, $p = 0.00008$, respectively]. There was no difference between the Write Ink and Write No Ink conditions [$t(39) = 0.220$, $p = 0.827$]. The main effect of age group was not significant [$F(2,37) = 1.496$, $p = 0.237$, *post hoc* power 0.298], nor was the two-way interaction [$F(4,74) = 0.806$, $p = 0.526$, *post hoc* power 0.246].

Left Middle Intraparietal Sulcus

A different pattern of results emerged from this region compared with our other ROIs. First, the main effect of age group was significant [$F(2,38) = 3.543$, $p = 0.039$, *post hoc* power 0.624] (**Figure 6A**). A *post hoc* independent samples *t*-tests revealed that the difference between adults (M = 0.785, SD = 0.220) and older children (M = 0.580, SD = 0.184) was significant [$t(26) = 2.678$, $p = 0.013$] but that the difference between older children and younger children was not [$t(25) = 1.731$, $p = 0.096$] ($p_{bonferroni} = 0.05/2 = 0.025$). Second, the main effect of condition was marginally significant [$F(2,76) = 2.632$, $p = 0.079$, *post hoc* power 0.509] (**Figure 6B**). The LmIPS response was greater during the Write Ink condition (M = 0.806, SD = 0.441) than during the Write No Ink condition (M = 0.624, SD = 0.421) [$t(40) = 2.033$, $p = 0.049$]. The difference between the Write Ink condition and the Watch Ink condition (M = 0.647, SD = 0.319) was marginally significant [$t(40) = 1.786$, $p = 0.082$]. The difference between Write No Ink and Watch Ink was not significant [$t(40) = 0.256$, $p = 0.800$].

Most importantly, however, the ANOVA revealed a significant two-way interaction between age group and condition [$F(2,76) = 2.926$, $p = 0.026$, *post hoc* power 0.762; **Figure 6C**]. The LmIPS response differed as a function of condition in the adults [$F(2,26) = 7.719$, $p = 0.002$], but not in the younger children [$F(2,24) = 1.071$, $p = 0.359$], or in the older children [$F(2,26) = 0.358$, $p = 0.703$]. In adults, the LmIPS response decreased linearly from Write Ink (M = 1.057, SD = 0.333) to Write No Ink (M = 0.783, SD = 0.471) to Watch Ink (M = 0.517, SD = 0.278) [$F(1,13) = 48.359$, $p = 0.00001$]. The LmIPS response during Write Ink was greater than during Watch Ink in adults [$t(13) = 6.954$, $p = 0.00001$]. The LmIPS response during Write Ink was greater in adults than in the older children (M = 0.598, SD = 0.437) and greater than in the younger children as well (M = 0.759, SD = 0.439) [$t(26) = 3.122$, $p = 0.004$ and $t(25) = 1.994$, $p = 0.057$, respectively].

Left Posterior Intraparietal Sulcus

The ANOVA from this region demonstrated no significant main effects [condition: $F(2,74) = 2.122$, $p = 0.127$, *post hoc* power 0.422; age group: $F(2,37) = 0.032$, $p = 0.968$, *post hoc* power 0.054] and no significant interaction between the factors [$F(4,74) = 1.382$, $p = 0.248$, *post hoc* power 0.410].

Frontal Motor Cortex

Left Dorsal precentral Gyrus

The ANOVA from this region revealed a main effect of condition [$F(2,74) = 4.324$, $p = 0.017$, *post hoc* power 0.735; **Figure 7**]. The LdPG response was greater during the Write Ink (M = 1.327, SD = 0.665) condition than during the Watch Ink (M = 0.960, SD = 0.665) condition [$t(39) = 2.973$, $p = 0.005$]. There was no difference between the Write Ink and Write No Ink (M = 1.152, SD = 0.626) conditions [$t(39) = 1.264$, $p = 0.214$]. There was no difference between the Write No Ink and Watch Ink conditions [$t(39) = 1.667$, $p = 0.104$]. The main effect of age group was not significant [$F(2,37) = 1.035$, $p = 0.365$, *post hoc* power 0.217], nor was the interaction [$F(4,74) = 1.842$, $p = 0.130$, *post hoc* power 0.534].

Left Ventral Precentral Gyrus

In this region, the two main effects were not significant [condition: $F(2,74) = 1.325$, $p = 0.272$, *post hoc* power 0.278; age

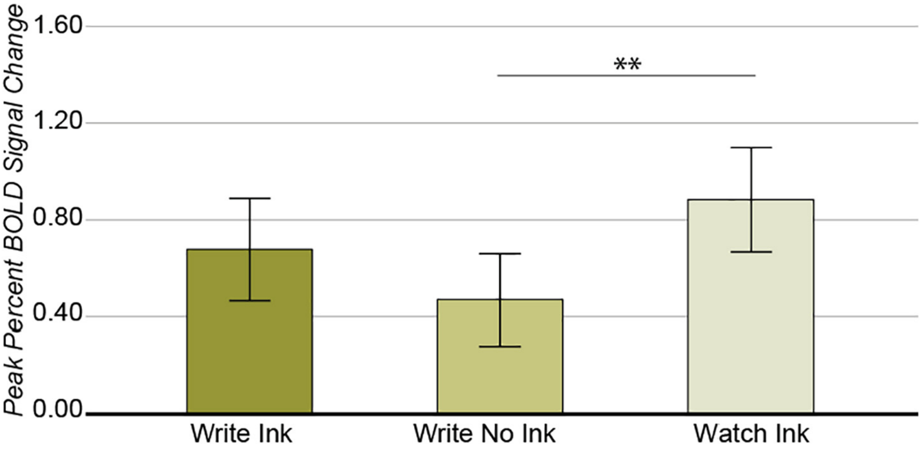

FIGURE 4 | Left posterior fusiform gyrus. Main effect of CONDITION. Error bars represent 95% confidence intervals. **$p < 0.01$.

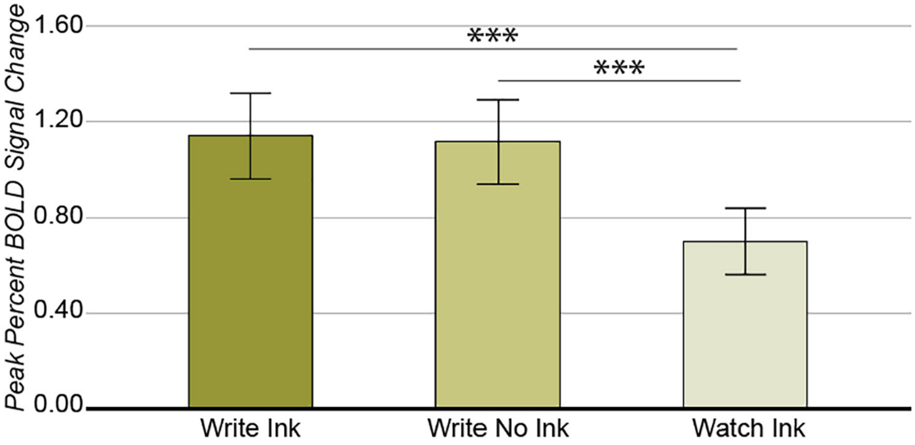

FIGURE 5 | Left anterior intraparietal sulcus. Main effect of CONDITION. Error bars represent 95% confidence intervals. ***$p < 0.001$.

group: $F(2,37) = 0.468$, $p = 0.630$, *post hoc* power 0.121]. The two-way interaction was significant [$F(4,74) = 2.638$, $p = 0.041$, *post hoc* power 0.711; **Figure 8**]. The LvPG response differed among conditions in the adults [$F(2,24) = 11.998$, $p = 0.0002$], but not in the younger children, [$F(2,24) = 1.880$, $p = 0.174$] or in the older children [$F(2,26) = 0.845$, $p = 0.441$]. In the adults, the LvPG response was greater during the Write Ink condition (M = 1.145, SD = 0.541) than during the Watch Ink condition (M = 0.643, SD = 0.499) [$t(12) = 4.633$, $p = 0.001$]. There was no difference between the Write Ink and Write No Ink (M = 1.128, SD = 0.524) conditions [$t(12) = 0.138$, $p = 0.892$]. There was no difference between the Write No Ink and Watch Ink conditions [$t(13) = 1.527$, $p = 0.151$].

Correlations With Behavior

Age

We evaluated the Pearson correlation between age and activation during the Write Ink condition using only the child data. We performed this correlation in only the LmIPS and LvPG given that these were the only ROIs that demonstrated an interaction between age and condition. We combined the two child age groups, i.e., younger and older, into one group because we did not observe any differences between these two age groups in the prior analyses. All correlations between activation and age were not significant, all *ps* > 0.05.

Literacy

We evaluated the partial correlation between a literacy composite score and activation during the Write Ink condition, controlling for age (see section "Materials and Methods: Statistical Analyses: Correlations with Behavior"). We used only the child data because we were concerned with the relationship between the neural system supporting handwriting and literacy during early reading development. We performed this analysis in the Write Ink condition only because we were concerned with the relationship between neural response during handwriting and literacy, while we had no specific hypotheses concerning relationships with the neural response in our control conditions.

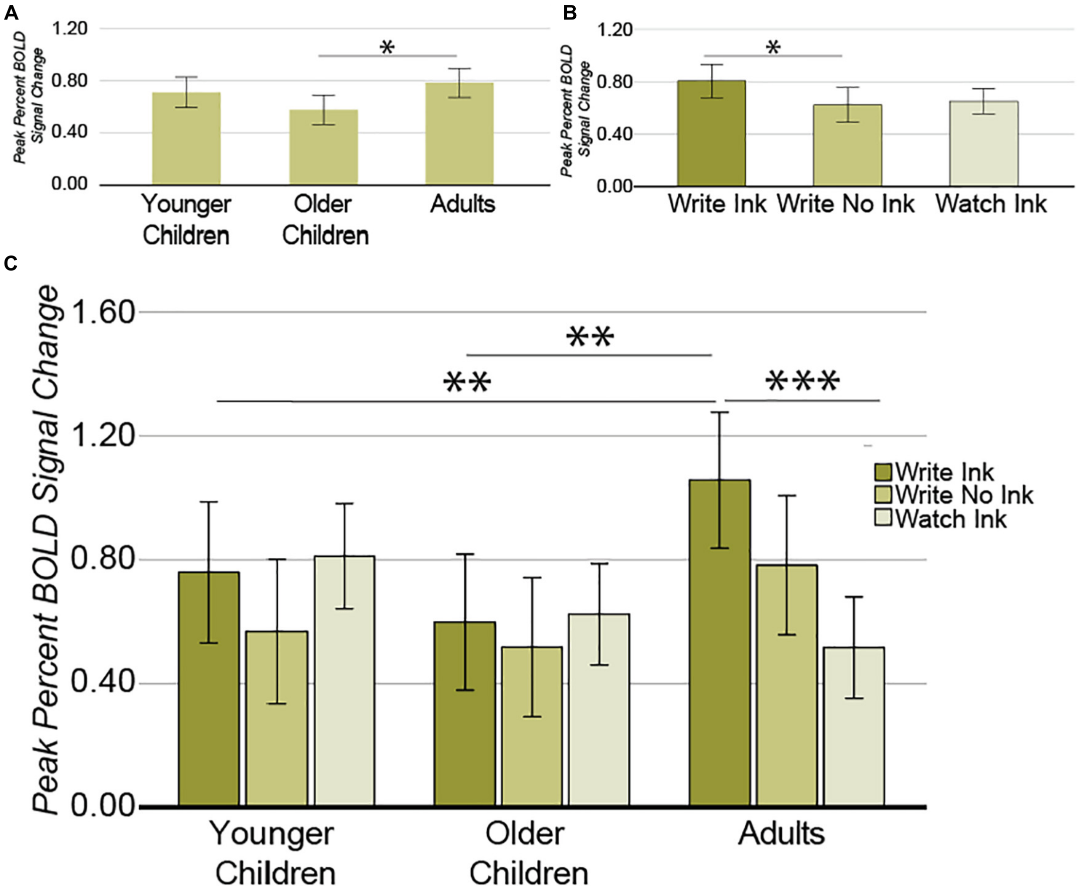

FIGURE 6 | Left middle intraparietal sulcus. **(A)** Main effect of AGE GROUP. **(B)** Main effect of CONDITION. **(C)** Interaction between AGE GROUP and CONDITION. Error bars represent 95% confidence intervals. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

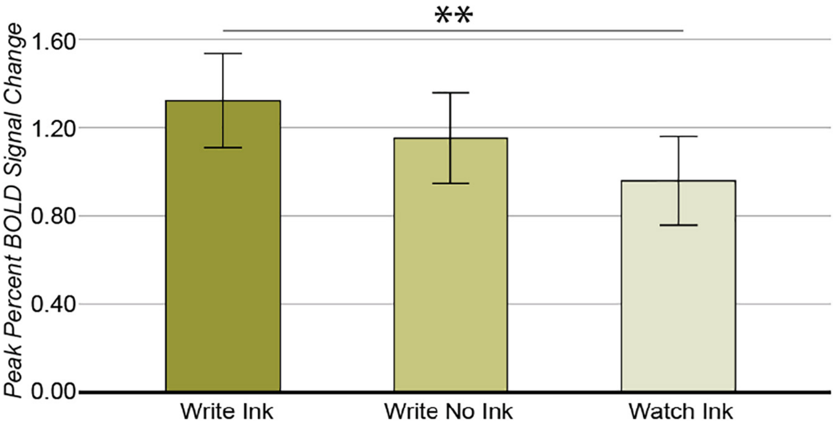

FIGURE 7 | Left dorsal precentral gyrus. Main effect of CONDITION. Error bars represent 95% confidence intervals. **$p < 0.01$.

We found a positive correlation between Literacy and LmIPS activation during Write Ink ($r = 0.447$, $n = 27$, $p = 0.022$). As literacy increased, activation in the LmIPS increased (**Figure 9**). The correlation between Literacy and LvPG activation during Write Ink was not significant ($r = 0.237$, $n = 27$, $p = 0.244$).

The literacy composite score is an average of four independent assessments related to early reading development. We performed an additional exploratory analysis in the ROIs where activation during Write Ink correlated with the composite literacy score. We correlated each individual assessment score with

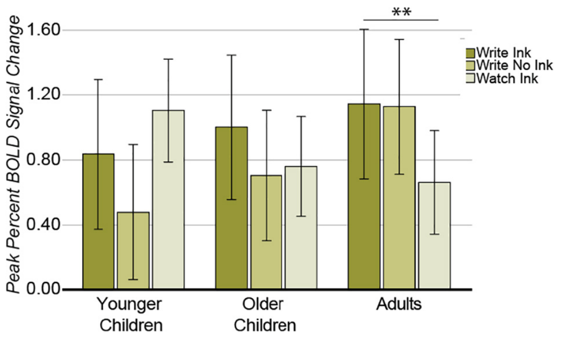

FIGURE 8 | Left ventral precentral gyrus. Interaction between AGE GROUP and CONDITION. Error bars represent 95% confidence intervals. $^{**}p < 0.01$.

activation to determine if there were certain aspects of literacy development that were related to activation in LmIPS in our child sample. We found a significant correlation between WJ-IV Achievement: Letter-Word Identification and LmIPS activation ($r = 0.515$, $n = 27$, $p = 0.007$). No other individual assessment correlated with LmIPS activation during Write Ink, all $ps > 0.05$.

DISCUSSION

Our goal with the present work was to provide information concerning the development of the neural system supporting handwriting in young children in the early stages of learning to write. We compared functional activation in 5–8-year-old children during fMRI scanning to activation in adults during handwriting and two sensorimotor control tasks. The sensorimotor control tasks allowed us to assess to what degree cortical regions associated with handwriting were related to the sensory (in this case visual) and/or motor components of handwriting. We focused our analyses on regions that have been shown to be related to the sensorimotor element of handwriting and tested whether the involvement of these regions in the sensorimotor element differed among young children and adults. Our results demonstrated that frontal motor and anterior parietal regions responded preferentially for the motor component while ventral regions responded preferentially for the visual component in both children and adults. We found a significant difference between children and adults in activation during handwriting in the left middle intraparietal sulcus (LmIPS) and left ventral precentral gyrus (LvPG), suggesting that the dorsal neural system that supports handwriting is still developing in children ages 5–8 years of age. Furthermore, we found that parietal and frontal activation correlated with a literacy composite score in our child sample, suggesting that the individual differences in parietal and frontal responses during handwriting were related to individual differences in emerging literacy skills. Our results are consistent with literature suggesting a prolonged developmental trajectory for parietal function relative to ventral-temporal function and suggest that the neural system that supports handwriting is related to early reading development.

Adult Activation During Handwriting: Consistency With Prior Work

Activation during handwriting in the adult group was consistent with prior literature that has demonstrated a gradient of functional selectivity where dorsal/anterior brain regions are related to motor processing while ventral/posterior brain regions are related to visual processing (James and Gauthier, 2006; Planton et al., 2013, 2017; Vinci-Booher et al., 2019). In the current study, frontal and anterior parietal ROI responses were greatest during motor actions (Write Ink and Write No Ink) while ventral-temporal ROI responses were greatest in the visual-only condition (Watch Ink) in both child and adult participants.

The frontal motor ROI responses were greatest in the motor conditions relative to the visual-only condition. For both the dorsal and ventral precentral gyrus ROIs (i.e., LdPG and LvPG), activation was greater during Write Ink compared to Watch Ink and was not different during Write Ink than during Write No Ink. In the LdPG, activation was greater during Write Ink than during Watch Ink with no significant difference between Write Ink and Write No Ink. The same result was observed in the LvPG in the adult group. These results suggest that activation in the frontal motor cortex, specifically in the precentral gyrus, during adult-like handwriting is related to the execution of the motor action, consistent with prior works on handwriting (Planton et al., 2013; Kadmon Harpaz et al., 2014; Longcamp et al., 2014; Yuan and Brown, 2014; Vinci-Booher et al., 2019) and the literature on frontal motor cortex more broadly (Schieber, 2001; Graziano, 2006; Meier et al., 2008).

The parietal ROI responses demonstrated an anterior-posterior gradient along the IPS with anterior regions being related to motor processing, similar to prior works (Purcell et al., 2011; Thaler and Goodale, 2011; Planton et al., 2013; Kadmon Harpaz et al., 2014; Longcamp et al., 2014; Yuan and Brown, 2014; Haar et al., 2015; Vinci-Booher et al., 2019; Vinci-Booher and James, 2020b). The anterior IPS response was greater during Write Ink and Write No Ink compared to Watch Ink and the middle IPS activation decreased linearly from Write Ink to Write No Ink to Watch Ink in the adults. The posterior IPS response, however, was not significantly different across conditions, suggesting that posterior IPS does not necessarily prefer a motor condition to a visual-only condition. This suggests that the more anterior ROI was more strongly driven by the motor component relative to the posterior ROI, similar to prior work in adults using the MRItab (Vinci-Booher and James, 2020b).

The ventral-temporal ROI responses demonstrated a preference for the visual-only condition relative to the motor conditions; their responses were greater during Watch Ink than during Write Ink and Write No Ink. This result is consistent with literature demonstrating that the ventral-temporal cortex is largely involved in perceptual processing of sensory information, particularly visual information (Mishkin et al., 1983; Goodale and Milner, 1992). However, this result is also inconsistent with this literature because we found no significant difference in ventral-temporal response between the Write Ink and Write No Ink conditions. A difference between the Write Ink and Write No Ink conditions in ventral-temporal response would

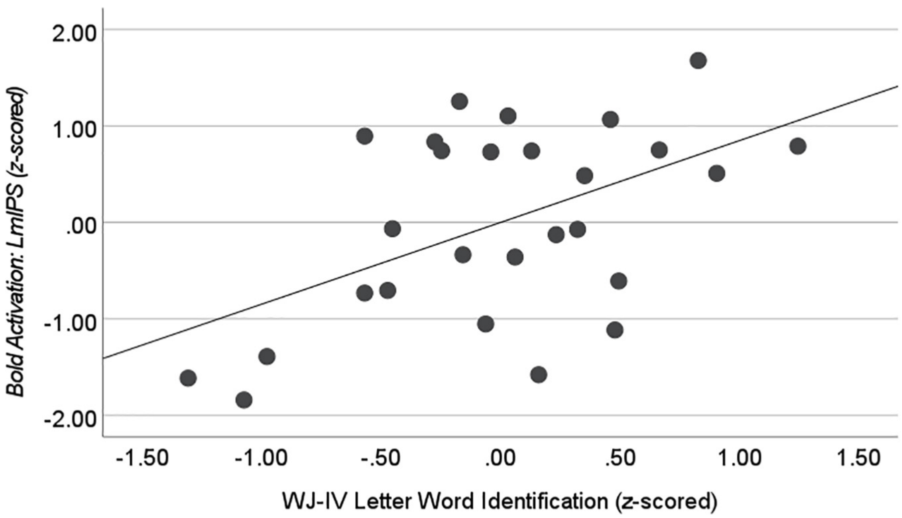

FIGURE 9 | Correlation with WJ-IV Letter Word Identification during Write Ink. Activation in the left middle intraparietal sulcus (LmIPS) correlated with performance on the WJ-IV Letter Word Identification in the child participants after controlling for age (r = 0.515, n = 27, p = 0.007).

be expected because the letter produced during handwriting in the Write Ink condition is visually available to the participant while it is not available in the Write No Ink condition. Indeed, one of our prior studies demonstrated that the ventral-temporal cortex response was sensitive to visual images of letters that occur during handwriting, reporting a greater ventral-temporal response during Write Ink than during Write No Ink (Vinci-Booher et al., 2019). This apparent inconsistency can be rectified by noting that the experimental set-up in prior works does not allow participants to see their hands during handwriting, rendering the Write No Ink condition void of any letter-related visual input (e.g., Tam et al., 2011). The experimental set-up in the current study, however, allowed participants to see their hands during handwriting; in other words, participants watched their hand make the motions necessary to produce a written letter during the Write No Ink condition in the current study. Thus, our findings, in the context of the prior work discussed, suggest that activation in the ventral-temporal cortex during handwriting is sensitive to both visual input of the letter-form and also the visual input of one's hand creating that form.

Children Display Adult-Like Activation in Ventral-Temporal Cortex but Not Parietal or Frontal Cortex During Handwriting

Our results demonstrated that the magnitude of response in the ventral-temporal cortex was at an adult-like level by 4.5 years of age during handwriting; however, it is important to note that the visual processes being performed in the ventral-temporal cortex likely continue to change past 4.5 years of age. For example, prior work using this same child participant cohort demonstrated that the ventral-temporal cortex response was greater when children saw their own handwritten letters than when they saw typed letters and that the reverse was true by 6.5 years of age (Vinci-Booher and James, 2020a). Additionally, we note that neural processing for visual perception of common objects, such as faces and places, in the ventral-temporal cortex develops throughout childhood and adolescence (Golarai et al., 2007; Scherf et al., 2007) as does processing for written words (Centanni et al., 2017) but see Dehaene-Lambertz et al. (2018). In the context of prior works, our results suggest that ventral-temporal cortex may already be responding during handwriting, as it does in adults, but likely still undergoes changes in sensitivity to visual stimuli at later ages.

Our results clearly demonstrated that handwriting-related function in the parietal cortex was still developing in our child sample. We found a significant difference in activation magnitude among our age groups in the left middle intraparietal sulcus (LmIPS). Activation in the LmIPS was dependent on an interaction between age group and condition such that its response was greatest during Write Ink in the adult group. In adults, the LmIPS response was greater during Write Ink when compared to Write No Ink and Watch Ink while there were no significant differences among these conditions in either child group.

Prior work in adult participants has demonstrated that activation along the left intraparietal sulcus is more closely associated with handwriting than drawing, indicating that one of the crucial differences between the neural system that supports these activities is parietal function (Yuan and Brown, 2014, 2015; Ose Askvik et al., 2020). Perhaps the most notable differences between handwriting and drawing are, first, that handwriting is more strongly associated with language than drawing and, second, that handwriting becomes an over-practiced skill whereas drawing typically remains under-practiced. It is unlikely that the condition and age group interaction that we observed in LmIPS activation was related to the association of handwriting with language because our conditions specifically manipulated the sensorimotor aspects of handwriting, leaving the language association in each condition. Therefore, the condition differences observed in LmIPS activity in adults were not likely due to an association with language in the Write Ink condition that was not present in the Write No Ink and Watch Ink conditions. We interpret the greater activation in LmIPS during Write Ink in adults compared to children to be associated with the performance of an over-practiced task, a task that would not be over-practiced in 5–8-year-old children. Although children begin to learn the difference between handwriting and drawing as young as 3 years old based on behavioral measures (Treiman and Yin, 2011; Otake et al., 2017), their productions are far from being over-practiced and our results suggest that during handwriting children are likely relying on a neural system similar to the neural system used for drawing in adults.

The neural response during handwriting in the left frontal motor cortex also exhibited developmental differences, but only for the ventral precentral gyrus (LvPG) and not the dorsal precentral gyrus (LdPG) ROI. In the LvPG, activation in adults was greater during Write Ink than during Watch Ink, but there was no difference between these two conditions in either child group. The response in adults suggests that the LvPG is associated with the execution of the motor action, similar to the LdPG. However, unlike the LdPG, the LvPG is not yet adult-like in our child sample, suggesting that ventral portions of the precentral gyrus undergo a more prolonged developmental trajectory than dorsal portions of the precentral gyrus.

Activation in LpIPS and LdPG Correlates With Literacy in Children

Our results demonstrated a significant correlation between a literacy composite score and activation in the left posterior intraparietal sulcus (LpIPS) and between the same literacy composite score and activation in the left dorsal precentral gyrus (LdPG). The composite literacy score was created by averaging across several literacy-related subtests of the WJ-IV, including subtests that assessed reading real and non-real words as well as spelling real and non-real words. When we tested for correlations between the subtests that were used in the composite score, we found that the LpIPS and LdPG correlations were driven by the children's scores on the Letter-Word Identification subtask. The Letter-Word Identification was the subtest that assessed reading real words and, for younger children, often includes only letter identification items. Our results, therefore, suggest that activation in the LpIPS and LdPG during handwriting is related to letter recognition and word reading ability.

A substantial line of research suggests that learning to read is accompanied by changes in ventral-temporal function during passive word reading tasks (Centanni et al., 2018; Chyl et al., 2018; Dehaene-Lambertz et al., 2018; Lerma-Usabiaga et al., 2018; Nordt et al., 2018; Kubota et al., 2019; Brem et al., 2020; Liebig et al., 2021). We, therefore, had expected to find a correlation between literacy and ventral-temporal activation during handwriting; however, we instead found a correlation between literacy and dorsal motor activation during handwriting. This suggests that activation in ventral-temporal and dorsal motor cortex is different during passive reading tasks than it is during active production tasks, even when both tasks contain letters and words.

Studies that have investigated dorsal motor activity during handwriting suggest that activation in the dorsal motor cortex during handwriting may be related to letter recognition, similar to our results. One set of studies investigated activation in dorsal motor regions, specifically the LdPG and LaIPS, in adults as they wrote individual letters of the alphabet (i.e., a, s) in different letter-forms (i.e., a A) (Rapp and Dufor, 2011; Dufor and Rapp, 2013). Results demonstrated that the response in these dorsal motor regions during handwriting was related to the identity of the letter (i.e., a vs. s) and not to the different letter-forms (i.e., a vs. A). This result suggests that activation in the dorsal motor cortex during handwriting may be related to letter recognition and, remarkably, may not be related to the specification of the hand movements required to produce a letter-form. Such a result fits nicely with a large body of work that has interpreted activation in dorsal motor regions during passive letter perception as signifying the involvement of the motor system in letter recognition (Longcamp et al., 2003, 2005, 2006, 2008; James and Gauthier, 2006; James and Atwood, 2009; James, 2010, 2017; James and Engelhardt, 2012; Vinci-Booher and James, 2020a).

CONCLUSION

The current study is the first study to investigate the neural correlates of handwriting in typically developing children under the age of 8 years old. Prior work has suggested that the adult neural system supporting handwriting is already in place by 8 years of age. Here, we demonstrated that parietal and frontal motor regions are not yet adult-like by 5 years of age, suggesting that the neural system supporting handwriting changes during the early elementary school years. Further, we found a positive correlation between dorsal neural activity and early literacy skills. Our results are consistent with the broad developmental trend whereby function in ventral-temporal cortex resembles adult function earlier than function in the parietal cortex when examined past the age of 2 years old.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Indiana University Institutional Review Board. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin. Children 7 years and older provided written assent.

AUTHOR CONTRIBUTIONS

SV-B contributed to all aspects of the manuscript, including the original conception of the study, the design, data collection, analyses, writing the original draft of the manuscript, and revisions. KJ contributed to conceptual development of the work, the design, data collection, and the writing of the manuscript.

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Conflict of Interest: This report makes use of a patented MRI-compatible device (US Patent No. 62/370, 372). The patent is owned by the Trustees of Indiana University (Inventors: Sturgeon, Shroyer, SV-B, and KJ).

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Predicting Reading From Behavioral and Neural Measures – A Longitudinal Event-Related Potential Study

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Fluent reading is characterized by fast and effortless decoding of visual and phonological information. Here we used event-related potentials (ERPs) and neuropsychological testing to probe the neurocognitive basis of reading in a sample of children with a wide range of reading skills. We report data of 51 children who were measured at two time points, i.e., at the end of first grade (mean age 7.6 years) and at the end of fourth grade (mean age 10.5 years). The aim of this study was to clarify whether next to behavioral measures also basic unimodal and bimodal neural measures help explaining the variance in the later reading outcome. Specifically, we addressed the question of whether next to the so far investigated unimodal measures of N1 print tuning and mismatch negativity (MMN), a bimodal measure of audiovisual integration (AV) contributes and possibly enhances prediction of the later reading outcome. We found that the largest variance in reading was explained by the behavioral measures of rapid automatized naming (RAN), block design and vocabulary (46%). Furthermore, we demonstrated that both unimodal measures of N1 print tuning (16%) and filtered MMN (7%) predicted reading, suggesting that N1 print tuning at the early stage of reading acquisition is a particularly good predictor of the later reading outcome. Beyond the behavioral measures, the two unimodal neural measures explained 7.2% additional variance in reading, indicating that basic neural measures can improve prediction of the later reading outcome over behavioral measures alone. In this study, the AV congruency effect did not significantly predict reading. It is therefore possible that audiovisual congruency effects reflect higher levels of multisensory integration that may be less important for reading acquisition in the first year of learning to read, and that they may potentially gain on relevance later on.

Keywords: N1 print tuning, MMN, audio-visual integration, EEG, ERP, reading, development, longitudinal

INTRODUCTION

Developmental dyslexia is usually identified after a child has started to learn to read at school. This delayed identification comes with a delay of supportive measures and an increase of the reading deficits compared to typically developing children. Given that dyslexia is thought to arise from preexisting neurocognitive deficits, there is great interest in finding longitudinal predictors of reading development that may be used for the early identification of dyslexia. In addition to behavioral predictors, such as phonological deficits, cognitive neuroscience research also identified several unimodal neural measures that may improve longitudinal prediction of reading development compared to behavioral measures alone (e.g., Hoeft et al., 2007; Maurer et al., 2009). Given the multimodal nature of reading, and particularly the importance of print-to-sound mapping (Ehri and Wilce, 1985), the question arises whether neural measures of audiovisual integration can further improve the prediction of reading development. In addition to the potential practical significance of reading predictors, they are also theoretically relevant, as they point to processes that are particularly important for reading acquisition at certain stages of reading development and may further be used to guide age-specific interventions.

Several longitudinal studies have examined early behavioral predictors of later reading abilities. To date, the best behavioral predictors of reading outcome in alphabetic languages are recognized to be rapid automatized naming (RAN; i.e., the ability to quickly and accurately name a series of items, e.g., pictures or familiar objects), phonological awareness (the ability to identify and manipulate the sound units of a word), letter knowledge and vocabulary (Juel, 1986; Wolf, 1986; Wimmer et al., 1991; Bowey, 1995; Wagner et al., 1997; de Jong and van der Leij, 1999; Catts et al., 2001; Pennington and Lefly, 2001; Schatschneider et al., 2004; Lepola et al., 2005; Puolakanaho et al., 2007; Georgiou et al., 2008; Torppa et al., 2012; Brem et al., 2013). The relative importance of these cognitive skills may change depending on the orthographic depth of a particular writing system, with rapid naming being a more important predictor than phonological awareness in more transparent languages like Finnish, Italian or German (Moll et al., 2014; Zoccolotti et al., 2014; Schmalz et al., 2015). Based on such findings, behavioral tests have been developed to assess the risk for developing dyslexia shortly before school entry (e.g., Jansen et al., 2002). However, despite encouraging results, considerable variance in reading development remained unexplained, and the question arose whether prediction could be improved by measuring neurocognitive processes that underly phonological and orthographic processing (Vandermosten et al., 2015) more directly.

Several neuroimaging studies have provided evidence that concurrent reading skills or future reading development can be predicted based on either spatially (e.g., Hoeft et al., 2007, 2011; Raschle et al., 2011, 2012; Karipidis et al., 2018) or temporally sensitive (e.g., Maurer et al., 2009) neural measures. While both approaches are theoretically relevant, temporally sensitive EEG measures have a practical advantage due to their easier and less expensive application, and therefore the focus of the following literature review is on EEG studies. In EEG studies, two neural measures have been mainly discussed as possible early predictors of later reading outcome. One of them being a visual, negative component of the event-related potential (ERP), known as N170, N1 or N1 print tuning (Bach et al., 2013; Brem et al., 2013), and the other one being a negative component of the auditory ERP, namely mismatch negativity (MMN, Maurer et al., 2009). However, to our knowledge the predictive values of these two measures have not been tested in the same study with the same children.

The N1 component of the visual ERP peaks at around 150–250 ms after stimulus presentation and is characterized by posterior negativity and fronto-central positivity, thought to be generated by sources in bilateral occipito-temporal regions (e.g., Bentin et al., 1999; Tarkiainen et al., 1999; Brem et al., 2005, 2009; Parviainen et al., 2006; Maurer et al., 2007). Although elicited by visual stimuli in general, the N1 is enhanced for expertise-related stimuli compared to low-level visual control stimuli (Rossion et al., 2003). In the area of reading, words that are presented visually elicit a larger N1 than symbol strings (Bentin et al., 1999; Maurer et al., 2005a,b; Brem et al., 2006) or false-font strings (Brem et al., 2010; Hasko et al., 2013; Eberhard-Moscicka et al., 2014, 2016), an effect that has been called N1 print tuning, and that is thought to reflect visual expertise for letter strings (Maurer et al., 2005b, 2006). This neural specialization for print is not only present in adult expert readers (Maurer et al., 2005a; Brem et al., 2006; Mahé et al., 2012), but also in beginning readers (Eberhard-Moscicka et al., 2014; Zhao et al., 2014) and most strikingly already in illiterate kindergarten children after only a short grapheme–phoneme training (Brem et al., 2010). Print tuning has been shown to be reduced in children with dyslexia (Maurer et al., 2007) and to correlate with concurrent reading skills (Eberhard-Moscicka et al., 2014). Next to this visual expertise account, there is another account of N1 print tuning that is believed to reflect the print-to-sound mapping (Brem et al., 2013). This account has previously been used to explain the often reported left-lateralization of the N1 print tuning (Maurer and McCandliss, 2007). Importantly, previous studies pointed toward the predictive value of the N1 print tuning that can serve as an early predictor of the later reading outcome (Brem et al., 2010; Bach et al., 2013).

The MMN is a negative component in a difference ERP between deviant and standard auditory stimuli that peaks at around 100–250 ms at fronto-central electrodes. The fronto-central negativity is accompanied by a positivity at temporal/mastoid electrodes reflecting auditory sources and possibly an involvement of frontal cortices (for a review, see Alho, 1995). The MMN is evoked automatically in an oddball condition where infrequent deviant stimuli are embedded among frequently occurring standard stimuli and is thought to measure sensory memory (Näätänen and Alho, 1997; Näätänen et al., 2005). It is independent of attention, which makes it a successful tool to investigate phoneme specialization in young children (for a review, see e.g., Näätänen et al., 2007) who are easily distracted or sometimes difficult to motivate to participate in experimental tasks. To date, MMN has been widely used in research with preschoolers (e.g., Maurer et al., 2003; Lee et al., 2012;

Lovio et al., 2012) and school-age children (e.g., Kraus et al., 1999; Cheour et al., 2000; Maurer et al., 2009; Datta et al., 2010; Jost et al., 2015). The MMN has been shown to be reduced in dyslexia for speech and non-speech stimuli (e.g., see Gu and Bi, 2020 for a recent meta-analysis). In preschool children, the amplitude and the degree of the left-lateralization of the late MMN improved the prediction of reading ability over behavioral measures, but lateralization was the only measure capable of predicting long-term reading outcomes in fifth grade (Maurer et al., 2009). Prospective prediction of reading or reading-related skills was also obtained from measures of auditory processing in infants (Molfese, 2000; Lyytinen et al., 2004; Guttorm et al., 2010).

While N1 and MMN measures have been shown to be able to prospectively predict reading development, they are unimodal measures that do not reflect an essential aspect of learning to read, which is the linking of visual and auditory information (Blomert, 2011). It is believed that this bimodal grapheme–phoneme integration is an emergent property of learning to read which may develop inadequately in dyslexic children (Blau et al., 2010) and adults (Blau et al., 2009), presumably due to lacking specialization at the neuroanatomical level. Brain regions that are believed to play a role in the binding of grapheme–phoneme pairs have been located to temporal and occipital brain areas (Raij et al., 2000; van Atteveldt et al., 2004). One way of investigating the audiovisual (AV) integration is by comparing the neural response of incongruent and congruent audiovisual stimuli, the so-called AV congruency effect. This AV congruency effect has been demonstrated at the more basic level of letter-speech sound pairs (van Atteveldt et al., 2007; Doehrmann and Naumer, 2008; Karipidis et al., 2017) but also at the level of word-speech sound pairs (Jost et al., 2013). While theoretical arguments point to the potential use of AV integration measures for predicting reading, only few studies have been conducted so far. In one study, an ERP congruency effect after an artificial letter training in kindergarten improved prediction of poor reading in a small sample of children who were followed up half a year after the onset of reading training at school (Karipidis et al., 2018). In our own study, we found no clear association between audiovisual integration and concurrent reading fluency in first grade children (Jost et al., 2013), thus leaving it an open question whether such an association would emerge only later in the course of reading acquisition. Furthermore, as previous studies indicated the predictive power of basic unimodal visual (i.e., N1 print tuning; Bach et al., 2013; Brem et al., 2013) and auditory (i.e., MMN; Maurer et al., 2009) neural measures, the question arises as to the relative contribution of unimodal visual and auditory measures and a bimodal measure of audiovisual integration regarding their prediction of the later reading outcome.

Thus, the current study made use of behavioral and neural measures from children tested in first grade (previously reported in Jost et al., 2013, 2015; Eberhard-Moscicka et al., 2014, 2016) to predict reading skills of the same children who were followed up in fourth grade as part of the current study. Unlike some of the previously used EEG indices (Eberhard-Moscicka et al., 2014, 2016), this study employed the whole-scalp topographic approach (as also reported in Jost et al., 2013, 2015) to account for different scalp-distribution patterns across all the three neural measures tested. Moreover, to obtain the typical MMN topography (i.e., fronto-central negativity and lateral/mastoid positivity, e.g., Maurer et al., 2003; Kujala et al., 2007; Näätänen et al., 2007; Zevin et al., 2010) additional filter settings (cf. Jost et al., 2015) were applied to the MMN data. The goals of the study were to investigate: How well do behavioral measures collected at the end of first grade predict the reading outcome at the end of fourth grade (aim 1); How much of the variance in reading at the end of fourth grade can be attributed to all the three neural measures from first grade (aim 2); Whether neural measures add to the prediction over behavioral measures (aim 3).

MATERIALS AND METHODS

Participants

We report data of 51 native (Swiss-)German-speaking children (21 girls and 30 boys; 4 left-handed, 5 dyslexics, i.e., below 10th percentile). Children were tested longitudinally; the first assessment took place after 1 year of formal reading instruction (i.e., at the end of first grade, mean age 7.6 years, range 6.7–8.5 years), whereas the second assessment took place at the end of fourth grade (mean age 10.5 years, range 9.6–11.2 years). From an original group of 70 children, seven dropped out of the study, one transferred to another school, two needed to repeat a grade, six were excluded due to a low number of accepted trials in either the N1 task (four children were below 26 trials) or in the MMN task (two children were below 70 trials), and three participants were above three standard deviations in the Global Field Power (GFP) of the time window of interest in either of the three EEG tasks. All subjects had normal or corrected-to-normal vision, and every child had an estimated non-verbal IQ equal or above 80 [i.e., not more than 1.333 *SD* below the normative mean in HAWIK-IV (*M* = 100, *SD* = 15), subtest: block design, Petermann and Petermann (2010), corresponding to the English version of the Wechsler Intelligence Scale for Children]. The study protocol was approved by the local ethics committee. Consent was obtained orally from children and in written form from their parents. Moreover, children's parents filled out a background questionnaire screening for a history of neurological diseases and psychiatric disorders.

Procedure

In first grade, all the children participated in a behavioral and an EEG session (previously reported in Jost et al., 2013, 2015; Eberhard-Moscicka et al., 2014, 2016), while in fourth grade they participated in a behavioral session only. At both time points (i.e., at the end of first and fourth grades) the behavioral session lasted about 1.5 h and took place either at schools (in a separate room provided by schools), at the Department of Psychology at the University of Zurich or at participants' homes. The EEG session was administrated using one of two identical portable EEG systems (Electrical Geodesics, Inc., EGI). The recording was approximately 3.5 h long and was administered either in a separate room provided by schools or in the EEG laboratory at the Department of Psychology at the University of Zurich. Before using a room at the schools, a standard quality check was applied

TABLE 1 | Behavioral and neural measures used in the regression approach.

	M (SD)	**Correlations**			
Measures		**Reading fluency in fourth grade**	**N1 print tuning in first grade (GFP)**	**Filtered MMN in first grade (GFP)**	**AV congruency in first grade (GFP)**
Reading fluency in fourth grade					
SLRT I word-reading (correct per 1 min)	107.7(29.9)	1.00	0.38^{2}	−0.22	−0.21
SLRT-II word-reading (correct per 1 min)	75.6(19.4)				
SLRT I text-reading (correct per 1 min)	126.9(30.4)				
SLS sentence-reading (correct per 3 min)	50.0(10.7)				
Reading fluency in first grade					
SLRT I word-reading (correct per 1 min)	35.5(20.9)	0.56^{1*}	0.34^{3}	−0.14	−0.11
SLRT-II word-reading (correct per 1 min)	30.3(15.6)				
SLRT I text-reading (correct per 1 min)	47.9(33.2)				
SLS sentence-reading (correct per 3 min)	18.8(9.4)				
RAN in first grade					
RAN one syllable animals naming (time in sec)	69.5(18.2)	-0.55^{2}	−0.21	0.10	0.08
RAN three syllable animals naming (time in sec)	90.2(26.8)				
RAN lower case letter naming (time in sec)	39.7(9.8)				
RAN digit naming (time in sec)	40.7(12.1)				
Phonological processing in first grade					
BAKO phoneme deletion (correct items/max: 7)	4.5(1.7)	0.37^{2}	−0.06	−0.23	−0.08
BAKO pseudoword segmentation (correct items/max: 8)	4.8(1.5)				
Vocabulary in first grade					
HAWK-IV, vocabulary (raw score)	26.7(6.1)	0.42^{2}	0.09	−0.00	0.02
Block design in first grade					
HAWK-IV, block design (raw score)	33.5(11.0)	0.05	0.06	−0.16	−0.08
Auditory memory span in first grade					
HAWIK-IV, digit span backward (raw score)	5.8(1.2)	0.30^{3}	0.18	−0.19	−0.10
HAWIK-IV, digit span forward (raw score)	6.5(1.0)				

$^{1}p < 0.001$; $^{2}p < 0.01$; $^{3}p < 0.05$; asterisk depicts significant $^{*}p < 0.005$ Bonferroni corrected value.
Standard score: vocabulary 11.16 (2.44), block design 12.12 (3.00), digit span (backward and forward) 10.33 (2.07).

to ensure the absence of 50 Hz noise. As a compensation for the participation in the study, every child received a written report about his/her reading skills and a book voucher of 40 CHF at the first assessment at the end of first grade and of 30 CHF at the second assessment at the end of fourth grade.

Behavioral Session

During the behavioral assessment, the child was seated opposite the experimenter and performed a set of cognitive tasks. All the tasks were rehearsed according to test guidelines to make sure that every child understood the instructions. The measures collected during the behavioral session assessed different aspects of German language processing. In first and fourth grades, measures of sentence- and word-reading fluency (Mayringer and Wimmer, 2005; Landerl et al., 2006; Moll and Landerl, 2010) were collected. Next to the reading fluency measures also RAN (Landerl, 2001; Landerl et al., 2013), phonological awareness (Stock et al., 2003), vocabulary, auditory memory span and block design as a measure of non-verbal IQ (Petermann and Petermann, 2010), as well as spelling (Moll and Landerl, 2010) were assessed in first grade (see **Table 1** for a detailed list of subtests and **Supplementary Material T1** for bivariate correlations between behavioral measures in first grade). The spelling task proved to be too difficult for the first graders, hence could not be considered in further analyses.

The measure of reading fluency in fourth grade was based on average scores of four z-transformed tests of word, text, and sentence reading (see also **Table 1**). Scores for correct words per minute were computed for the two subtests of the Lese- und Rechtschreibtest (Landerl et al., 2006) and one subtest of the Salzburger Lesetest II (Moll and Landerl, 2010). The score for correct sentences per minute was computed based on the Salzburger Lesescreening 1-4 (Mayringer and Wimmer, 2005).

EEG Session

During the EEG recording, children were seated 80 cm away from the computer screen. Every child performed two unimodal (i.e., N1 and MMN) and one bimodal (i.e., AV) EEG tasks (described below) that were presented in a pseudo-randomized order. To avoid fatigue, children were allowed to take breaks between experiments and compliance during the experiments was monitored by means of a digital camera. Before every experiment began, children were instructed on task demands. Additionally, as opposed to the passive MMN task, for the active N1 and AV tasks children performed a practice experimental run that lasted about 1 min.

EEG Tasks

Visual one-back N1 task

The visual N1 task (see also Eberhard-Moscicka et al., 2014, 2016) assessing specialization for print took about 20 min. In this task, children were presented with familiar German words (high frequency of occurrence in the textbooks of children aged 6–8, M = 161.86/Mio, ChildLex Lexical Database, Schroeder et al., 2015), unfamiliar false-font strings matched to the letters appearing in German words (false-font characters were designed for the purpose of this study where each alphabetical letter had its unique false-font correspondent), English words and pseudowords and were asked to press a mouse button for immediate repetitions (**Figure 1A**). English word and pseudoword stimuli are not part of this study, hence will not be described in detail here (for a detailed description we refer the reader to Eberhard-Moscicka et al., 2016). Due to the limited number of English words that we expected children to know at the follow-up session (Eberhard-Moscicka et al., 2016), we limited the number of items per condition to 14. The 14 stimuli per condition were repeated six times (84 stimuli per condition) and presented in six blocks (the order of conditions was counterbalanced). In each condition, 12 immediate repetitions serving as targets were presented. To be consistent with previous studies (e.g., Maurer et al., 2005a,b, 2006, 2007), the stimuli were presented in a block design and the block order was counterbalanced across subjects. Stimuli were presented in black (Arial, bold, font size 28, uppercase letters) and appeared in the middle of a white rectangular box (85 mm × 47 mm) in the center of a gray background. Each stimulus was presented for 500 ms and was followed by a mean inter-stimulus interval of 1500 ms (jittered between 1250 and 1750 ms). The stimuli were matched for string length and contained 3.9 letters/false-font characters on average (range: 3–5; average length and height: 31.9 mm × 7 mm). In addition, German words, pseudowords and English words were matched for number of letters, frequency of letters and number of syllables. In this paper, we focus on the N1 print tuning effect in the native German language, i.e., the difference between German words and false-font strings, thus only data of these experimental stimuli will be analyzed and discussed here.

Oddball auditory mismatch negativity task

The auditory MMN task (see also Jost et al., 2015) assessing phoneme specialization took approximately 15 min. In this passive task, children were asked to avoid motion and watch a silent cartoon while in the background they were presented with repetitive standard and rare deviant sound stimuli. The phonemes presented were one standard “da” and two deviants “ta” (a common phoneme in the native German language) and “tha” (a common phoneme in the non-native English language, not part of this study, hence not discussed here, for details we refer the reader to Jost et al., 2015). The natural speech stimuli were matched for vowel onset and duration, as well as for maximal intensity (Praat software, Boersma, 2001) and were presented in a traditional oddball paradigm where the deviant stimuli occurred 9.4% of the time. The stimuli were presented binaurally through speakers placed in front of the subject and next to the laptop playing a silent cartoon. A total of 1600 standard (“da”) and 300 deviant (150 deviant “ta” and 150 deviant “tha”) stimuli were presented for 170 ms and followed by a 280 ms inter-stimulus interval (**Figure 1B**). Stimulus order was pseudo-randomized so that at least two standards were played between two deviants. Here, we focus on the MMN in the native German language, that is, the difference between deviant “ta” and standard “da,” hence only data of these experimental stimuli will be analyzed and discussed.

Audiovisual detection task

The audiovisual (AV) detection task (see also Jost et al., 2013) assessing the integration of visual and spoken words lasted for about 24 min. In this task children were asked to respond to a rare (9%) target word “PINK” by pressing a response pad button. The stimuli presented were 10 familiar German words (high frequency of occurrence in the textbooks of children aged 6–8, M = 95.37/Mio, ChildLex Lexical Database, Schroeder et al., 2015), 10 unfamiliar English words (pronunciation according to German grapheme–phoneme correspondence rules and phonetic inventory) and 10 unfamiliar English words (pronunciation not according to German grapheme–phoneme correspondence rules or phonetic inventory). Similarly to the visual one-back N1 task, the number of unique stimuli was limited to 10 per word list due to the limited sample of English words that the children were expected to know at the follow-up session and due to the German word stimuli and English word stimuli matching procedure. English words are not part of this study, hence will not be discussed in more detail (for details we refer the reader to Jost et al., 2013). Stimuli were presented either in the auditory (A), visual (V) or audiovisual (AV) mode (**Figure 1C**). The bimodal stimuli were either matching (AVM) or non-matching (AVN). As there was only one target word, the bimodal targets were always matching. Same as for the visual one-back N1 task, the visual stimuli were presented in black (Arial, bold, font size 28, uppercase letters) and appeared in the middle of a white rectangular box (85 mm × 47 mm) in the center of a gray background. The auditory stimuli, spoken by a German-English bilingual male speaker, were scaled to the same length (Praat software, Boersma, 2001). As such, visual as well as auditory stimuli were presented for 600 ms and were followed by a mean inter-stimulus interval of 700 ms. To avoid fatigue, the experiment was divided into two parts (each about 12 min) and children were allowed to take a short break after 6 min of the task. 80 trials were presented for each of the 12 stimulus types (4 modalities × 3 word types). Every word was presented 24 times in the visual (8 unimodal V, 8 bimodal matching, 8 bimodal non-matching) and 24 times in the auditory modality (8 unimodal A, 8 bimodal matching, 8 bimodal non-matching). Given the overlap in the audiovisual

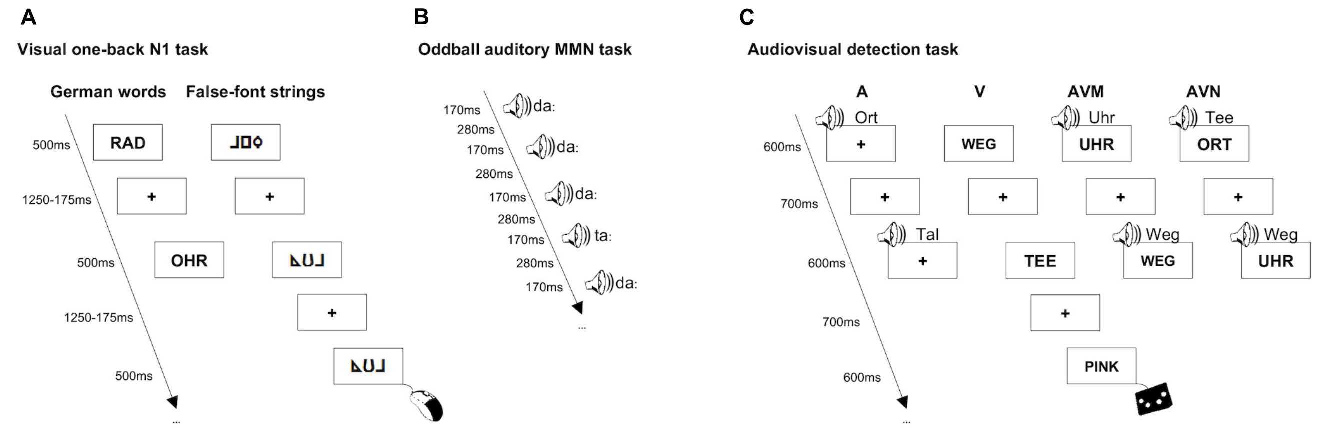

FIGURE 1 | First grade children performed two unimodal and one bimodal EEG tasks that were presented in a pseudo-randomized order. In the visual one-back N1 task they were viewing German words and false-font strings and were instructed to press a mouse button for immediate repetitions **(A)**. In the oddball auditory MMN task they were watching a silent cartoon while in the background they were presented with repetitive standard “da” and rare deviant “ta” sound stimuli **(B)**. In the audiovisual detection task German words were presented either in the auditory, visual, audiovisual matching or audiovisual non-matching mode and children were asked to press the response pad button whenever they saw or heard the target word “PINK” **(C)**.

matching condition, there were 40 trials where the same word appeared either in the visual or auditory modality. As such, a total of 960 word stimuli and 96 target stimuli were presented in a block design (cf. Kronschnabel et al., 2013; Karipidis et al., 2017; block order was counterbalanced across subjects) in either of the four different stimulus conditions (i.e., A, V, AVM, and AVN). The stimuli were matched for string length and contained 4.4. letters on average (range: 3–7; average length and height: 35.9 mm × 7 mm). In this paper, we focus on the AV congruency effect in the native German language, i.e., the difference between the AVN and AVM German word stimuli, thus only data of these experimental stimuli will be analyzed and discussed here.

EEG Recording and Processing

Continuous 128-channel EEG (HydroCel GSN, EGI NA 300 amplifier) was recorded using one of the two identical portable EGI systems. EEG was recorded against the Cz reference, at a sampling rate of 250 Hz, with high- (0.1 Hz) and low-pass (100 Hz) filter settings. As modern high-input impedance amplifiers and their accurate digital filters for power noise provide excellent EEG signal collection even at higher electrode impedances (Ferree et al., 2001), the electrode impedance was kept below 50 kΩ (cf. Maurer et al., 2005a; Franklin et al., 2007; Rihs et al., 2007; Hämäläinen et al., 2015; Karipidis et al., 2017). The raw data of the two unimodal EEG experiments (i.e., N1 and MMN tasks) was preprocessed using BESA software (including eye blink correction, MEGIS Software, Gräfelfing, Germany, for details see also Eberhard-Moscicka et al., 2014; Jost et al., 2015), while the raw data of the bimodal AV task was preprocessed with Vision Analyzer software (including eye blink correction, Brain Products GmbH, for details see also Jost et al., 2013). Apart from filter settings (see below), the remaining preprocessing steps were identical for all the three EEG experiments, i.e., after channels with extensive artifacts were spline interpolated, the continuous EEG was corrected for eye blinks and trials with artifacts exceeding the max-min difference of 180 μV in any channel were automatically excluded before averaging. For the N1 and AV tasks, the corrected files were digitally low- (30 Hz) and high-pass filtered (0.3 Hz). To obtain the typical MMN topography (i.e., fronto-central negativity and lateral/mastoid positivity, e.g., Maurer et al., 2003; Kujala et al., 2007; Näätänen et al., 2007; Zevin et al., 2010) the EEG-data of the MMN task were digitally low-pass filtered with 30 Hz and high-pass filtered with 3 Hz (hereafter referred to as filtered MMN), as described in Jost et al. (2015). The data was further segmented (−150 ms prior and 850 ms following the stimulus onset) and transformed to the average reference (Lehmann and Skrandies, 1980). The recording reference was used as an additional electrode for further data processing. Including and following the average reference step, the ERPs of all the three experimental tasks were further pre-processed in Vision Analyzer Software. Furthermore, the ERPs were corrected for the amplifier delay of 8 ms (induced by the anti-alias filters of EGI NA300 amplifiers with the current sampling rate; for details see Update to Advisory Notice, 26 November 2014, Electrical Geodesics Inc.; cf. Pegado et al., 2014) and a constant stimulus release delay of 20 ms for the N1 and AV tasks and 24 ms for the MMN task. In the final pre-processing step, the ERPs of all conditions of interest (i.e., German words, and false-font strings for the N1 task, standard “da” and deviant “ta” for the MMN task, as well as AVN German words and AVM German words for the AV task) were averaged separately for each experimental task, after target stimuli of the N1 and AV tasks were automatically excluded. Difference ERPs between conditions of interest (i.e., German words – false-font strings for the N1 task, deviant “ta” – standard “da” for the MMN task and AVN German words – AVM German words for the AV task) were computed, before individual grand averages were calculated.

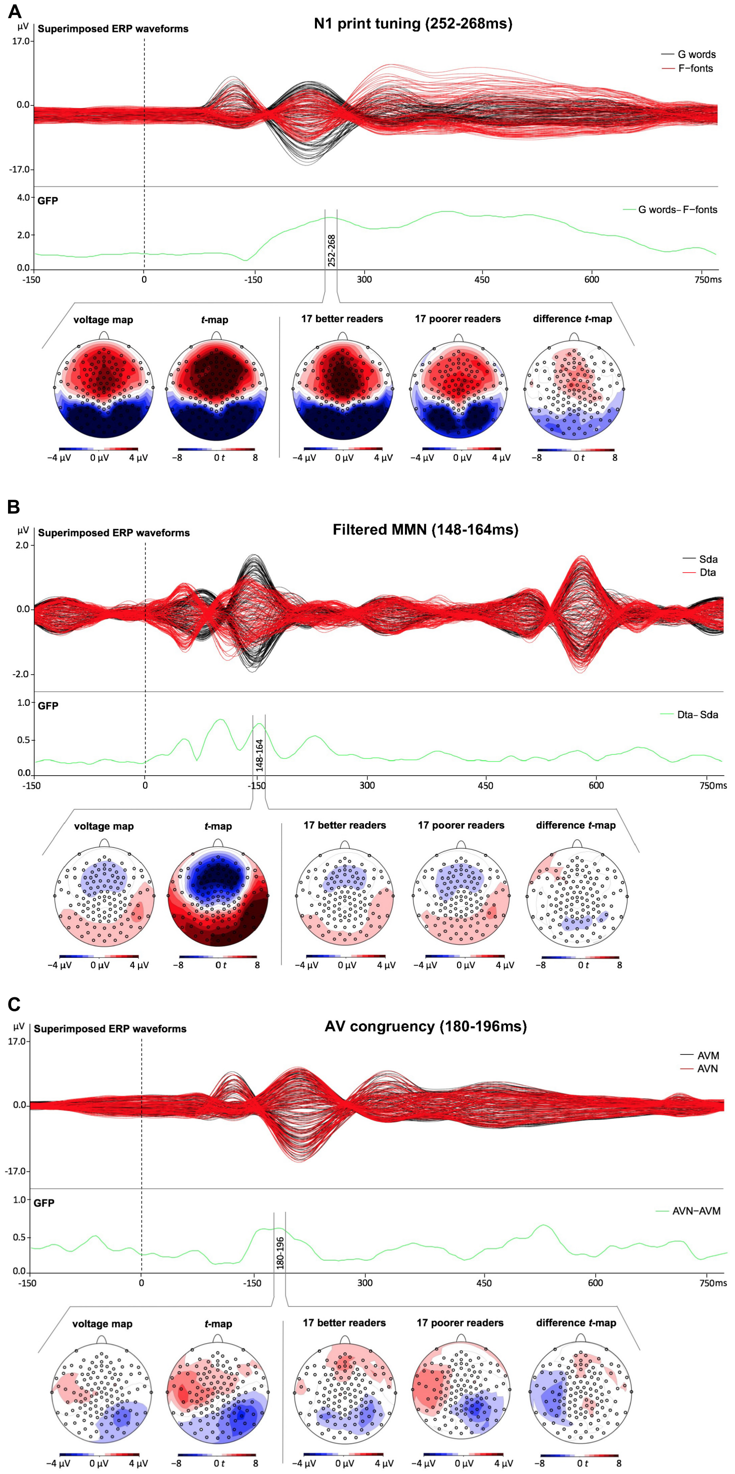

FIGURE 2 | Superimposed event related potential (ERP) waveforms for all the three experimental tasks as well as voltage maps and corresponding *t*-maps across all children and difference *t*-maps of the time segments of interest for the lowest third of poorer and the highest third of better readers. The green line corresponds to the GFP measure of the effects of interest. **(A)** Visual one-back N1 task (black lines correspond to German words and red lines to False-font strings). The green line corresponds to the GFP measure of the effects of interest, i.e., N1 print tuning – indexed by the difference between German words and false-font strings. **(B)** Oddball auditory MMN task (black lines correspond to standard “da” and red lines to deviant “ta” stimuli). The green line corresponds to the GFP measure of the effects of interest, i.e., filtered MMN – indexed by the difference between deviant “ta” and standard “da” stimuli. **(C)** Audiovisual detection task (black lines correspond to audiovisual matching and red lines to audiovisual non-matching German words). The green line corresponds to the GFP measure of the effect of interest, i.e., AV congruency effect - indexed by the difference between audiovisual matching and audiovisual non-matching German words.

EEG Analysis

We investigated N1 print tuning (indexed by the difference between German words and false-font strings), filtered MMN (indexed by the difference between deviant "ta" and standard "da") and AV congruency effects (indexed by the difference between AVN German words and AVM German words). The time windows of interest were equally long for all the three EEG tasks (i.e., five time points) and were based on the GFP peaks (i.e., peak ± two time points) of the effects of interest (i.e., N1 print tuning: 252–268 ms, filtered MMN: 148–164 ms, and AV congruency: 180–196 ms, see **Figure 2**). The chosen time windows coincide with previous studies (N1 print tuning: e.g., Maurer et al., 2006, 2007; Brem et al., 2010, 2013; Araújo et al., 2012; Eberhard-Moscicka et al., 2014, 2016; MMN: e.g., Näätänen et al., 2004; Froyen et al., 2008; Jost et al., 2015; Justen and Herbert, 2018; and AV congruency: e.g., Jost et al., 2013; Karipidis et al., 2017). Given that the aim of this paper was to investigate the early basic processes; early time windows were chosen for all the three neural measures (the analysis on the late AV congruency effect is reported in the **Supplementary Material A2**). The measure used in the analyses was global field power (GFP; Lehmann and Skrandies, 1980). This whole-scalp topographic measure appears best suited in a study combining different neural measures that follow different scalp-distribution patterns. The GFP represents the spatial standard deviation of the electric field at the scalp (Lehmann and Skrandies, 1980) and has the advantage of being reference-independent (Michel et al., 2004), and thus making it more comparable to the results of previous studies (e.g., Zevin et al., 2010; Jost et al., 2013, 2015).

Statistical Analysis

Multiple regression analyses were run to predict whether behavioral and neural measures collected at the end of first grade contributed to the explained variance in the reading outcome in fourth grade (aims 1 and 2). A stepwise multiple regression was run to explore if neural measures can improve prediction over behavioral measures (aim 3). All the steps are detailed in the Results section.

RESULTS

How Much Variance in Fourth Grade Reading Can Be Explained by the First Grade Behavioral Measures?

Multiple regression was run to explore how much variance in reading in fourth grade can be predicted by the five behavioral measures collected at the end of first grade. Overall, more than 46% of the entire variance in reading at the end of fourth grade could be attributed to the behavioral measures collected at the end of first grade [$F(5,45) = 7.925$, $p < 0.001$, $R^2 = 0.468$]. Importantly, while RAN ($p = 0.002$), block design ($p = 0.006$) and vocabulary ($p = 0.007$) significantly contributed to the explained variance in reading, auditory memory span and phonological processing were not significant (both p's > 0.221; see also **Table 2** and **Figure 3A**).

TABLE 2 | Multiple regression analyses (method enter).

Measures	Reading fluency (fourth grade)	*B*	*SE B*	β
Behavioral (first grade)	Constant	−0.34	0.54	
	RAN	−0.50	0.15	-0.42^1
	Block design	−0.03	0.01	-0.40^2
	Vocabulary	0.06	0.02	0.37^2
	Auditory memory span	0.18	0.14	0.16
	Phonological processing	0.17	0.15	0.16
Neural (first grade)	Constant	0.05	0.70	
	N1 print tuning	0.29	0.10	0.40^1
	Filtered MMN	−0.88	0.43	-0.27^2
	AV congruency	−0.17	0.20	−0.11

$^1p < 0.005$, $^2p < 0.05$.

Topographic Distribution of the Basic Unimodal and Bimodal Neural Measures

Both unimodal measures of N1 print tuning and filtered MMN showed typical topographic distributions, with N1 print tuning showing a posterior negativity and fronto-central positivity and filtered MMN showing fronto-central negativity and lateral/mastoid positivity (**Figure 2**). AV congruency showed left fronto-temporal positivity and right occipito-temporal negativity (**Figure 2**). While the measures of N1 print tuning and filtered MMN were highly significant at multiple occipito-temporal [N1: $t_{(max)} = -12.70$, $p < 0.001$; MMN: $t_{(max)} = 9.66$, $p < 0.001$] and fronto-central electrodes [N1: $t_{(max)} = 10.52$, $p < 0.001$; MMN: $t_{(max)} = -9.25$, $p < 0.001$], AV congruency showed weaker effects, nevertheless still highly significant at right occipito-temporal electrodes [$t_{(max)} = -4.35$, $p < 0.001$] and significant at left temporal electrodes [$t_{(max)} = 3.44$, $p < 0.002$, see **Figure 2**].

How Much Variance in Reading Can Be Explained by the Basic Neural Measures?

Parallel to the behavioral measures, a multiple regression was run to investigate how much variance in reading fluency in fourth grade can be attributed to the neural measures recorded at the end of first grade. Overall, the three neural measures tested significantly predicted the reading outcome in fourth grade [$F(3,47) = 4.776$, $p = 0.005$, $R^2 = 0.234$], nevertheless leaving over 70% of unexplained variance. Moreover, only the two unimodal measures of N1 print tuning ($p = 0.004$) and filtered MMN ($p = 0.047$) significantly predicted reading outcome in fourth grade, while the bimodal measure of AV congruency did not ($p = 0.403$, see **Table 2**). Furthermore, while higher GFP values in N1 print tuning were associated with better reading, this direction was opposite for filtered MMN

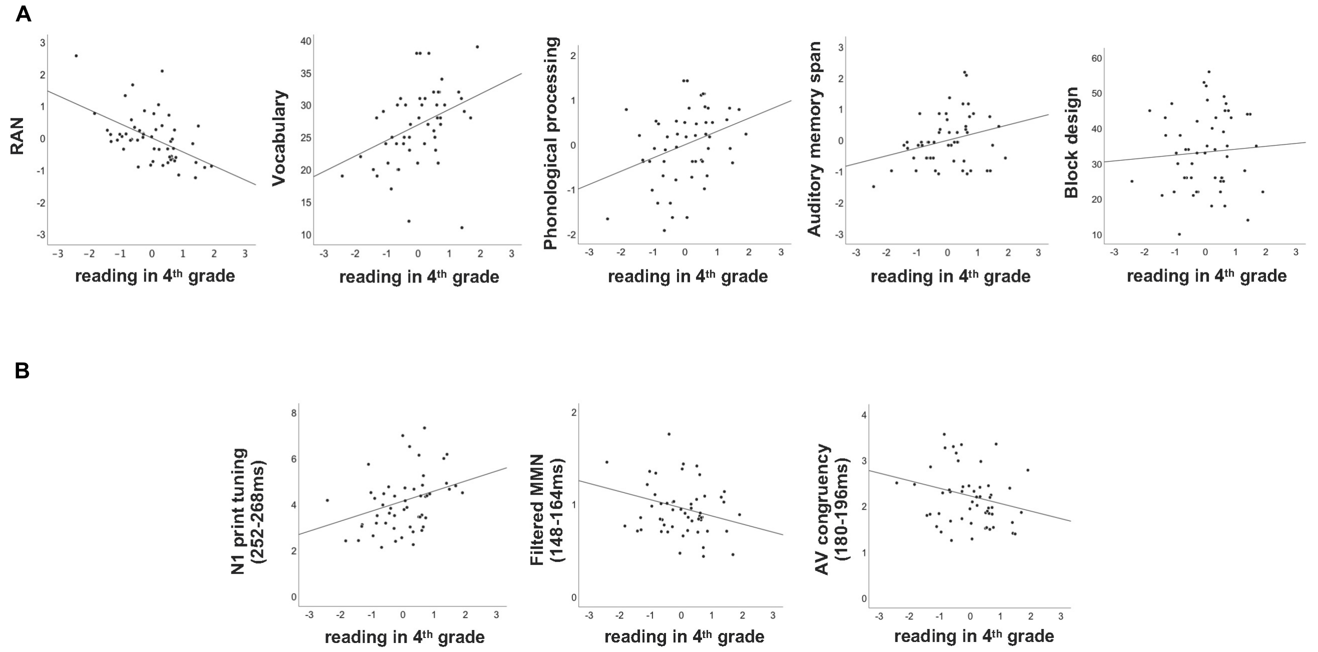

FIGURE 3 | Scatterplots of behavioral **(A)** and neural **(B)** measures collected at the end of first grade and the reading outcome tested at the end of fourth grade. Reading in fourth grade is shown on the *x*-axis (z-transformed), while the behavioral and neural measures are plotted on the *y*-axes (see **Table 1** for the units).

as well as AV congruency (**Figure 3B**). For better illustration, an independent sample *t*-test was run to explore whether the neural measures tested differentiated between the lowest and the highest third of extreme readers. Only N1 print tuning significantly differentiated between the two extreme groups of readers [$t(32) = -2.894$, $p = 0.007$], while filtered MMN and AV congruency were trends [filtered MMN: $t(32) = 1.763$, $p = 0.087$; AV congruency: $t(32) = 1.980$, $p = 0.056$; see also; **Figure 2**].

Can Basic Neural Measures Improve Prediction Over Behavioral Measures?

Further, we wanted to test whether basic neural measures recorded early in the course of reading acquisition (i.e., at the end of first grade) can improve prediction of the future reading outcome over behavioral measures alone. To this end, the significant behavioral predictors of RAN, block design and vocabulary were entered first, while the significant neural predictors, N1 print tuning and filtered MMN, were added in an additional block in a forward regression model. The result showed that beyond the behavioral measures of RAN, block design and vocabulary, the two unimodal neural measures of N1 print tuning and filtered MMN explained 7.2% additional variance in reading ($\Delta R^2 = 0.072$, $p = 0.008$, see also **Table 3**). Importantly, this combination of the behavioral and neural measures explained 57% of the entire variance in reading [$F(5,45) = 11.982$, $p < 0.001$, $R^2 = 0.571$], suggesting that combining behavioral and neural measures can improve prediction over behavioral measures alone.

TABLE 3 | Results of the forward regression combining the significant behavioral and neural predictors.

	Measures	*B*	*SE B*	β
Model 1	Constant	−0.68	0.51	
	RAN	−0.59	0.14	-0.50^1
	Vocabulary	0.06	0.02	0.40^1
	Block design	−0.03	0.01	-0.31^2
Model 2	Constant	−1.50	0.57	
	RAN	−0.53	0.14	-0.44^1
	Vocabulary	0.06	0.02	0.39^1
	Block design	−0.03	0.01	-0.31^2
	N1 print tuning	0.20	0.08	0.28^2
Model 3	Constant	−0.75	0.60	
	RAN	−0.49	0.13	-0.41^1
	Vocabulary	0.07	0.02	0.43^1
	Block design	−0.03	0.01	-0.36^1
	N1 print tuning	0.24	0.07	0.32^1
	Filtered MMN	−0.93	0.34	-0.28^1

$^1p < 0.009$, $^2p < 0.05$.

DISCUSSION

The goal of the present study was to investigate the predictive power of behavioral and basic neural measures collected at the early stage of reading acquisition on reading outcome 3 years later. Given that the predictive value of these basic neural measures across several years were of main interest of this study, the reading measures in fourth grade were chosen as the outcome measures. Specifically, we tested whether next to the so far investigated unimodal measures of N1 print tuning and filtered MMN, the bimodal measure of audiovisual congruency effect can contribute to the prediction of the later reading outcome, and whether the neural measures can improve prediction of the later reading outcome over behavioral measures alone. RAN, block design and vocabulary were the strongest predictors, explaining over 46% of the entire variance in reading. In line with earlier studies, both unimodal measures of N1 print tuning and filtered MMN predicted reading, yet contrary to our expectation, the bimodal measure of AV congruency effect did not add to the explained variance in the later reading outcome. Most importantly, beyond the behavioral measures of RAN, block design and vocabulary, the two unimodal neural measures of N1 print tuning and filtered MMN explained 7.2% additional variance in reading.

Rapid Automatized Naming – The Best Predictor of the Reading Outcome at the End of Fourth Grade

A considerable number of studies have identified behavioral predictors for later reading outcome (e.g., Catts et al., 2001; Schatschneider et al., 2004; Torppa et al., 2012; Brem et al., 2013). In accordance with previous literature (Compton, 2000; Manis et al., 2000; Compton et al., 2001; Wimmer and Mayringer, 2002; Lepola et al., 2005; Torppa et al., 2012; Brem et al., 2013), we found RAN to be the best predictor of the later reading outcome. Next to RAN, also phonological awareness and vocabulary have been shown to predict the later reading outcome (Wagner et al., 1997). A systematic meta-analytic review pointed out the pivotal role of phonemic awareness as a predictor of individual differences in reading development (Melby-Lervåg et al., 2012). However, in our sample of children phonological processing and auditory memory span did not contribute to the explained variance, while next to RAN, also vocabulary and block design were significant predictors of the reading outcome in fourth grade. The lack of predictive value of phonological skills in our study may be explained by three factors. First, RAN is particularly important for reading fluency, while the predictive value of phonological skills seems relatively stronger for reading accuracy and spelling rather than for reading fluency (Moll et al., 2014). Second, RAN seems to be a relatively better predictor than phonological awareness in consistent (shallow) orthographies compared to inconsistent (deep orthographies; Moll et al., 2014; Schmalz et al., 2015). Third, there are studies suggesting that phonological awareness may be a poorer long-term predictor when compared to RAN (Wagner et al., 1997; Georgiou et al., 2008).

The direction of the predictive effect of block design on reading in fourth grade was negative, meaning that children with a lower performance in the block design task showed better reading performance in fourth grade. Importantly, block design was not a significant predictor of reading in isolation, and its predictive value only became significant in combination with RAN and vocabulary. Moreover, the unexplained variance by RAN and vocabulary also correlated with the block design task. This indicates that visuospatial skills, as measured by the block design, interact with the predictive value of RAN and vocabulary.

Unimodal Neural Measures of N1 Print Tuning and Mismatch Negativity but Not the Bimodal Measure of Audiovisual Congruency Predict Reading Outcome at the End of Fourth Grade

N1 print tuning was the most robust predictor of the later reading outcome among the neural measures. Also, previous studies emphasized the predictive value of N1 print tuning in learning to read (Bach et al., 2013; Brem et al., 2013; González et al., 2016; Soto et al., 2018). Moreover, previous studies indicated diminished sensitivity for print in young dyslexic children (Maurer et al., 2007) that may normalize with progressing reading experience (Maurer et al., 2011), but dyslexic adults still show deficient sensitivity for print (Helenius et al., 1999; Shaywitz and Shaywitz, 2005; Mahé et al., 2012). These results, together with the finding of clear structural and functional alterations in the left occipito-temporal cortex (Specht et al., 2009; Raschle et al., 2011) of preschool children with a familial risk of dyslexia and two longitudinal studies indicating the predictive power of the N1 print tuning for the later reading outcome (Brem et al., 2010; Bach et al., 2013), emphasize the importance of the potential power of print sensitivity as an index for successful reading acquisition.

A number of previous studies indicated the predictive value of auditory ERPs for language development (Molfese, 2000; Guttorm et al., 2005; Maurer et al., 2009; Choudhury and Benasich, 2011; Hämäläinen et al., 2015; Linnavalli et al., 2017). In our study, the (filtered) MMN was a significant predictor of the later reading outcome, but the negative beta-value with larger MMN associated with poorer reading contrasted results from previous studies (Maurer et al., 2009). The reason for the unexpected direction might be that the MMN was obtained only after applying a strong high-pass filter of 3 Hz that eliminated the overlapping positive mismatch response (MMR; Jost et al., 2015). A positive MMR has previously been interpreted as an immature mismatch response, as it was found in children, but not in adults (Maurer et al., 2003). It is possible that the positive MMR response was not entirely removed and that the correlation with reading skills may be driven by the original (immature) positive MMR rather than the filtered MMN. Although the correlation between positive MMR and fourth grade reading was not significant ($r = -0.075$, $p = 0.600$), a group contrast between good and poor readers showed a nominally larger MMR for the good readers, supporting the idea that the correlation between filtered MMN and reading may be driven by an incompletely removed positive MMR (see **Supplementary Materials A1** and **F1**). Moreover, the effect of the filtered MMN on later reading was rather weak, as it only occurred together with the other predictors, but not when added as a single predictor.

As previous studies indicated the crucial role of the integration of auditory and visual linguistic inputs for reading (Ehri, 2005;

Blau et al., 2009, 2010; Blomert, 2011), this study aimed at investigating whether AV congruency effects could predict reading better than the so far investigated unimodal measures on N1 print tuning (Bach et al., 2013; Brem et al., 2013; Eberhard-Moscicka et al., 2014) and MMN (Maurer et al., 2009). To date, this question has been addressed by a single study with a smaller sample size that used artificial-letter training (Karipidis et al., 2018). However, unlike the previous study, we did not find any significant prediction of later reading skills by the AV congruency effect around 200 ms. Moreover, the group contrast suggested a larger AV congruency effect for poor readers than good readers, contrasting previous results that showed larger congruency effects for typically reading children (Blau et al., 2010) and adults (Blau et al., 2009), but not for their dyslexic peers. Moreover, a larger AV congruency effect was found in children who became good readers compared to those who became poor readers (Karipidis et al., 2018). As the time window selected in our study (180–196 ms) was earlier than in the study by Karipidis et al. (2018), the neural processes measured may reflect different aspects of audiovisual integration. We therefore performed an additional analysis (see **Supplementary Material F2**) with the STEN toolbox (Knebel and Notter, 2018) that indicated a second, later time window (late AV congruency: 544–560 ms). As such, parallel to the main analysis, an additional analysis was run in order to investigate whether the later time window of the AV congruency effect would yield a significant result. Again, the (late) AV congruency effect did not predict later reading (see the **Supplementary Material A2**), even though the effect tended to be larger in good readers compared to poor readers (see **Supplementary Material F2**), similar to previous studies (Blau et al., 2009, 2010; Karipidis et al., 2018).

Importantly, in accordance with the main analysis, also the multiple regression analysis with the (late) AV congruency effect indicated that only the two unimodal measures of N1 print tuning ($p = 0.002$) and filtered MMN ($p = 0.039$) but not the bimodal measure of (late) AV congruency effect ($p = 0.873$) were predictive of the future reading outcome (see **Supplementary Material T2**). Yet, these results do not generally contradict the notion of letter-sound integration constituting an emergent property of learning to read (Blau et al., 2009, 2010). They may rather suggest that first grade might be too early to study multisensory integration processes at the word level; and/or that audiovisual integration at this stage might be more basic, and AV integration effects at the level of letters and phonemes may be better predictors of reading acquisition (Karipidis et al., 2018). It also seems plausible that neural processes underlying audiovisual integration of words may become more important predictors later on during reading acquisition.

Basic Neural Measures Can Improve Prediction of the Future Reading Outcome Over Behavioral Measures Alone

We found that N1 print tuning and filtered MMN improve prediction of the future reading outcome over behavioral data alone. This is in line with previous studies that showed improved prediction of reading development, if neural measures were added to behavioral measures (Hoeft et al., 2007; Maurer et al., 2009; Brem et al., 2013). While the current findings confirm the results of previous investigations (Brem et al., 2013) by showing that N1 print tuning explains additional variance of future reading skills, the current results also extend those previous studies by showing that N1 print tuning has predictive value not only before the start of formal schooling but also in the first phase of learning to read at school. Moreover, the results of the current study suggest that MMN measures potentially add explanatory power for predicting reading skills, although the underlying processes measured in the current study may rather be tied to an immature mismatch response than to processes tapped in previous studies. Taken together, these results indicate the potential value of combining measures from different methods (i.e., neural and behavioral) to advance prediction of the future reading outcome. This predictive value of the neural measures shall be of particular importance in preliterate children, where behavioral measures are typically of limited applicability. A practical implementation may entail development of targeted intervention programs that may include, yet are not limited to, grapheme–phoneme trainings that can be applied early in the course of development, as has been demonstrated by, e.g., Karipidis et al. (2017) with kindergarten children.

CONCLUSION

To our knowledge, no study to date has combined visual, auditory and audiovisual neural measures together with behavioral measures to investigate their predictive value for later reading skills in a larger sample of children. Although these results shall be interpreted with caution, this study provides important information on the predictive power of the basic neural and behavioral measures and that the neural measures can improve prediction over behavioral measures alone.

DATA AVAILABILITY STATEMENT

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request. Requests to access the datasets should be directed to AE-M, aleksandra.eberhard@neuro.unibe.ch.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by University of Zurich Ethics Commission, Faculty of Arts and Social Sciences, Zurich. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

AE-M, LJ, and UM contributed to the material preparation, data collection, and performed the analyses. AE-M wrote the first draft of the manuscript. All authors contributed to the study conception, design, and commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.733494/full#supplementary-material

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REVIEW
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How Learning to Read Changes the Listening Brain

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Reading acquisition reorganizes existing brain networks for speech and visual processing to form novel audio-visual language representations. This requires substantial cortical plasticity that is reflected in changes in brain activation and functional as well as structural connectivity between brain areas. The extent to which a child's brain can accommodate these changes may underlie the high variability in reading outcome in both typical and dyslexic readers. In this review, we focus on reading-induced functional changes of the dorsal speech network in particular and discuss how its reciprocal interactions with the ventral reading network contributes to reading outcome. We discuss how the dynamic and intertwined development of both reading networks may be best captured by approaching reading from a skill learning perspective, using audio-visual learning paradigms and longitudinal designs to follow neuro-behavioral changes while children's reading skills unfold.

Keywords: reading development, dyslexia, audio-visual plasticity, reading-induced plasticity, dorsal and ventral reading networks

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INTRODUCTION

Despite standardized curricula and teaching programs at school, children reach very different levels of reading fluency. Proficiency in reading determines personal achievement not only during primary and secondary education but also societal attainment later in life (UNESCO, 2006; Hudson et al., 2009; Livingston et al., 2018; Kortteinen et al., 2020). This especially affects the 5–10% of children with developmental dyslexia who struggle to acquire fluent reading skills despite adequate intellectual abilities and schooling opportunities (Blomert, 2005; Shaywitz and Shaywitz, 2008). Here we focus on neuro-behavioral processes characterizing the acquisition of early reading skills, and their relevance to explaining individual differences in children's reading fluency at the level of visual words and pseudowords.

The acquisition of reading requires years of practice and is accompanied by a gradual re-shaping of existing dorsal spoken language and ventral visual brain networks into an integrated audio-visual reading network. Thus, when a child learns to read, striking changes occur in higher-order visual regions of the (left) ventral occipito-temporal cortex (vOTC) which becomes increasingly responsive to and specialized in written text perception (Maurer et al., 2006; Brem et al., 2009; Ben-Shachar et al., 2011; Dehaene-Lambertz et al., 2018). Furthermore, while forming associations between text and speech sounds, auditory/speech sensitive regions in the posterior superior temporal cortex (pSTC) become linked to these higher-order visual regions and start responding to written text in addition to spoken language (van Atteveldt et al., 2004, 2009, 2010; Froyen et al., 2009; Brennan et al., 2013; McNorgan et al., 2013, 2014; Kronschnabel et al., 2014; Bonte et al., 2017; Caffarra et al., 2021). The emergence of these audio-visual response characteristics arguably reflects a form of neural plasticity that is central to reading acquisition, with reduced or less automatic text-induced audio-visual linking in dyslexic readers and illiterates (Blomert, 2011; Dehaene et al., 2015). Individual differences in reading skills along a continuum from poor (dyslexic) to excellent readers, may thus scale with the capacity of the brain regions involved in auditory and visual perception to accommodate reading-induced changes. This may hold across largely different writing systems, with cultural variability mainly affecting the representational level at which written to spoken language associations are formed (Perfetti, 2003; Rueckl et al., 2015; Feng et al., 2020). Here we argue that understanding why some children thrive while others keep on struggling to read requires approaching reading-induced neuro-behavioral changes from a dynamic skill learning perspective, employing auditory and/or visual learning paradigms and multi-level longitudinal studies.

DEVELOPMENTAL DYSLEXIA

Developmental dyslexia provides a good model for investigating the role of the dorsal and ventral brain networks in reading development as most dyslexic readers show difficulties in handling the sound structure of spoken language (Snowling, 1980, 2013; Shaywitz et al., 1998; Goswami, 2003; Lyon et al., 2003) and in forming associations between (clusters of) letters and speech sounds (Blomert and Willems, 2010; Blomert, 2011; Kronschnabel et al., 2014). It remains debated whether the convergence of written to spoken language representations is a universal signature of proficient reading (Blomert, 2011; Rueckl et al., 2015), with a possible language-specific grain size of convergence (Ziegler and Goswami, 2005), or alternatively, is most relevant for explaining individual differences and dyslexia in orthographies with fairly regular letter-speech sound mappings, such as Dutch, German, or Hungarian, and less for languages with irregular mappings, such as English (Nash et al., 2016; Clayton and Hulme, 2017).

A major challenge in understanding dyslexia lies in its highly heterogeneous behavioral manifestation. Suggested causes include – but are not limited to – deficits in letter-speech sound integration (Snowling, 1980; Blomert, 2011), poorly specified and/or less categorical speech representations (Snowling, 1998; Serniclaes et al., 2004), impaired access to speech representations (Ramus and Szenkovits, 2008), impaired temporal sampling of speech (Goswami, 2011), inadequate implicit auditory regularity detection (Ahissar, 2007), impaired processing of brief sounds (Tallal and Piercy, 1973), visual dysfunctions (Bosse et al., 2007), or more general deficits in magnocellular functions (Livingstone et al., 1991), automation processes (Nicolson and Fawcett, 1999), or attentional mechanisms (Bosse et al., 2007; Shaywitz and Shaywitz, 2008; Vidyasagar and Pammer, 2010; Lobier et al., 2012). So far these different possibilities have been mostly studied in isolation and typically using cross-sectional experimental designs that may not have the sensitivity to reveal the underlying multifaceted and individually variable developmental dynamics. It is therefore promising that an increasing number of labs and research consortia have started longitudinal neuroimaging studies following children during different stages of reading development (van der Leij et al., 2013; Lyytinen et al., 2015; Wang et al., 2017, 2020; Dehaene-Lambertz et al., 2018; Vanderauwera et al., 2018; Chyl et al., 2019; Moulton et al., 2019; van de Walle de Ghelcke et al., 2020; Zuk et al., 2020, see Chyl et al., 2021 for a recent review of longitudinal neuroimaging studies on reading development and dyslexia). These studies are crucial to understanding how individual differences in reading trajectories and outcome can be positioned within the interactive development of the brain's spoken and written language networks (Pugh et al., 2001; Sandak et al., 2004). Recent work has further highlighted that individual differences in reading outcomes are likely rooted in multiple genetic and environmental factors that interactively influence structural and functional brain changes while children learn and develop (Raschle et al., 2011; Wang et al., 2017; Yu et al., 2018b, 2020; Zuk et al., 2020). For example, a child with a parent or sibling with dyslexia has about 40–50% chance of also developing dyslexia. Neuro-behavioral risk factors, such as phonological processing difficulties, associated with this familial risk (Snowling and Melby-Lervåg, 2016) may be moderated by protective factors such as strong verbal reasoning, vocabulary and attention skills, or a positive self-concept (Cavalli et al., 2016; Haft et al., 2017). As a result of these complex interactive developmental processes, reading variability is continuous in nature (Pennington, 2006; van Bergen et al., 2014; Peters and Ansari, 2019). At the same time, dyslexia is typically diagnosed based on a specific cut-off, most commonly scoring 1,5 standard deviations below the age-group average on a battery of reading and/or spelling tests (American Psychiatric Association, DSM-5 Task Force, 2013). In clinical practice, such an arbitrary cut-off criterion is currently unavoidable, but at a scientific level, the variability and continuity in reading skills requires a shift from a dichotomous classification of reading as poor versus fluent toward a multi-deficit spectral view of reading (Pennington, 2006; van Bergen et al., 2014; Protopapas and Parrila, 2018; Peters and Ansari, 2019). Here, reading fluency is represented on a spectrum ranging from poor to fluent, with dyslexia lying on one end of the spectrum rather than being defined as a qualitatively discontinuous condition. This approach takes into account individual differences in reading proficiency observed across both poor and fluent readers (Aravena et al., 2013; Žarić et al., 2014; Fraga-González et al., 2015; Romanovska et al., 2021) and explains how the frequently reported comorbidity between developmental disorders, such as between dyslexia, dyscalculia, and attention deficit hyperactivity disorder (ADHD), may result from shared neurobiological and/or environmental risk factors (Pennington, 2006; Landerl and Moll, 2010; van Bergen et al., 2014; Peters and Ansari, 2019).

SPEECH PERCEPTION IN THE DORSAL LANGUAGE NETWORK

By the time children start to learn to read, neural functions for speech perception and production have already gone through several years of functional refinement. Spoken language functions thus form a linguistic basis for reading acquisition both from a phylogenetic and an ontogenetic perspective (Dehaene et al., 2015). Since the first neuroimaging findings in the 1990s, numerous studies have been designed with the aim to delineate the brain's spoken language system. One of the pioneering studies in this domain showed that listening to speech elicits extensive and bilateral activation in the superior temporal cortex (STC), including primary areas on Heschl's gyrus (HG), the planum temporale (PT), and along the superior temporal gyrus (STG) and superior temporal sulcus (STS; see **Figure 1**; Binder et al., 1994). Building on this work, advances in, among others, functional magnetic resonance imaging (fMRI) and Electrocorticography (EGoG) methodology have enabled delineating a more fine-grained functional architecture of speech sound representations in the superior temporal cortex (Chang et al., 2010; Mesgarani et al., 2014; Leonard et al., 2016). One relevant new insight emerging from this work is the finding that the auditory representations of speech along the posterior and lateral STG are not restricted to low-level acoustic-phonetic speech features (Jäncke et al., 2002; Obleser and Eisner, 2009), but include higher-order perceptual levels of representation that are strongly modulated by a listener's behavioral goals, learning and contextual information (Formisano et al., 2008; Bonte et al., 2009, 2014; Mesgarani and Chang, 2012; Rutten et al., 2019; Yi et al., 2019; Levy and Wilson, 2020). Most interesting with respect to reading development is the observation of perception-related shifts in the auditory cortical representation of speech resulting from visual presentation of text (Bonte et al., 2017) and other types of multisensory context information, including videos of a speaker articulating words or pseudowords (Kilian-Hütten et al., 2011; Ozker et al., 2017, 2018). While it remains debated whether and how learning to read changes the representation of speech (Dehaene et al., 2015; Mitterer and Reinisch, 2015), the modulatory effect of audio-visual mappings between text and spoken language does suggest reading-induced plasticity at the level of the auditory cortex (Bonte et al., 2017; see also Karipidis et al., 2017, 2018; Joo et al., 2021).

Further support for a key role of the superior temporal cortex in learning to read comes from developmental neuroimaging studies showing that the strength and/or extent of speech evoked responses in this region is associated with children's reading level (Parviainen et al., 2011; Brennan et al., 2013; Conant et al., 2014; Lohvansuu et al., 2018), and phonological skills (Turkeltaub et al., 2003; Conant et al., 2014; Bonte et al., 2016; Randazzo et al., 2019). Moreover, children with dyslexia (Schulte-Körne et al., 1998; Bonte and Blomert, 2004; Frey et al., 2019; Schaadt and Männel, 2019; Gu and Bi, 2020; Virtala et al., 2020), or at familial risk for developing dyslexia (Vandermosten et al., 2020) may show reduced or less discriminable auditory cortical responses to speech. Such functional changes may be the result of less efficient speech sound learning during early development. Indeed, a reduced, or a slower build-up of, sensitivity to statistical regularities in speech sound structures has been observed in adults (Noordenbos et al., 2013; Schmalz et al., 2017; Zhang et al., 2021) and children (Bonte et al., 2007; Gabay et al., 2015) with dyslexia. Evidence further suggests that atypicalities in brain responses to speech (Vandermosten et al., 2020), and to basic sound features (Hakvoort et al., 2014) may be associated with a familial risk for dyslexia without being predictive of children's later reading outcomes. Thus, atypicalities in auditory cortical responses to speech, together with commonly observed

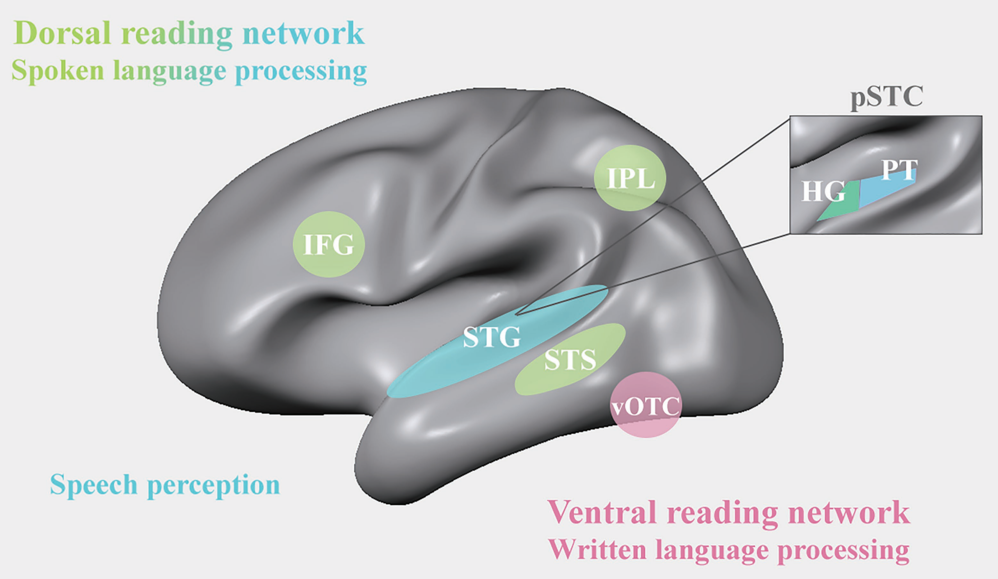

FIGURE 1 | A representation of the dorsal (green) and ventral (pink) reading networks of the brain's audio-visual reading network. IFG: inferior frontal gyrus; IPL: inferior parietal lobe; STG: superior temporal gyrus; STS: superior temporal sulcus; vOTC: ventral occipito-temporal cortex; pSTC: posterior superior temporal cortex; HG: Heschl's gyrus; PT: planum temporale.

phonological processing difficulties in children at familial risk for dyslexia (Snowling and Melby-Lervåg, 2016), likely present a vulnerability or risk factor for reading problems that will lead to dyslexia if not mitigated by protective factors. This phonological risk factor may also show in anatomical characteristics of speech sensitive superior temporal cortex (STC). In fact, there is a long tradition of relating morphological variability of the PT to language dysfunctions in dyslexia (Geschwind and Levitsky, 1968; Galaburda et al., 1985; Galaburda, 1989; Leonard et al., 2006) as well as to inter-individual variability in auditory and language skills (Golestani et al., 2011).

A relation between reading development and morphological characteristics of the superior temporal cortex can be located within a more general pattern of protracted, experience-related changes in pSTC morphology, which have been observed to continue well into the third decade of life, particularly in the left hemisphere (Giedd et al., 1999; Sowell et al., 2003; Gogtay et al., 2004). Similarly, while the global signature of speech evoked STC responses is in place in infancy (Dehaene-Lambertz and Pena, 2001), its functional characteristics continue to change well beyond primary school years (Sharma et al., 1997; Pang and Taylor, 2000; Bonte and Blomert, 2004; Brauer et al., 2008; Bonte et al., 2013; Chyl et al., 2017). Such an extended developmental time course may allow a prolonged process of functional specialization during which auditory and visual language input contributes to the shaping and fine-tuning of pSTC brain circuitry (Johnson, 2001, 2011; Werker and Hensch, 2015). Indeed, a recent study exploring grey matter volume in 8-year-old children of varying reading fluency found that right STG grey matter volume differentiates fluent from dysfluent readers, with the former group showing higher grey matter volume in this region compared to the latter group (Martins et al., 2021). So far, however, there is no unequivocal evidence linking morphological pSTC features to its functional characteristics or to individual children's language skills. Early research specifically reported a hemispheric asymmetry of the PT region, with the left PT covering a larger surface area compared to the right PT in 65% of a sample of 100 brains (Geschwind and Levitsky, 1968). Soon after, studies emerged suggesting that the same asymmetry is not present in readers with dyslexia who instead were found to have more symmetrical PT areas in both hemispheres or to show the opposite, right-ward, asymmetry (Galaburda et al., 1985; Galaburda, 1989). It was therefore argued that reading difficulties in dyslexia may be associated with morphological differences of the PT. However, the finding of a different PT asymmetry in readers with dyslexia has not been systematically replicated (Leonard et al., 1993, 2006; Schultz et al., 1994; Beaton, 1997; Carrion-Castillo et al., 2020) and may instead depend on more general factors, such as gender (Altarelli et al., 2014), family history of dyslexia (Vanderauwera et al., 2018), handedness (Beaton, 1997), or methodological discrepancies in the anatomical criteria used to delineate the PT (Ramus et al., 2018). Thus, similar to behavioral and functional STC signatures of phonological processing difficulties, differences in PT morphology may reflect a neurobiological risk factor for later reading problems rather than characterizing all individuals with developmental dyslexia.

AUDIO-VISUAL PROCESSING IN THE DORSAL AND VENTRAL READING NETWORKS

The protracted functional and morphological development of the pSTC in the posterior dorsal network may be key to the gradual build-up of neural associations between visual symbols and corresponding spoken language representations and, on a more general level, the strong bi-directional influences between reading and spoken language development (Morais et al., 1979; Perfetti et al., 1987; Sandak et al., 2004; Blomert, 2011; Rueckl et al., 2015). Evidence of a gradual strengthening of audio-visual associations throughout the first years of reading development – extending well beyond the initial phase of learning to map letter(s) to their corresponding speech sound(s) – comes from EEG studies employing audio-visual oddball paradigms. These studies have found that the neural time-window of audio-visual integration changes from later to earlier (Froyen et al., 2009; Žarić et al., 2014) and becomes narrower/more time-sensitive (Žarić et al., 2014) over the course of (reading) development. Moreover, the latency of integrative letter-speech sound responses has been found to deviate in dyslexic compared to typical readers (Froyen et al., 2011; Žarić et al., 2014; Jones et al., 2016; Moll et al., 2016) with a speeding up of these responses after 6 months of intensive letter-speech sound training in dyslexic children (Žarić et al., 2015). Suggestive evidence for a direct influence of visual text on pSTC responses to speech comes from the observation that pSTC activation increases in response to matching (congruent) compared to non-matching (incongruent) letter-speech sound pairs and speech alone (Raij et al., 2000; van Atteveldt et al., 2004; Blau et al., 2010; van Atteveldt and Ansari, 2014; Karipidis et al., 2017). Furthermore, these cross-modal modulations in the STC were found to scale with phonological skills (McNorgan et al., 2013) and reading experience (McNorgan et al., 2014) in typical readers, and to be reduced in dyslexic readers (Blau et al., 2009, 2010; Kronschnabel et al., 2014; Ye et al., 2017). Similarly, we recently observed that cortical activation in bilateral STG in response to paired text and ambiguous speech sound stimuli correlates with children's letter-speech sound mapping fluency (Romanovska et al., 2021).

While the pSTC seems to be especially relevant for the processing of already learnt letter-speech sound associations (van Atteveldt et al., 2004; Blau et al., 2010), the inferior parietal lobe (IPL) may mediate the initial establishment of these associations (Hashimoto and Sakai, 2004; Booth et al., 2007; Bonte et al., 2017; Wise Younger et al., 2018). In typically reading adults, text-induced shifts in superior temporal cortical responses to ambiguous speech sounds seem to be "installed" via functionally correlated activity in the IPL (Bonte et al., 2017), and learning of novel symbol-sound mappings is modulated by parietotemporal brain stimulation (Wise Younger et al., 2018). Furthermore, continued reading development in children is associated with a reduction in IPL activation in response to text and audio-visual phonological processing, as well as with a reduction in reading-related IPL to vOTC connectivity (Wise Younger et al., 2017; Dehaene-Lambertz et al., 2018; Yu et al., 2018a; Moulton et al., 2019). Studies comparing brain activation within this region between readers with and without dyslexia have found reduced IPL activation in both, adults and children with dyslexia (Hoeft et al., 2007; Richlan et al., 2009; Paz-Alonso et al., 2018), with a possibly more pronounced group difference in children (Richlan et al., 2011). Next to a specific contribution to (the learning of) letter-speech sound mapping, the IPL has been associated with other linguistic functions including semantic processing (Shaywitz and Shaywitz, 2008; Paz-Alonso et al., 2018) as well as with more general cognitive functions including visual attention (Vidyasagar, 1999; Saalmann et al., 2007). The involvement of the IPL in both letter-speech sound mapping and visual attention is interesting also with respect to the frequent co-occurrence of dyslexia and, especially the inattentive subtype of, ADHD (Greven et al., 2011; Hendren et al., 2018; Plourde et al., 2018).

The anterior part of the dorsal network houses the inferior frontal gyrus (IFG) which is increasingly recruited while beginning readers improve their reading ability and phonological skills (Turkeltaub et al., 2003). Functional connectivity between IFG and IPL has been associated with phonological processing skills during early reading development (Yu et al., 2018a), while functional connectivity between IFG and STG has been found to correlate with reading fluency measures and to be reduced in dyslexic readers (**Figure 2**; Schurz et al., 2015). Furthermore, studies have shown reduced activation in the left IFG (Cao et al., 2006; Richlan et al., 2009; Richlan, 2012, 2019) but increased activation in left pre-motor regions in dyslexic compared to typical readers (Richlan et al., 2010; Wimmer et al., 2010). The increased left-premotor activation is interesting as, next to the suggested compensatory function of the right IFG in dyslexic readers (Hoeft et al., 2011), it may provide a window on possible alternative reading strategies or paths to improving learning outcomes via sensorimotor training, including, for example, the active pronunciation, or writing of letters (Torres et al., 2021). Within the developing reading network, the IFG may be involved in the learning of novel audio-visual associations (Hein et al., 2007), phonologic-orthographic regularity of words (Pugh et al., 1997), and semantic and phonological processing of written and spoken words (Fiez, 1997; Poldrack et al., 1999; Booth et al., 2001; Burton, 2001; Turkeltaub et al., 2003; Sandak et al., 2004). These different levels of analysis are compatible with a more general role of the left IFG in unifying different types of linguistic and non-linguistic information into multi-level integrated language representations (Hagoort, 2005).

A core area for developing fluent reading in the ventral reading network is the putative visual word form area (VWFA) within the left vOTC. This area has been shown to become increasingly specialized for text over the course of reading development (Maurer et al., 2006; Brem et al., 2009; Ben-Shachar et al., 2011; Dehaene-Lambertz et al., 2018) and to be less active in dyslexic readers (**Figure 2**; Paulesu, 2001; Hoeft et al., 2007; Richlan et al., 2009; Wimmer et al., 2010; Dehaene and Cohen, 2011). The central function of this specific occipito-temporal region in written text processing most likely relates to its close functional interaction with regions in the dorsal language network, including the STS, pSTG, IPL, and IFG (Richlan, 2012; Monzalvo and Dehaene-Lambertz, 2013; Schurz et al., 2015; Yu et al., 2018a). Accordingly, the functional specialization of the left vOTC is thought to be shaped by communication via direct white matter connections to these key speech processing areas (Hannagan et al., 2015; Saygin et al., 2016; Moulton et al., 2019). Indeed, in literate participants in alphabetic languages, activation in this region has been linked to categorical perception of phonemes (Conant et al., 2014), phonological processing (Romanovska et al., 2021), and to be modulated by audio-visual speech-text stimuli (McNorgan and Booth, 2015). Moreover, developmental studies report more overlap in activation in response to both, auditory and visual word stimuli in the vOTC and STG in children compared to adults (Booth et al., 2001), with a gradual transition from multi-modal to primarily unimodal processing with continued (reading) development (Church et al., 2008). Its lasting functioning as a multi-modal language area is also indicated by the involvement of the left vOTC during braille reading or reading via soundscapes in the congenitally blind (Büchel et al., 1998; Burton et al., 2002; Reich et al., 2011; Striem-Amit et al., 2012) and its responsiveness to both (braille) reading and grammatical processing of spoken sentences in congenitally blind braille readers but not in sighted readers (Kim et al., 2017).

One important open question is the extent to which the commonly observed reduced recruitment of regions within the dorsal and ventral reading networks in dyslexic readers constitute risk and/or protective factors in the etiology of dyslexia, or alternatively reflect consequences of a history of reading problems (see e.g., Huettig et al., 2018). Longitudinal studies following children with/without family risk of dyslexia over the course of reading development will be important to disentangle the contribution of each of these factors to explaining individual differences. Available evidence suggests that pre-readers categorized at high versus low family risk for developing dyslexia, show activation differences in similar brain regions as dyslexic versus typical readers (**Figure 2**). These include reduced activity in key spoken language and reading networks (Debska et al., 2016), and more specifically in the left vOTC (Plewko et al., 2018), and (letter and) speech sensitive left STC (Maurer et al., 2003; Raschle et al., 2012; Plewko et al., 2018) alongside reading outcome related group differences in white matter diffusivity between left ventral visual and frontal regions (Vandermosten et al., 2015; Vanderauwera et al., 2017). Specifically, family risk was found to be associated with a reduced distinctiveness of STC speech representations in 7 to 8-year-old children (Vandermosten et al., 2020), and reduced left temporo-parietal cortical activity during phonological processing in pre-readers (Yu et al., 2018a). Neither of these diminished speech/phonology evoked functional responses was found to be predictive of children's later reading problems. On the other hand, brain

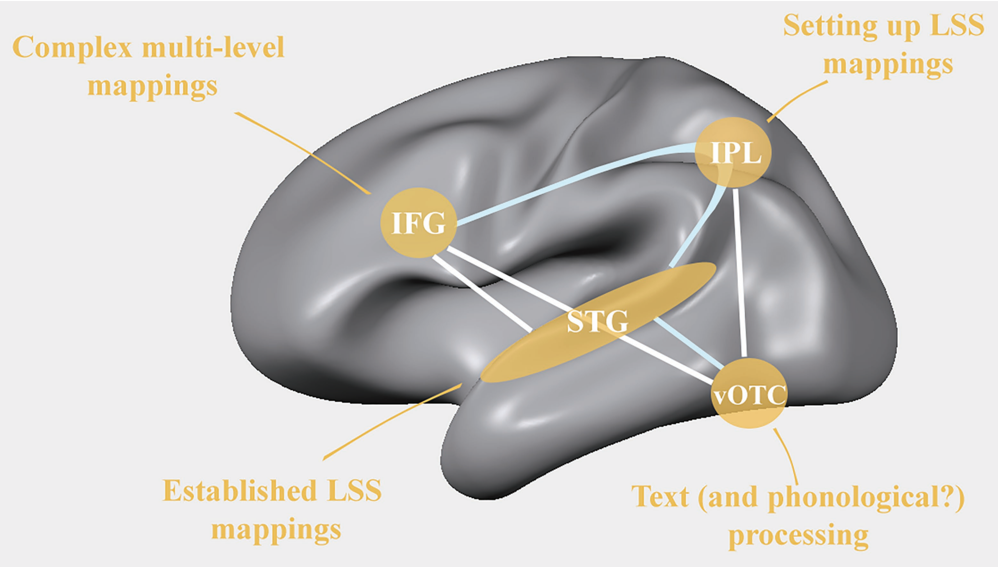

FIGURE 2 | Areas where reduced cortical activation has been reported in readers with dyslexia alongside frequently observed differences in functional (white lines) and structural (light blue lines) connectivity between readers with and without dyslexia. IFG: inferior frontal gyrus; IPL: inferior parietal lobe; STG: superior temporal gyrus; vOTC: ventral occipito-temporal cortex; LSS: letter-speech sound.

activation of the right IFG during phonological processing and vowel perception tasks (Leppänen et al., 2011; Yu et al., 2020) as well as changes in white matter diffusivity in tracts connecting the dorsal and ventral reading systems (Wang et al., 2017) in at-risk children who do versus do not develop reading difficulties have been reported to differ from children without familial risk. The nature of developmental changes in network dynamics and compensatory mechanisms children develop to aid reading, will likely differ depending on family risk of dyslexia, as well as additional social and environmental risk and protective factors.

DEVELOPMENTAL DYNAMICS OF THE DORSAL AND VENTRAL READING NETWORKS

When learning to read, children initially rely mostly on the dorsal network (**Figure 3**, top row; Booth et al., 2001; Pugh et al., 2001; Turkeltaub et al., 2003; Sandak et al., 2004), presumably employing the IPL in particular to map letters and eventually letter strings onto corresponding speech sounds (Shaywitz and Shaywitz, 2008; Grainger and Ziegler, 2011; Moulton et al., 2019). With continued practice, both ventral and dorsal networks are shaped by the incremental development of phonological awareness and integrated representations of orthographic, phonological, and semantic features of words (Pugh et al., 2013). Effortful letter-for-letter reading and emerging phonological and orthographic knowledge create and strengthen functional (Schlaggar and McCandliss, 2007; Price and Devlin, 2011; Dehaene et al., 2015; Yu et al., 2018a; Moulton et al., 2019) and structural (Yeatman et al., 2012; Vandermosten et al., 2012b; Gullick and Booth, 2014; Myers et al., 2014; Moulton et al., 2019) links between the dorsal and ventral systems. Ample evidence suggests that this leads to a gradual re-shaping of dedicated areas for visual text processing in the left vOTC (Pugh et al., 2001; Maurer et al., 2006, 2008; Brem et al., 2009, 2010; Price and Devlin, 2011; Fraga González et al., 2014, 2016, 2017; Lochy et al., 2016; Karipidis et al., 2017, 2018; Pleisch et al., 2019).

While there is discussion about the extent to which reading acquisition also changes auditory speech representations (Dehaene et al., 2015; Mitterer and Reinisch, 2015; Bonte et al., 2017), recent neuroimaging findings in children indeed suggest these types of changes in the STG (Karipidis et al., 2017, 2018; Joo et al., 2021). For example, 7–12-year-old typical readers have been found to automatically engage the left STG while processing visually presented words, with stronger left STG responses in better readers (Joo et al., 2021). Research employing artificial script learning paradigms in pre-readers has shown higher right STG activation in response to trained versus untrained letter-symbol pairs in children who were faster in learning these associations (Karipidis et al., 2017). Moreover, left PT activation has been found to differentiate future fluent and poor readers, with an increased PT activation in response to congruent compared to incongruent letter-symbol pairs in future fluent readers and a trend toward the opposite response pattern in future poor readers (Karipidis et al., 2018).

Based on longitudinal evidence, the strength of functional connectivity between the IPL and vOTC is suggested to be key to successful audio-visual integration of letters and speech sounds during initial reading development and to shaping the left vOTC for automatized, fluent reading (Wise Younger et al., 2017; Yu et al., 2018a). Once fluent reading is achieved, the ventral network ensures rapid and automatized recognition and processing of

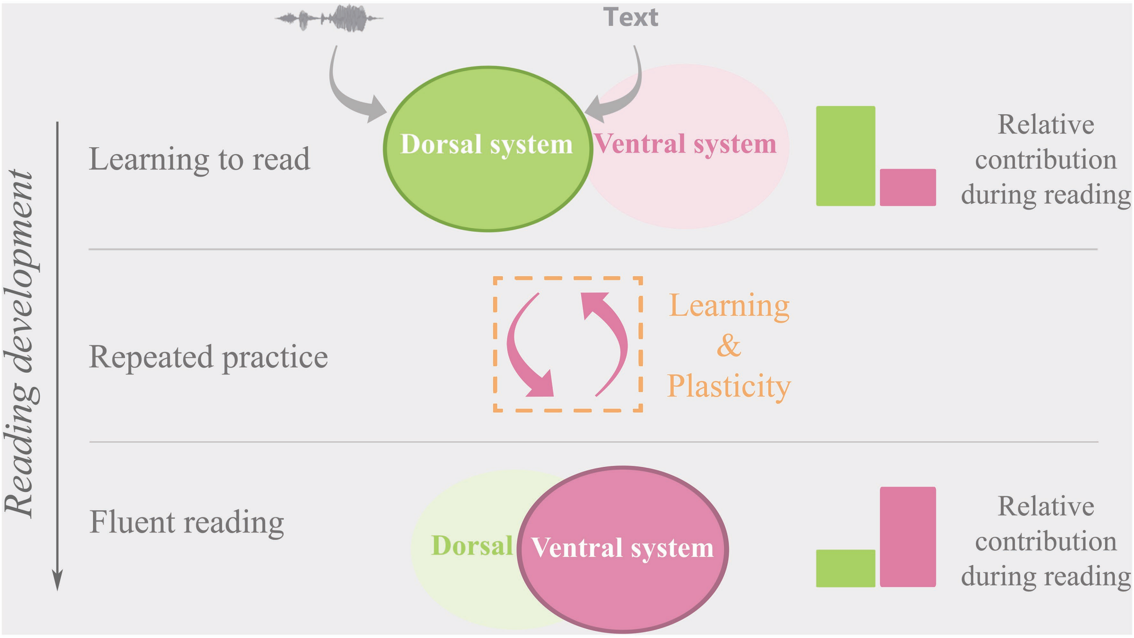

FIGURE 3 | A representation of the relative dorsal (green) and ventral (pink) cortical reading network contribution over the course of reading development.

text and becomes the dominant system used for reading (**Figure 3**, bottom row; Shaywitz et al., 2002; McCandliss et al., 2003; Sandak et al., 2004; Cohen and Dehaene, 2009). While the contribution of the dorsal network to fluent reading at this stage may be reduced, areas within the network continue to be employed especially for reading difficult, irregular words, or novel pseudowords (Pugh et al., 2001; Simos, 2002). In line with the proposed developmental shift to predominant reliance on the ventral system in fluent readers, increased connectivity between the IPL and vOTC is linked to better reading fluency and phonological skills in 5 to 6-year-olds (Yu et al., 2018a; Moulton et al., 2019), while decreased connectivity between these areas has been associated with larger gains in reading fluency in 8 to 14-year-old children (Wise Younger et al., 2017). These findings suggest a dynamic relationship between the dorsal and ventral networks where the strength of their inter-connectedness follows a non-linear inverted-u-trajectory with reading development (see also skill learning perspective below). The developmental changes in functional connectivity are paralleled by changes in diffusivity in the white matter tracts connecting the key nodes of the dorsal and ventral reading networks (Yeatman et al., 2012; Myers et al., 2014; Vanderauwera et al., 2018) the developmental trajectories of which may be different for good versus poor readers (Yeatman et al., 2012).

SKILL LEARNING AND NON-LINEAR DEVELOPMENTAL CHANGES

When acquiring a new skill, children make use of both, active, explicit strategies as well as implicit, statistical/associative learning (Shrager and Siegler, 1998; Siegler, 2005; Siegler and Araya, 2005). During the initial stages of learning, the active strategies are relied upon the most, helping to establish rules necessary to acquire a skill (Crowley et al., 1997; Karni et al., 1998). Continued practice serves as input for the implicit learning mechanisms that are mainly used during a consolidation phase involving the mastering of a given skill (Crowley et al., 1997; Shrager and Siegler, 1998; Siegler and Araya, 2005). Models of skill learning further predict that, at the brain level, learning follows an initial phase of expansion (e.g., an increase in regional activity or cortical maps) with a subsequent renormalization (e.g., a reduction of regional activity or cortical maps; Wenger et al., 2017; Lövdén et al., 2020). While these models are mostly based on perceptual, motor skill learning (Karni et al., 1998; Wenger et al., 2017; Lövdén et al., 2020), and math learning (Shrager and Siegler, 1998; Siegler, 2005; Siegler and Araya, 2005), reading acquisition similarly involves an initial phase of explicit learning of letter-speech sound mappings followed by a slower consolidation phase involving the development of reading fluency with practice and experience. In fact, several neuroimaging studies have suggested that the acquisition of reading during primary school is accompanied by non-linear inverted-u-type changes in visual and auditory cortical responses to text and audio-visual letter-speech sound stimuli (Maurer et al., 2006, 2008, 2011; Price and Devlin, 2011; Fraga González et al., 2017; Dehaene-Lambertz et al., 2018; Fraga-Gonzalez et al., 2021). Similar non-linear changes have also been reported in connectivity between the reading networks. A longitudinal study investigating changes in structural connectivity between key areas of the ventral and dorsal reading networks in children aged 5 showed an increase in connectivity between the VWFA and left IPL during the first year of reading instruction, that correlated with reading ability (Moulton et al., 2019). Longitudinal studies of functional connectivity changes in 5-to-8-year-olds, have reported a developmental increase in connectivity strength between the left IPL and lateral posterior occipito-temporal cortex in children with above-average gains in phonological processing, with children who had below-average gains showing the opposite pattern (Yu et al., 2018a). By comparison, in older, 8-14-year-old, children a longitudinal decrease in functional connectivity between the IPL and fusiform gyrus was associated with reading gains. This reduction in connectivity was observed in children who showed the largest improvement in reading across sessions (Wise Younger et al., 2017). We therefore hypothesize that, next to regional brain changes, learning to read involves dynamic trajectories of functional connectivity, starting from less reliable dorsal-to-ventral connectivity at the onset of reading instruction (i.e., no robust associations between written and spoken language), to an increase (expansion) in connectivity strength with initial reading acquisition (e.g., Yu et al., 2018a; Moulton et al., 2019), followed by a decrease in (renormalization) connectivity with repeated practice (e.g., Wise Younger et al., 2017). Once reading has become fully automatized, fast and fluent reading is mainly taken over by the ventral system (Pugh et al., 2001; Sandak et al., 2004).

Changes in cortical activation in the regions of the ventral and dorsal reading networks as well as the connectivity patterns between these areas could reflect their gradual specialization for reading. Thus, after initially establishing broad and varied links between written and spoken language, similar to model of sensory and motor skill learning (Lövdén et al., 2020), only the most efficient links may be reinforced through repeated reading practice. This selection process may shape the specialization and consolidation of local representations of visual text in the vOTC (Maurer et al., 2006; Brem et al., 2009; Ben-Shachar et al., 2011; Dehaene-Lambertz et al., 2018) and of text-to-spoken language mappings in the pSTC (Froyen et al., 2009; Brennan et al., 2013; McNorgan et al., 2014; Caffarra et al., 2021). Local specialization, in turn, may be characterized by narrowing of response properties – that is, increased sensitivity to text compared to other visual stimuli (Dehaene-Lambertz et al., 2018) – and increased local processing speed (e.g., within the vOTC Johnson, 2001). These local and interregional developmental changes in the reading network may follow non-linear inverted-u-type trajectories (Froyen et al., 2009; Fraga González et al., 2017; Fraga-Gonzalez et al., 2021), but also other types of (non)linear trajectories (Bonte et al., 2016; Dehaene-Lambertz et al., 2018).

Individual differences in the time course of reading development will inevitably affect the timing and pattern of changes in the dorsal and ventral reading networks. The time it takes to become a fluent reader is influenced by (but not limited to) genetic (Hawke et al., 2006; Keenan et al., 2006; Friend et al., 2008) and socio-economic factors (Noble et al., 2006a,b; Aikens and Barbarin, 2008). Especially individuals with (familial risk of) dyslexia may require an extended period for speech structure and audio-visual learning (e.g., Karipidis et al., 2018; Zhang et al., 2021). A longitudinal investigation of children with and without dyslexia showed delayed development of functional connectivity between vOTC and IFG between ages 6 to 8 in dyslexic compared to age-matched typical readers, reaching the same level of connectivity by age 12 (Morken et al., 2017). Aberrant functional connectivity between vOTC and the dorsal network has also been reported in cross-sectional studies, with dyslexic children showing less robust connectivity between the left vOTC, IFG, and IPL (**Figure 2**; van der Mark et al., 2011; Finn et al., 2014; Schurz et al., 2015). The connectivity patterns in these studies reveal alternate functional connectivity between the vOTC and the dorsal system, as well as connectivity to right hemisphere areas, arguably as a result of differences in the developmental trajectories in poor and fluent readers. Developmental changes in functional connectivity between the IPL and left vOTC may be key for a successful switch to automatized, ventral processing of text in typical readers (Wise Younger et al., 2017). However, dyslexic readers and at-risk pre-readers may develop different functional and structural (Steinbrink et al., 2008; Rimrodt et al., 2010; Vandermosten et al., 2012a, 2015, 2017; Cui et al., 2016; Langer et al., 2017; Vanderauwera et al., 2017) connectivity patterns between the ventral and dorsal reading networks, potentially as a compensatory reaction to difficulties with quick, automatized text processing in the vOTC.

INVESTIGATING TEXT-SPEECH SOUND LEARNING MECHANISMS

In line with the idea that the brain's reading network is formed through the association of written to spoken language representations, our understanding of individual differences in reading development will benefit from a detailed understanding of learning processes underlying the formation of these associations. Studies investigating dyslexia intervention targeting letter-speech sound automatization, have shown improvements in reading outcome and in brain responses associated with letter-speech sound integration following intervention (Žarić et al., 2015; Fraga González et al., 2016, 2017). However, typically used outcome measures of letter-speech sound integration (e.g., (in)congruency effects of learnt associations) yield variable neuro-behavioral differences in group comparisons of typical readers compared to dyslexic readers at different ages, and pre-readers at high versus low familial risk (Blau et al., 2010; Richlan et al., 2011; Žarić et al., 2014; Karipidis et al., 2018; Plewko et al., 2018). It is difficult to assess children's underlying letter-speech sound mappings in these paradigms in a way that is not biased by context variables, such as task strategies and (self-beliefs regarding) the ability to perform the experimental task. Interestingly, longitudinal behavioral evidence suggests that pre-literate children's ability to learn letter-speech sound associations – rather than their current knowledge of these associations – permits predicting individual differences in early reading skills (Horbach et al., 2015, 2018).

A promising platform to investigate audio-visual learning mechanisms can be found in artificial symbol – (speech) sound training and phonetic recalibration paradigms. Artificial symbol – sound training involves mapping known speech sounds onto novel visual symbols, thus directly targeting reading-related learning skills. Despite the observed association between pre-literate children's symbol-sound learning performance and their early reading skills (Horbach et al., 2015, 2018), no group differences in the overall ability to learn novel letter-speech sound pairs have been observed between 7- to 11-year-old children with dyslexia (Aravena et al., 2013; Law, 2018) and at-risk pre-readers (Karipidis et al., 2018) compared to their age-matched peers. Group differences have been found to emerge under time constraints (i.e., rapid naming of the letter-speech sound pairs; Aravena et al., 2013 but see Law, 2018) and when the newly learnt letter-speech sound mappings needed to be applied to another task (e.g., reading names of familiar objects using the artificial script; Aravena et al., 2013; Karipidis et al., 2018; Law, 2018). Also, the use of these mappings for decoding, including blending phonemes into syllables and word reading, has been found to predict children's future reading problems (Gellert and Elbro, 2017). Together, these findings suggest that reading problems may especially occur if a child faces difficulties in consolidating or automatizing letter-speech sound mappings rather than in creating these mappings in the first place (Blomert and Willems, 2010; Blomert, 2011; Kronschnabel et al., 2014).

Another paradigm that enables examining perceptual mechanisms associated with short-term audio-visual learning is phonetic recalibration (also "perceptual learning," Samuel and Kraljic, 2009; Vroomen and Baart., 2012). Recalibration refers to a shift in an individual's perception of ambiguous speech induced by the presentation of disambiguating visual input, such as lip-read speech (Bertelson et al., 2003; Vroomen and Baart., 2012), spoken word context (Norris et al., 2003), overt speech articulation (Scott, 2016), or text (Bonte et al., 2017; Keetels et al., 2018; Romanovska et al., 2019). In the classical paradigm, an ambiguous speech sound, e.g., /a?a/ midway between /aba/ and /ada/ is combined with a disambiguating video of a speaker articulating "aba" or "ada." The subsequent perception of the ambiguous speech sound in auditory-only trials is temporarily biased in the direction of the video – that is, it will be perceived as /aba/ following an "aba" video and as /ada/ following an "ada" video. This perceptual shift is accompanied by a measurable shift in fMRI activation patterns in early and higher-order auditory cortex (Kilian-Hütten et al., 2011). Namely, multi-voxel pattern analysis of left PT and HG activity, enabled to significantly distinguish whether, on a given trial, participants perceived the ambiguous /a?a/ sound as either /aba/ or /ada/. In other words, the same ambiguous /a?a/ sound was represented differently depending on the disambiguating video it had been coupled with. This shift indicates that the two modalities have been successfully combined and a new audio-visual association created.

An alternative to the classical recalibration paradigm – text-based recalibration – employs text as the disambiguating visual information, tapping into the mechanisms of reading-induced audio-visual plasticity. An fMRI study exploring text-based recalibration in typically reading adults found that text-induced perceptual shifts in the auditory cortical representations of ambiguous speech is mediated by the bilateral IPL (Bonte et al., 2017). Behavioral evidence has further suggested an absence of this text-induced perceptual shift in adult dyslexic readers (Keetels et al., 2018) while lip-read information was found to yield similar shifts in dyslexic and fluent readers (Baart et al., 2012; Keetels et al., 2018). Surprisingly, 8 year-old dyslexic children instead were found to show comparable text-based recalibration to their typically reading peers (Romanovska et al., 2019), emphasizing the importance of studying audio-visual learning processes across multiple age groups. At the same time, we found different cortical activation patterns accompanying these comparable behavioral text-based recalibration effects in children with and without dyslexia (Romanovska et al., 2021). Children with dyslexia showed less vOTC activation during audio-visual integration of letters and ambiguous speech compared to typically reading children. Moreover, cortical activation within this region was correlated with individual differences in reading fluency and phonological processing across groups. Additionally, across groups, higher bilateral STG activation was associated with less fluent letter-speech sound integration (Romanovska et al., 2021). These findings point to a relative difference in fluent versus less fluent reader's reliance on brain areas in the ventral and dorsal reading networks. Because the interplay between both networks is still being refined during initial reading development, less fluent readers may engage the dorsal reading network to a higher extent to successfully map letters and speech sounds. Once a more fixed and mature connectivity pattern has been established, group differences may emerge as a result of discrepant interactions between the dorsal and ventral systems in dyslexic adults (van der Mark et al., 2011; Finn et al., 2014; Schurz et al., 2015).

CONCLUSION

Reading development is a highly dynamic and individually variable process illustrating an impressive capacity of the brain to accommodate the requirements of a culturally acquired skill. These changes are shaped around the formation of solid associations between dorsal spoken language representations and ventral visual representations that become tuned to written language. Individual differences in the brain's capacity to accommodate these changes, together with compensatory strengths, such as positive self-beliefs, strong verbal reasoning, vocabulary and attention skills, presumably result in the observed high variability in children's reading outcome. The observed interactions between the dorsal and ventral reading networks may be best understood from a skill learning perspective involving non-linear developmental changes triggered by the initial acquisition of basic reading skills and their subsequent consolidation with reading practice. Within this framework, variability across typical and dyslexic readers can be characterized by individual learning trajectories with some children facing difficulties especially while learning basic reading skills, including letter-speech sound mappings, and others struggling to make the switch toward consolidating, fine-tuning or generalizing the learned skills and mappings.

One key challenge for the scientific study of reading is understanding which of the observed neuro-behavioral differences between (groups of) readers reflect vulnerabilities or risk factors for developing reading problems versus strengths or compensatory factors, or, especially in older children and adults, consequences of a history of reading problems. Promising experimental paradigms to disentangle these different explanatory possibilities are learning paradigms, such as artificial script learning and text-based recalibration that permit to trace children's actual learning trajectories. Ideally, these types of paradigms should be combined with a longitudinal multi-level approach incorporating developmental dynamics at various levels including genetic, social environmental, cortical and subcortical brain changes as well as cognitive and behavioral factors (van Atteveldt et al., 2021). This approach ideally integrates developmental changes across both domain-specific and domain-general functional networks, for example, reading, math, and executive function, thereby acknowledging the multi-deficit spectral view of specific learning disorders including dyslexia (Pennington, 2006; van Bergen et al., 2014; Peters and Ansari, 2019). A detailed understanding of children's learning trajectories across multiple levels and functions starting from the early stages of reading (precursor) skills, will help improve early prediction and, ultimately, prevent the accumulation of reading problems via individualized tailoring of reading support and intervention.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Atypical Relationships Between Neurofunctional Features of Print-Sound Integration and Reading Abilities in Chinese Children With Dyslexia

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Conquering print-sound mappings (e.g., grapheme-phoneme correspondence rules) is vital for developing fluent reading skills. In neuroimaging research, this ability can be indexed by activation differences between audiovisual congruent against incongruent conditions in brain areas such as the left superior temporal cortex. In line with it, individuals with dyslexia have difficulty in tasks requiring print-sound processing, accompanied by a reduced neural integration. However, existing evidence is almost restricted to alphabetic languages. Whether and how multisensory processing of print and sound is impaired in Chinese dyslexia remains underexplored. In this study, we applied a passive audiovisual integration paradigm with functional magnetic resonance imaging to investigate the possible dysfunctions in processing character-sound (opaque; semantics can be automatically accessed) and pinyin-sound associations (transparent; no particular meaning can be confirmed) in Chinese dyslexic children. Unexpectedly, the dyslexic group did not show reduced neural integration compared with typically developing readers in either character or pinyin experiment. However, the results revealed atypical correlations between neural integration and different reading abilities in dyslexia. Specifically, while the neural integration in the left inferior frontal cortex in processing character-sound pairs correlated with silent reading comprehension in both children with and without dyslexia, it was associated with morphological awareness (semantic-related) in controls but with rapid naming (phonological-related) in dyslexics. This result indicates Chinese dyslexic children may not use the same grapho-semantic processing strategy as their typical peers do. As for pinyin-sound processing, while a stronger neural integration in the direction of "congruent > incongruent" in the left occipito-temporal cortex and bilateral superior temporal cortices was associated with better oral reading fluency in the control group, an opposite pattern was found in dyslexia. This finding may reflect dyslexia's dysfunctional recruitment of the regions in grapho-phonological processing, which further impedes character learning.

Keywords: audiovisual integration, character, Chinese, dyslexia, individual differences, pinyin

HIGHLIGHTS

- Neurofunctional correlates of print-sound integration in Chinese children with and without dyslexia are investigated.
- Dyslexic children show atypical relationships between neural audiovisual integration and reading abilities.
- Chinese children with dyslexia are likely to use inefficient strategies to process characters and pinyin.

INTRODUCTION

Reading consists of multiple cognitive processes, and it takes years of formal instruction to achieve a high proficiency. In this process, establishing robust links between orthographic and phonological representations (e.g., grapheme-phoneme correspondence [GPC] rules) is one initial and fundamental step (Perfetti and Harris, 2013). Behavioral and neuroimaging studies of alphabetic languages have revealed that it is critical to conquer the GPC rules to develop fluent reading skills. The failure will impede building efficient grapho-semantic mapping and eventually result in reading difficulties (Shaywitz, 1998; Blomert, 2011; Richlan, 2019; Di Folco et al., 2021). Nowadays, most researchers agree that the manifestation of dyslexia is associated with linguistic features in a given language (Richlan, 2020). However, while existing evidence is almost restricted to alphabetic orthographies, the question of whether and to what extent print-sound integration is impaired in Chinese children with dyslexia remains underexplored, especially at the neurofunctional level.

Chinese has a morpheme-based logographic writing system (Perfetti et al., 2013). In addition to phonological information, semantics is strongly involved in even the most fundamental processing—character recognition (Bi et al., 2007; Yang et al., 2013; Zhao et al., 2014; Liu et al., 2017; Guan et al., 2020). At the behavioral level, longitudinal and meta-analytic studies have demonstrated the importance of both phonological-related (e.g., phonological awareness [PA], rapid naming [RAN]) and semantic-related (e.g., morphological awareness [MA]) skills in Chinese reading development (Lei et al., 2011; Pan et al., 2016; Liu et al., 2017; Ruan et al., 2018). However, it should also be noted that the tasks used in these studies required explicit processing of the written scripts. A similar situation exists at the brain level. Previous functional magnetic resonance imaging (fMRI) studies revealed hypoactivation in the left inferior and middle frontal areas during visual rhythming and lexical decision in children with dyslexia, suggesting dysfunctions of the neural substrates underlying both print-to-sound and print-to-meaning mappings in tasks requiring explicit processing (Siok et al., 2004; Liu et al., 2012; Cao et al., 2017). Paralleling the fMRI research, structural and diffusion imaging studies also provided evidence on alterations in morphometry of these regions and white matter tracts connecting them (Siok et al., 2008; Xia et al., 2016; Su et al., 2018). Hence, while these findings indicate deficits in grapho-semantic and grapho-phonological processing in Chinese children with dyslexia, the question of whether implicit and automatic processing is impaired remains largely unknown.

In this study, we adopted a passive fMRI audiovisual paradigm (i.e., without explicit phonological or semantic judgment), which is appropriate for investigating automaticity in reading-related processing. This paradigm has been used in shallow orthographies such as Dutch and demonstrated the impaired letter-sound automatized integration as a likely proximal cause of dyslexia that is independent of phonological processing deficits (Blau et al., 2008, 2009, 2010). This paradigm's basic logic is that if a brain area integrates auditory and visual inputs or is involved in the subsequent higher-level cognitive processes, its activation should differ between the congruent and incongruent conditions. This effect is usually named "congruency effect" when the activation in the congruent condition is stronger than the incongruent condition and is named "incongruency effect" otherwise. Here we used the term "audiovisual integration effect" (or "neural integration" for short), given that both directions indicate multimodal information integration somehow. Since this effect can be observed even when no task or a passive task is used, researchers regard it to reflect implicit processing (van Atteveldt et al., 2007b; Blau et al., 2010). To date, the neural integration has been demonstrated in skilled adult readers and typically developing children (van Atteveldt et al., 2004, 2007a; Blau et al., 2010; van Atteveldt and Ansari, 2014).

Of importance, direction and strength of the neural integration are affected by several factors, such as characteristics of participants and orthographic depth of languages (Blau et al., 2009, 2010; Kronschnabel et al., 2014; Holloway et al., 2015; Wang et al., 2020). For example, individuals with dyslexia showed an atypical pattern in brain areas such as the superior temporal cortex (STC) (Blau et al., 2009, 2010). This anomaly was driven by hypo-activation in the congruent condition along with hyper-activation in the incongruent condition in dyslexia, indicating reduced neural integration and lack of suppression, respectively. In terms of orthographic depth, investigations were administered with Chinese adults (Xu et al., 2019) and typically developing children recently (Xia et al., 2020). In particular, Xia et al. (2020) used Chinese characters and pinyin (a transparent alphabetic coding system that represents the pronunciations of characters, which is taught at the earliest stage of Chinese reading development and used as a scaffold in learning new characters) as experimental materials and observed a significant audiovisual integration effect in the direction of "congruent < incongruent" in the left inferior frontal cortex (IFC) and bilateral STC in processing character-sound associations. Moreover, neural integration in the left IFC in response to character-sound pairs and that in the left STC in response to pinyin-sound pairs were associated with children's performance in silent reading comprehension that relies on grapho-semantic mapping and oral word reading fluency that relies on grapho-phonological processing, respectively. This pattern is likely to be driven by stimuli's linguistic properties, including orthographic transparency and involvement of semantics. Using the same experimental design, the current fMRI study aimed to examine whether the neural audiovisual integrations of character-sounds and pinyin-sounds are impaired in Chinese dyslexia and how they associate with different levels of reading abilities.

Notably, while group comparison has been widely used to identify neural deficits in dyslexia, approaches focusing on individual differences also provide invaluable insights. In this case, investigating brain-behavior correlation is a useful strategy (Pernet et al., 2009; Jednorog et al., 2015), with which two primary patterns can be identified. The first is a universal brain-behavior correlation regardless of reading status (dyslexia vs. control), indicating that the same neural system supports the cognitive processing in both groups. For example, children's PA is correlated with the microstructural feature of the left arcuate fasciculus, even after controlling group effect (Vandermosten et al., 2012; Su et al., 2018). Alternatively, there could be distinct ways in which reading abilities correlated with brain measures between children with and without dyslexia, indicating dysfunction or compensation (Rumsey et al., 1999; Pernet et al., 2009; Hoeft et al., 2011; Tschentscher et al., 2018). For example, while typical readers rely more (higher regional cerebral blood flow) on the left inferior parietal lobule (IPL), higher activation in this area is associated with worse reading performance in dyslexia (Rumsey et al., 1999). However, previous studies commonly conducted correlation analyses while pooling individuals from different groups. Since the participants were selected on purpose, between-group differences could drive the significant correlations (Blau et al., 2010). As mentioned above, this issue can be addressed by controlling the effect of group in the statistic model or directly comparing the correlation within the dyslexic group and that within the typical readers.

To summarize, the main aim of this study was to investigate the possible impairments in Chinese children with dyslexia in implicit processing of print-sound associations and related information (e.g., semantics). We asked two specific questions. First, whether the neurofunctional correlates of print-sound integration differ between the dyslexics and controls. Second, whether the relationships between neural integration and reading abilities differ between groups. We adopted a passive fMRI audiovisual paradigm and used characters and pinyin—scripts with contrasting linguistic features—as experimental materials. Both group comparison and individual differences analytic approaches were performed. Based on the prior research in typically developing children (Xia et al., 2020), we predicted a reduced neural integration in Chinese children with dyslexia. In addition, dyslexic children might display atypical brain-behavior correlations or recruit other brain regions to integrate cross-modal information.

METHODS

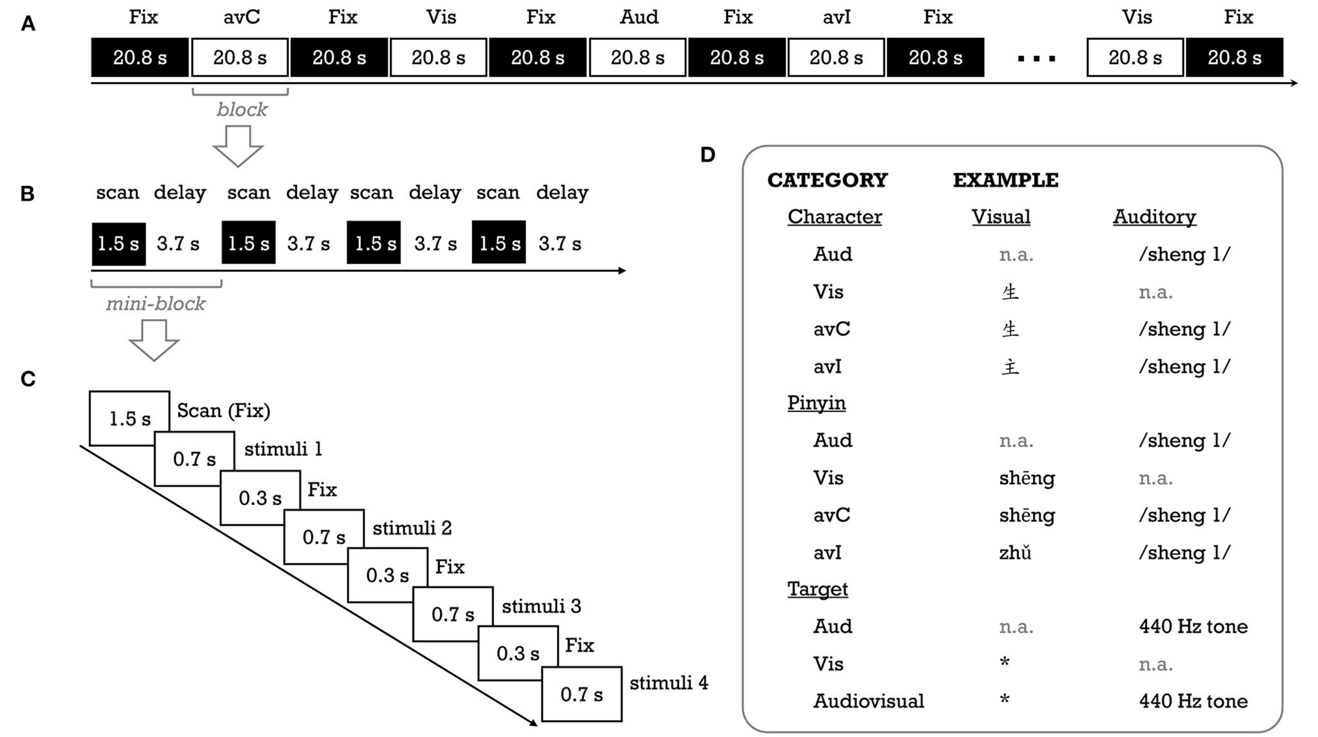
Participants and Behavioral Measures

In this study, dyslexia was operationalized by the criteria of having normal intelligence (≥80 on the abbreviated version of the *Chinese Wechsler Intelligence Scale for Children*; Wechsler, 1974) but manifesting reading difficulty (below −1 *SD* of the norm on a standardized reading screening task *Character Recognition*; Xue et al., 2013). On the other hand, each child in the control group should have normal intelligence (≥80) and a score above −0.5 *SD* of the norm on the reading screening task (the aim was to increase the gap in reading skills between groups). In addition, children in both groups should be right-handed (Oldfield, 1971) native speakers of Chinese, with normal hearing and normal or corrected-to-normal vision, and were free from neurological or psychiatric disorders. Finally, only the children that completed all the task fMRI runs, with an overall accuracy equal to or higher than 75% in the in-scanner passive task and <25% time-points labeled as outliers (i.e., "bad volume") in each run (data preprocessing section) were included.

Initially, one hundred children in grades 3–6 (including 45 dyslexia) were recruited from local elementary schools. According to the inclusion criteria described above, 23 dyslexic children (10 girls; age 111–144 months, M [SD] = 122 [10]) were included in the final analysis. Twenty-one dyslexic children were excluded due to uncompleted MRI data collection ($n = 9$), severe head motion artifacts ($n = 9$), or poor in-scanner performance ($n = 3$). One child with a history of dyslexia diagnosis but performed normally in the character recognition task at the time of data collection was also excluded (this child had received an intensive behavior intervention program). The controls were chosen to match the dyslexic group on grade, age, and sex. The final control group consisted of 22 typically developing children with qualified neuroimaging data (12 girls; age 118–140 months, M [SD] = 127 [6]).

Each child received a battery of behavioral tests on reading and cognitive-linguistic skills individually in a silent room on the same day of the MRI session. The reading measurements contained: (1) an untimed character naming task (*Character Recognition*) to estimate the number of characters children had conquered (Xue et al., 2013); (2) an oral word reading task (*Word List Reading*) to measure how fast the participant accurately retrieved phonological representations from visually presented high-frequency two-character words (Zhang et al., 2012); and (3) a timed comprehension task (*Silent Reading Comprehension*) to assess the proficiency of meaning access and semantic judgment (Lei et al., 2011). In addition, PA, RAN, and MA—the three most critical cognitive-linguistic skills in Chinese reading acquisition—were measured by *Phoneme Deletion* (Li et al., 2012), *Digit RAN* (Liu et al., 2017), and *Morphological Production* (Shu et al., 2006).

Written informed consents were obtained from all the children and their guardians after a detailed explanation of the



CATEGORY	EXAMPLE	
Character	Visual	Auditory
Aud	n.a.	/sheng 1/
Vis	生	n.a.
avC	生	/sheng 1/
avI	主	/sheng 1/
Pinyin		
Aud	n.a.	/sheng 1/
Vis	shēng	n.a.
avC	shēng	/sheng 1/
avI	zhǔ	/sheng 1/
Target		
Aud	n.a.	440 Hz tone
Vis	*	n.a.
Audiovisual	*	440 Hz tone

FIGURE 1 | Schematic description of the fMRI experimental procedure **(A–C)** for a run, a block, and a mini-block, respectively] and stimuli examples **(D)**. Aud, auditory; avC, audiovisual congruent; avI, audiovisual incongruent; Fix, fixation; Vis, visual. *Was the visual target of the fMRI task, without any meaning.

objectives and procedure of the study. After the experiment, each child received a book and a set of stationery as reward. This study was approved by the Institutional Review Board of the State Key Laboratory of Cognitive Neuroscience and Learning at Beijing Normal University. The data collection was conducted in 2018.

Experimental Design

This study adopted a passive audiovisual paradigm that had been widely used in the previous fMRI studies investigating the neural basis of letter-sound integration (**Figure 1**). The details about the stimuli and procedure can be found in Xia et al. (2020). In brief, 56 pictographic characters with high-frequency ($M \pm SD = 929 \pm 1486$ per million; Chinese Single-Character Word Database; https://blclab.org/pyscholinguistic-norms-database/; Liu et al., 2007) and are frequently used as radicals in phonograms were selected. These characters are visually simple (number of strokes: $M = 4.34$, $Range = 1–9$), learned early (age of acquisition: $M = 3$ years, $Range = 2–5$ years), and with high rating scores (7 as the highest value) on concreteness (5.76 ± 1.19) and imageability (5.96 ± 1.00). The pinyin spellings of these characters were used as the visual stimuli in the pinyin experiment. The auditory stimuli (duration: $M \pm SD = 476.3 \pm 87.5$ ms) were the characters' sounds (i.e., syllables). A native Chinese male recorded the audio files with a sampling rate of 44.1 kHz and 16-bit quantization. The sound files were then normalized to 85 dB and bandpass (100–4000 Hz) filtered with Audacity (https://www.audacityteam.org/).

The study consisted of four task fMRI runs, with the first and second runs for the pinyin experiment and the third and fourth runs for the character experiment. We used the fixed order to prevent priming from characters on visually presented pinyin stimuli. Two unimodal (auditory [Aud]; visual [Vis]) and two cross-modal conditions (congruent [avC]; incongruent [avI]) were created for each experiment (**Figure 1**). In this study, we focused on activation differences between the congruent against incongruent conditions—the neural integration. A block design was used to deliver stimuli. There were eight task blocks (duration = 20.8 s; two blocks for each condition) interleaved with nine rest blocks (duration = 20.8 s) in a single run. A task block contained four mini-blocks. A 1.5 s period was used to collect a whole-brain volume within each mini-block, and a silent period of 3.7 s was used to present stimuli (see "image acquisition" part). The stimuli were presented in white at the center of a black background ("*KaiTi*" font, 96 pt for characters; "*Century Schoolbook*" font, 90 pt for pinyin). A crosshair was presented at the center of the screen whenever there was no stimulus. To help children keep their attention on the stimuli while avoiding explicit congruency judgment, we used a target detection task (Blau et al., 2010). Specifically, in each task block, two out of 16 experimental stimuli were randomly replaced with the auditory target (440 Hz pure tone), visual target (an unpronounceable symbol) or their combination. The participant was asked to press a button with the right index finger as accurately and quickly as possible whenever the target appeared.

Image Acquisition

All brain images were collected at Beijing Normal University Imaging Center for Brain Research using a 3-Tesla Siemens MAGNETOM Trio Tim scanner with a 12-channel head coil. The children first attended a training session to get familiar with the experimental environment and the scanning noise. During the formal scan, foam pads were used to hold their heads secure during scanning to improve image quality. In addition, children could take a break between sequences to reduce the possible fatigue effect. For each participant, two functional runs for the pinyin experiment, one anatomical run for structural images, and two functional runs for the character experiment were administered sequentially. The quality of the brain images was evaluated immediately by a radiologist who was blinded to the details of this study.

The parameters of the functional images (Gradient Echo Planar Imaging [EPI]) were as follows, repetition time, 5.2 s; echo time, 32 ms; acquisition time, 1.5 s; flip angle, 90 degrees; slice thickness, 4.5 mm; interscan gap, 0.675 mm; voxel size, $3.0 \times 3.0 \times 4.5$ mm^3; 24 slices; 68 volumes.) Since this study contained auditory stimuli, to avoid artifacts induced by the noise during scanning, we used a sparse sampling design with 1.5 s for image collection and 3.7 s delay for stimuli presentation (Shah et al., 2000). The parameters of the structural images (Magnetization-Prepared Rapid Acquisition with Gradient Echo [MPRAGE]) were as follows, repetition time, 5.2 s; echo time, 3.39 ms; inversion time, 1.1 s; flip angle, seven degrees; slice thickness, 1.33 mm; interscan gap, 0 mm; voxel size, $1.3 \times 1.0 \times 1.3$ mm^3; 144 axial slices.)

Data Preprocessing

Functional data were analyzed with SPM12 (https://www.fil.ion.ucl.ac.uk/spm/). Three dummy scans were added at the beginning of each run to avoid the T1 equilibration effect. No additional volumes were discarded during the preprocessing. The sequence was corrected for head motion. The "bad volumes" were identified with ART-based outlier detection (https://www.nitrc.org/projects/artifact_detect). Considering the age range of participants, a liberal threshold (intensity > 9 *SD*; frame-to-frame head motion > 2 mm) was used. T1 images were segmented and used for transferring the fMRI data from native space to the standard Montreal Neurological Institute (MNI) space. The normalized images were smoothed with an 8-mm Full-Width Half-Maximum Gaussian kernel, and the resulting data were used in the subsequent model estimation. In the 1st level analysis, four experimental conditions, seven head motion parameters (three for translations, three for rotations, and one for framewise displacement), and the time point of each "bad volume" were included in the model. The contrast map in which the value of each voxel refers to "avC-avI" (i.e., positive value stands for higher activation in avC than avI; negative value stands for lower activation in avC than avI) was calculated for each child and used in the subsequent analyses.

Statistics

Deficits in reading and reading-related cognitive skills in children with dyslexia were examined at the behavioral level. We first performed descriptive statistics of multiple behavioral tasks in each group and then conducted group comparisons. Next, we calculated correlations between reading and cognitive-linguistic skills within each group and compared them between groups. The Spearman method was used for the variable that was not normally distributed. As for in-scanner performance, a correct response was defined as the button press to the target with a reaction time (RT) ranged from 200 to 2000 ms. Only correct trials were used to calculate the average RT. Finally, the effects of group and run and their interaction were examined on accuracy (ACC) and RT with analysis of variance (ANOVA).

We conducted brain analyses focusing on differences between the two cross-modal conditions for the character and pinyin experiments, respectively, with the same analytic approaches. The nuisance variables of age, sex, and performance IQ were controlled in all the analyses. First, a voxel-wise whole-brain 2 (group: control vs. dyslexic) × 2 (condition: avC vs. avI) ANOVA (i.e., the group comparison approach) was conducted to examine whether the brain regions showing neural integration in children with dyslexia were the same as those in the control group. Significant clusters were identified with the FWE-corrected threshold of p-cluster < 0.05 (p-voxel < 0.001 for height). These clusters were used as regions-of-interest (ROIs), and *post-hoc* t-tests were conducted to interrogate the effects. Complementary ROI analyses were performed to examine correlations between the neural integration with reading and reading-related cognitive-linguistic skills in each group, to identify the reading-related processes involved in audiovisual integration of character/pinyin for typical and dyslexic children, respectively. Once a significant correlation was revealed, we conducted a correlation coefficient comparison between groups.

Next, we used two individual differences approaches to examine the shared and different brain-behavior correlations in children with and without dyslexia in the character and pinyin experiments at the whole-brain level. First, to identify the shared neural basis associated with behavioral performance between groups, we conducted voxel-wise whole-brain regression analyses on the contrast maps of avC against avI across all the participants while controlling for the effects of group, age, sex, and performance IQ. Children's performance in *Word List Reading* and *Silent Reading Comprehension* tasks were used as regressors in separate models to examine the relationships between neural processing features during print-sound integration with reading abilities that rely more on grapho-phonological mapping and grapho-semantic mapping, respectively. Second, we examined whether the associations between neural integration and reading abilities differ between groups. Same as the previous analysis, we used *Word List Reading* and *Silent Reading Comprehension* as variates of interest in separate models, along with the factor of group and the interaction. In each analysis, an F-test was administered with the FWE-corrected threshold of p-cluster $<$ 0.05 (p-voxel < 0.001 for height), followed by ROI analysis to interrogate the significant effects.

To visualize the results, significant clusters were presented on a FreeSurfer surface template with BrainNet Viewer (Xia et al., 2013). Anatomical labeling was performed using the AAL atlas with DPABI (http://rfmri.org/dpabi).

TABLE 1 | Demographic and behavioral profiles.

Measures	Typical readers ($n = 22$)			Reading disorder ($n = 23$)			Comparison	
	Mean	*SD*	*Range*	*Mean*	*SD*	*Range*	t/X^2	*p*-value
Age (month)	127	6	118 ∼ 140	122†	10	111 ∼ 144	1.938	0.061
Sex (female/male)	12/10			10/13			0.552	0.556
Verbal IQ (standard score)	109	12	88 ∼ 139	97	11	67 ∼ 118	3.668	<0.001
Performance IQ (standard score)	115	13	82 ∼ 137	105	12	82 ∼ 135	2.512	0.016
Full-Scale IQ (standard score)	113	11	93 ∼ 130	101	9	84 ∼ 116	3.986	<0.001
Character recognition (item)	122	8	107 ∼ 140	86 †	11	53 ∼ 99	11.830	<0.001
Standard score	1.38	0.66	0.41 ∼ 2.43	−2.18	0.83	−4.520 ∼ −1.020	12.701	<0.001
Word list reading (word/minute)	94‡	16	72 ∼ 140	63	11	40 ∼ 83	7.612	<0.001
Standard score	0.95†	1.11	−0.38 ∼ 4.06	−1.584	0.67	−2.930 ∼ −0.130	7.278	<0.001
Silent reading comprehension (character/minute)	361‡	104	220 ∼ 565	163	56	70 ∼ 304	7.890	<0.001
Standard score	0.98‡	1.04	−0.38 ∼ 3.12	−1.083	0.57	−2.250 ∼ 0.430	7.998	<0.001
Phoneme deletion (item)	21†	4	7 ∼ 25	17†	6	1 ∼ 25	2.848	0.007
Rapid naming (second)	17	2	11 ∼ 20	22	4	15 ∼ 30	−5.481	<0.001
Morphological production (item)	24‡	3	20 ∼ 29	22	3	13 ∼ 28	2.927	0.005

†*Shapiro-Wilk* $p < 0.05$, $^{\ddagger}0.05 <$ *Shapiro-Wilk* $p < 0.01$.

All the behavioral and ROI analyses were administered with SPSS (v24; SPSS Inc., Chicago, IL, USA). Effects were considered significant at $p < 0.05$, and $0.05 < p < 0.1$ was considered indicative of a trend.

RESULTS

Behavior

Reading Measures and Group Comparisons

Statistical metrics including *M*, *SD*, *Range*, and result of the Shapiro-Wilk test of each behavioral measurement are presented in **Table 1** (see **Supplementary Figure 1** for plots). The dyslexic group performed worse in all the reading and reading-related cognitive tasks than the typically developing children (all *p*'s < 0.007). No significant between-group differences were found on age or sex (both *p*'s > 0.05). In addition, the IQs of all the children were within the normal range, while the typical readers had higher scores on both verbal and performance subscales.

Correlations Between Reading and Reading-Related Cognitive Skills

Both same and different correlations between reading and cognitive-linguistic skills were observed between children with and without dyslexia. In typical readers, character recognition was significantly correlated with MA ($r = 0.589$, $p = 0.004$) but not PA ($r = 0.117$, $p = 0.606$) or RAN ($r = -0.301$, $p = 0.174$). In dyslexics, however, this ability was associated with PA ($r = 0.489$, $p = 0.018$), but not RAN ($r = -0.269$, $p = 0.214$) or MA ($r = 0.008$, $p = 0.970$). The group difference on the correlation coefficients between character recognition and MA was significant ($Z = 2.09$, $p = 0.037$). A similar pattern was found in silent reading comprehension proficiency, where the scores were correlated with MA ($r = 0.456$, $p = 0.033$) in controls but not dyslexia ($r = -0.012$, $p = 0.957$). On the contrast, oral reading fluency was significantly correlated with RAN in both groups (controls: $r = -0.531$, $p = 0.012$; dyslexics: $r = -0.578$, $p = 0.004$).

In-Scanner Performance

The aim of using a passive target detection task was to ensure that the participant focused their attention on the stimuli delivered via auditory and visual modalities without performing explicit congruency judgment. The results revealed that children in both groups performed the task with high ACC (controls: *M* [*SD*] = 96.7% [2.9]; dyslexics: *M* [*SD*] = 92.4% [5.0]). In the ANOVA, the main effects of group were significant on both ACC ($p = 0.001$) and RT ($p = 0.012$). The *post-hoc* analyses showed that the children with dyslexia had lower accuracy and used more time to complete the tasks than the normal controls. The main effect of run was significant on RT ($p = 0.012$; faster as the experiment proceeds) but not on ACC ($p = 0.645$). No significant group × run interaction was observed on either ACC or RT (both *p*'s > 0.05).

fMRI

We used group comparison (ANOVA), and individual differences (brain-behavior correlation) approaches to investigate the impaired neurofunctional features accompanying print-sound integration in Chinese children with dyslexia. In this section, we first present the results of the character experiment, followed by the pinyin experiment.

Character: Whole-Brain ANOVA and ROI Analysis

In the voxel-wise whole-brain ANOVA, the left IFC and STC showed a significant main effect of condition that survived the FWE corrected *p*-cluster < 0.05 (*p*-voxel < 0.001 for height; **Table 2**; **Figure 2A**). The follow-up analysis revealed less activation in the congruent than incongruent conditions in both the controls (LIFC: $t = 4.361$, $p < 0.001$; LSTC: $t = 3.646$, $p =$

TABLE 2 | Significant clusters in the voxel-wise whole-brain analyses.

Experiment and contrast	Label	Brain area	$P_{\text{FWE-corrected}}$	Size	Peak *F*	X	Y	Z
Character								
Main effect of condition	LSTC	Left middle and superior temporal gyri	0.007	391	26.86	−60	−32	6
	LIFC	Left inferior frontal gyrus, opercular and triangular parts	0.024	281	23.90	−46	16	14
Pinyin								
Group difference in correlation	LOTC	Inferior and middle occipital gyri, fusiform gyrus	0.004	358	29.28	−44	−72	−2
Brain: avC-avI	LSTC	Left middle and superior temporal gyri	0.039	197	23.02	−52	−44	10
Behavior: *Oral reading fluency*	RSTC	Right superior temporal gyrus, Rolandic operculum	0.047	185	38.68	62	−8	4

The significant clusters were identified with the FWE-corrected threshold of p-cluster < 0.05 (p-voxel < 0.001 for height). Brain area labeling is based on the AAL atlas. Cluster size refers to the number of voxels.

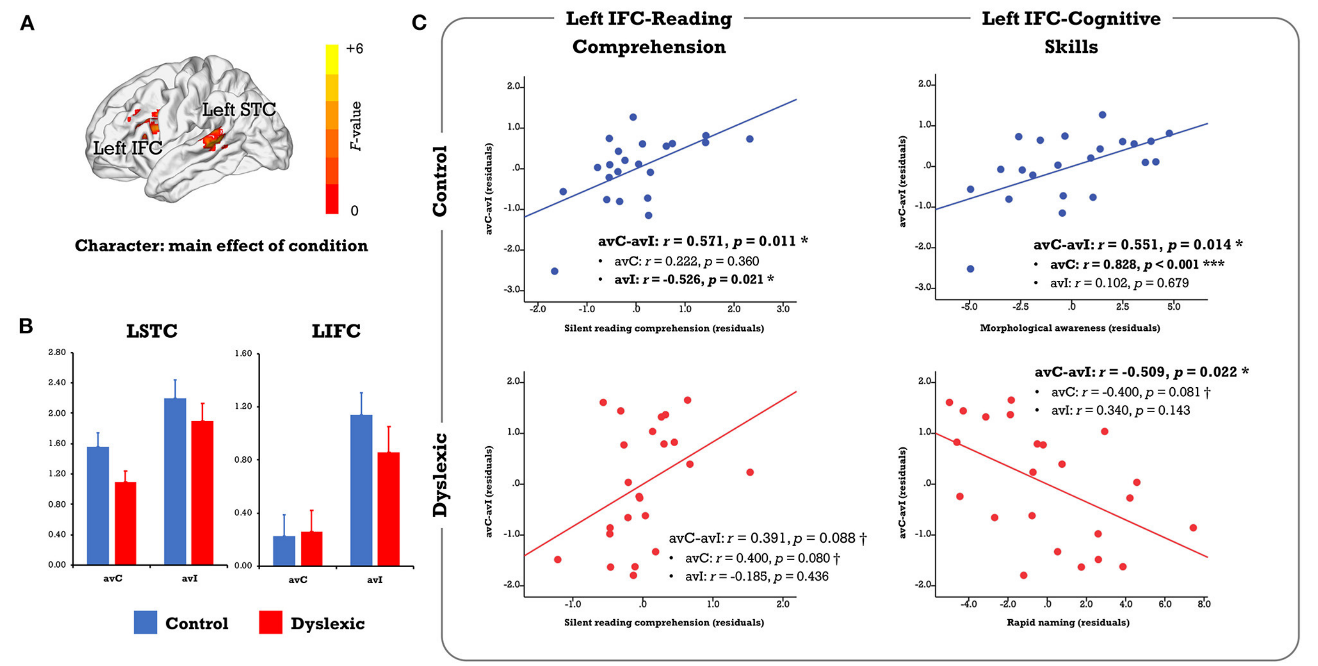


FIGURE 2 | (A) Results of the voxel-wise whole-brain ANOVA on the character conditions. Only clusters showing a significant main effect of condition were identified at the FWE corrected threshold of *p*-cluster < 0.05 (*p*-voxel < 0.001 for height). No region showed significant main effect of group or group × condition interaction. **(B)** The bar plots present brain activation in the audiovisual congruent and incongruent conditions for the control and dyslexic groups. **(C)** The scatterplots display correlations between the neural audiovisual integration effect (avC-avI) in the left IFC with silent reading comprehension proficiency and related cognitive-linguistic skills (morphological awareness, rapid naming). avC, audiovisual congruent; avI, audiovisual incongruent; IFC, inferior frontal cortex; STC, superior temporal cortex. $^{***}p < 0.001$, $^{*}p < 0.05$, $^{\dagger}p < 0.1$.

0.002) and the dyslexics (LIFC: $t = 2.346$, $p = 0.028$; LSTC: $t = 3.427$, $p = 0.002$; **Figure 2B**). No main effect of group or group × condition interaction survived the whole-brain FWE correction.

In the complementary ROI analysis, we observed similar correlations between the neural integration and reading comprehension proficiency in the left IFC in both groups (controls: $r = 0.571$, $p = 0.011$; dyslexics: $r = 0.391$, $p = 0.088$, marginally significant; **Figure 2C**). However, the relative contribution of each cross-modal condition was different. To be specific, the correlation was driven by the incongruent condition in typical readers (avC: $r = 0.222$, $p = 0.360$; avI: $r = -0.526$, $p = 0.021$) but was more related to the congruent condition in dyslexia (avC: $r = 0.400$, $p = 0.080$, marginally significant; avI: $r = -0.185$, $p = 0.436$). Between-group difference on the correlation coefficients between reading comprehension proficiency and brain activation in the incongruent condition was significant ($Z = 2.41$, $p = 0.016$). The distinct patterns of the correlations between the neural integration and reading-related cognitive skills further support the idea that different mechanisms underlie the integration-comprehension relationships in the two groups (**Figure 2C**): the neural integration in the left IFC was correlated with MA in the controls ($r = 0.551$, $p = 0.014$) but not in the dyslexics ($r = -0.025$, $p = 0.915$). Group difference on the correlation coefficients was significant ($Z = 2.01$, $p = 0.044$). On the other hand, the effect was correlated with RAN in

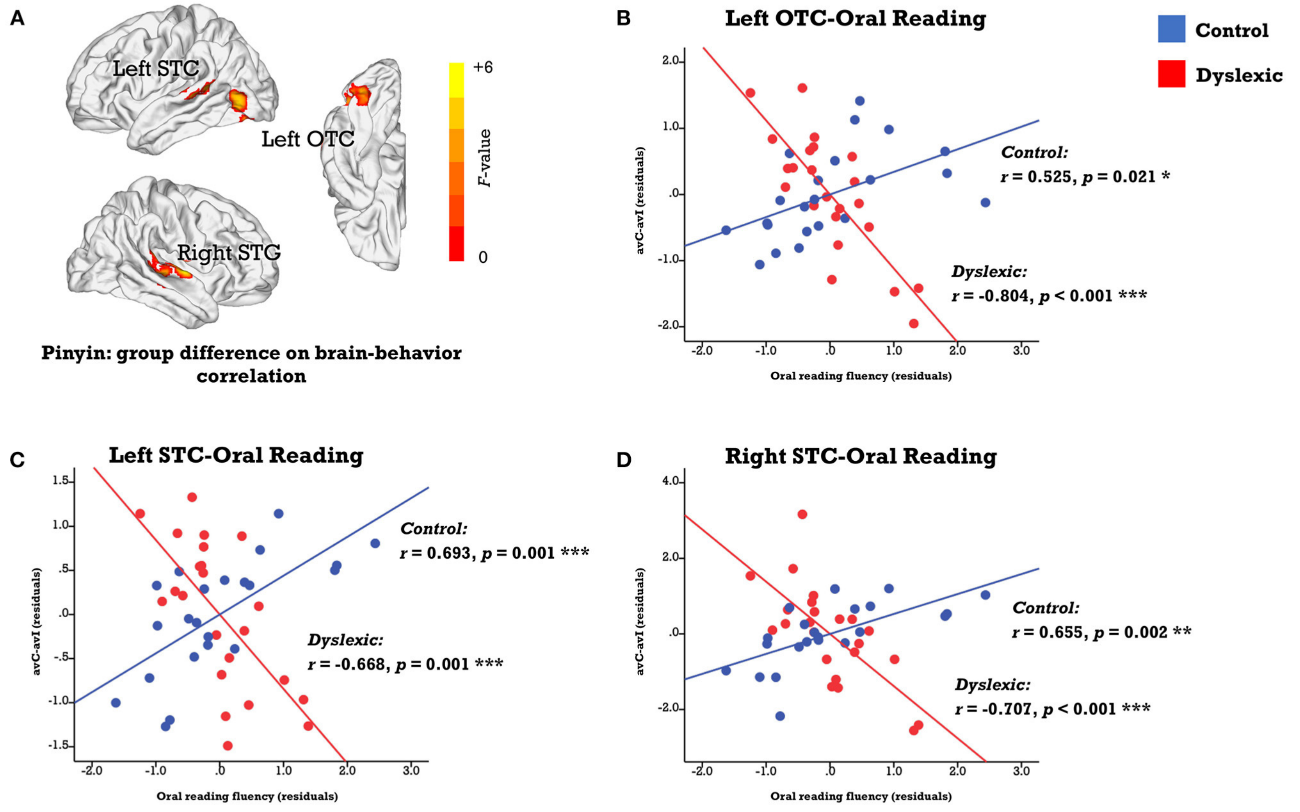


FIGURE 3 | (A) Brain map of regions showing significant between-group differences in the correlation between the audiovisual integration effect and oral reading fluency (FWE corrected p-cluster < 0.05, p-voxel < 0.001 for height). The scatterplots presents correlations in each group (blue: control; red: dyslexic) in the left OTC **(B)**, STC **(C)**, and right STC **(D)**. avC, audiovisual congruent; avI, audiovisual incongruent; OTC, occipito-temporal cortex; STC, superior temporal cortex. $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$.

the dyslexics ($r = -0.509$, $p = 0.022$) but not in the controls ($r = -0.338$, $p = 0.157$).

Character: Whole-Brain Group × Behavior Interaction

Regarding the individual differences approaches, no cluster survived the FWE-corrected threshold of p-cluster < 0.05 (p-voxel < 0.001 for height) in the analysis that investigated the same relationships between the neural integration and reading abilities across groups or that explored the correlation differences between groups.

Pinyin: Whole-Brain Group Comparison

The same analytic approaches were used in the pinyin experiment. In the voxel-wise whole-brain ANOVA, no regions showed significant main effect of group or condition or their interaction at the FWE corrected threshold of p-cluster < 0.05 (p-voxel < 0.001 for height).

Pinyin: Whole-Brain Group × Behavior Interaction and ROI Analysis

We investigated the neural deficits with the individual differences approaches in a whole-brain fashion. While no region displayed the same brain-behavior correlation across groups, clusters located in the left occipitotemporal cortex (OTC) and bilateral STC showed significant between-group differences in the correlation between the neural integration and oral reading fluency (FWE corrected p-cluster < 0.05, p-voxel < 0.001 for height; **Table 2**; **Figure 3A**). The subsequent analyses revealed positive brain-reading correlations in typical readers and negative correlations in children with dyslexia (**Figures 3B–D**; **Table 3**). Furthermore, the correlations in the left OTC (avC: $r = 0.685$, $p = 0.001$; avI: $r = 0.118$, $p = 0.631$) and STC (avC: $r = 0.588$, $p = 0.008$; avI: $r = -0.014$, $p = 0.956$) were driven by the congruent condition in the control group, while oral word reading fluency was not correlated with brain activation of the right STC in either the congruent condition ($r = 0.240$, $p = 0.321$) or incongruent condition ($r = -0.259$, $p = 0.284$). In contrast, in dyslexia, the correlations were driven by the incongruent condition (left OTC: $r = 0.674$; $p = 0.001$; left STC: $r = 0.445$, $p = 0.049$; right STC: $r = 0.543$, $p = 0.013$) but not the congruent condition (left OTC: $r = 0.026$, $p = 0.913$; left STC: $r = -0.050$, $p = 0.833$; right STC: $r = -0.181$, $p = 0.444$) in all three brain regions. Between-group differences on the correlations of the oral reading fluency and activation in the congruent condition in the left OTC ($Z = 2.54$, $p = 0.011$) and left STC ($Z = 2.26$, $p = 0.024$), and on the correlations of the oral reading fluency and activation

TABLE 3 | Brain-behavior correlations in the significant clusters in the voxel-wise whole-brain regression analyses.

Behavior:	**Group**	**Integration effect (avC-avI)**		**avC**		**avI**	
Oral reading fluency		***r*-value**	***p*-value**	***r*-value**	***p*-value**	***r*-value**	***p*-value**
L OTC	Control	0.525*	0.021	0.685**	0.001	0.118	0.631
	Dyslexic	−0.804***	< 0.001	0.026	0.913	0.674**	0.001
L STC	Control	0.693**	0.001	0.588**	0.008	−0.014	0.956
	Dyslexic	−0.668**	0.001	−0.050	0.833	0.445*	0.049
R STC	Control	0.655**	0.002	0.240	0.321	−0.259	0.284
	Dyslexic	−0.706***	< 0.001	−0.181	0.444	0.543*	0.013

*Age, sex, and performance IQ were controlled statistically. avC, audiovisual congruent; avI, audiovisual incongruent. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.*

in the in incongruent condition in the left OTC ($Z = -2.18$, $p = 0.029$) and right STC ($Z = -2.73$, $p = 0.006$) were significant.

Regarding correlations between the neural integration and reading-related cognitive-linguistic skills, the left STC was negatively associated with RAN in controls ($r = -0.479$, $p = 0.038$) and showed a trend positively correlated with RAN in dyslexics ($r = 0.394$, $p = 0.085$, marginally significant). The between-group difference was significant ($Z = -2.93$, $p = 0.003$).

DISCUSSION

This study investigated the neurofunctional features of implicit print-sound integration and their relationships with reading abilities in Chinese children with and without dyslexia. We adopted an fMRI audiovisual paradigm with a passive target detection task, where characters and pinyin—scripts with dramatically different orthographic depths—were used as experimental materials. Of importance, due to the morpho-syllabic nature of characters, semantic information can be automatically activated during character recognition, at least in typical readers. That is, this study enabled us to tap into the three-way relationship between orthography, phonology, and semantics in normal and impaired readers without demanding explicit phonological or semantic processing. Although no between-group differences on the audiovisual integration effect at the brain level were found, the results revealed strikingly atypical correlations between the neural integration of both character-sounds and pinyin-sounds with reading abilities in Chinese children with dyslexia. On the one hand, these anomalies indicate that children with dyslexia rely more on articulatory phonological information during implicit character processing, reflecting a less developed automatic grapho-semantic mapping and integration. On the other hand, it also suggests a malfunctional grapho-phonological mapping in dyslexia and implies that these children may have difficulty in developing the same pinyin processing strategy and transferring it to learning characters as their typically developing peers do.

Left IFC and Inefficient Grapho-Semantic Mapping in Chinese Dyslexia

First, this study revealed inefficient semantic information access from visual input in Chinese children with dyslexia. We observed slower silent reading comprehension in the dyslexia group. Moreover, while both character recognition accuracy and reading comprehension proficiency were associated with MA in typical readers, children with dyslexia showed significant correlations between reading abilities with other cognitive-linguistic skills instead of MA. Specifically, character recognition was correlated with PA, in line with the previous study with a large independent sample (Song et al., 2020). Regarding silent reading comprehension, although no correlation was significant, there was a trend with RAN, a phonological processing skill that consists of rapid and accurate phonological representation access, retrieval, and articulatory operations. This result is in line with recent studies in which phonological skill contributes to reading more at the early stages of reading acquisition, and the contribution of morphological processing skill increases as children grow (Liu et al., 2017). In addition to the direct effect, MA also mediates the effect of PA on reading (Pan et al., 2016).

Furthermore, we used a passive fMRI audiovisual paradigm to probe the neural bases of processing character-sound associations in Chinese children with and without dyslexia. In terms of brain activation in the left IFC and STC, dyslexic children seem to integrate information from auditory and visual modalities the same way as controls, reflected as a strong audiovisual integration effect in the direction of "congruent < incongruent." Moreover, the neural integration in the left IFC was associated with silent reading comprehension proficiency, regardless of reading status. However, between-group differences were uncovered in the subsequent ROI analyses. First, while the integration-comprehension association was driven more by the incongruent condition in typical readers, it was driven more by the congruent condition in children with dyslexia, suggesting dyslexic and typical children may use different strategies in processing characters and corresponding sounds, and this difference enlarges with reading abilities increasing within each group. Second, while the audiovisual integration effect in the left IFC was associated with MA in the control group, it was correlated with RAN in dyslexia. These findings indicate that articulatory phonological processing is more likely involved in implicit processing of character-sound pairs in children with dyslexia. In the previous studies investigating neural impairment in Chinese dyslexia, both hypo- and hyper-activation of the left frontal areas were reported (Siok et al., 2004; Liu et al., 2012; Cao et al., 2017). In a meta-analysis, different parts of the left IFC were distinguished based on functionality, where individuals with dyslexia displayed reduced activation in the ventral part associated with semantic processing but increased activation in the dorsal part that was associated with articulatory processing, presumably compensating for their less efficient grapho-semantic route (Richlan et al., 2011; Hancock et al., 2017). Given that the frontal region is multifunctional (Hagoort, 2014; Fedorenko and Blank, 2020), dyslexia may recruit it in reading-related processing in a different way compared with typical readers.

Of note, the in-scanner task used in this study did not require any sound-semantic or print-semantic processing. Nevertheless, since Chinese has a morpheme-based logographic writing system that involves semantic information even at the character processing level (Yang et al., 2013; Zhao et al., 2014; Liu et al., 2017; Guan et al., 2020), both phonological and semantic information could be accessed effortlessly, at least in typical readers who have received 4–5 years of formal instruction. Thus, it is reasonable to predict that semantic processing skill plays an equal or even more critical role in reading development than phonological processing skill, and its impairments will result in reading difficulties. In line with this hypothesis, previous studies of Chinese demonstrated morphological awareness uniquely predicted reading outcomes and dyslexia status (Pan et al., 2016; Ruan et al., 2018; Song et al., 2020). The current results also showed that while the left IFC was strongly involved in the character-sound integration in both groups, it was more associated with articulatory phonological processing in dyslexia and semantic-related morphological processing in typical children. The region is close to the one found to underlie morphological processing and show hypo-activation in children with dyslexia during tasks requiring explicit semantic processing (Liu et al., 2013; Zou et al., 2015).

In short, the findings of the character experiment suggest that Chinese children with dyslexia have yet to develop the same brain system for automated semantic access and integration during implicit character/word recognition as that in typically developing children. In contrast, these children are more likely to rely on an articulatory strategy by recruiting the multifunctional frontal area, which may underpin their slow reading comprehension.

Bilateral TPC, Left OTC, and Malfunctioning Grapho-Phonological Mapping in Chinese Dyslexia

In addition to the inefficient grapho-semantic mapping, this study also indicates that children with dyslexia may not develop a typical grapho-phonological mapping. At the behavior level, the dyslexic group performed worse in the tasks measuring oral reading fluency, PA, and RAN, in line with previous studies (e.g., Lei et al., 2011). In the pinyin experiment, we observed differential brain-behavior correlations in the classic reading-related areas, including the left OTC and bilateral STC. The morphometric measurements in these regions have also been associated with oral reading fluency in Chinese school-age children (Xia et al., 2018). In particular, the neural integration in the direction of "congruent > incongruent" in response to pinyin-sound pairs was positively associated with oral reading fluency in typical controls: the better the children performed in the oral word reading task, the higher the activation was in the congruent condition than incongruent condition. In contrast, the direction of the correlation was negative in dyslexia: children with higher reading fluency showed higher activation in incongruent than congruent conditions. Additionally, the correlations in the control group were driven more by individual differences in brain responses to the congruent stimuli. In contrast, the correlations in the dyslexic group were driven more by the incongruent condition. These findings suggest that while the same brain regions were recruited for both groups' implicit audiovisual integration of pinyin, children with dyslexia may use them differently.

The OTC and STC in the left hemisphere have been regarded as critical nodes in the classic reading network. Deficits in these areas have also been repeatedly reported in dyslexia (Richlan et al., 2009, 2011). On the one hand, the left OTC has been considered the interface for initially integrating orthographic, phonological, and semantic information (Price and Devlin, 2011). In addition, the left OTC contains a specific portion in the fusiform gyrus named Visual Word Form Area that has been found to respond specifically to word and word-like stimuli. The left STC, on the other hand, is a central area that represents phonological information (Boets et al., 2013; Glezer et al., 2016), including lexical tone—the supramarginal phoneme in tonal languages such as Chinese (Zhang et al., 2011; Si et al., 2017). The left STC is functionally and structurally connected to the left OTC, which can be shaped by learning grapho-phonological mappings (Thiebaut de Schotten et al., 2014; Stevens et al., 2017). In the current study, besides the left-hemispheric regions, the right STC also showed significant group differences in brain-behavior relationships. Although this region has been less frequently reported in previous studies in alphabetic languages, it subserves lexical tone processing in Chinese (Zhang et al., 2011; Si et al., 2017; Liang and Du, 2018). In addition, the cortical thickness of this area is also associated with oral reading fluency in typically developing Chinese children (Xia et al., 2018).

The differential relationship between the audiovisual integration effect during pinyin-sound processing and oral word reading fluency in dyslexia can be interpreted in at least two ways. First, suppose pinyin processing skill is a continuum, and dyslexia represents the lower end. In that case, the current finding then hints at the expansion and renormalization hypothesis of brain plasticity associated with skill learning (Wenger et al., 2017). That is, the growth curve of print-sound integration is an inverse U-shape. When the child starts learning pinyin, the brain response to incongruent audiovisual pairs is lower than congruent pairs. With learning, mismatched information extracted from visual and auditory modalities induces higher activation during integration. Then, children turn to focus on overlearned visual scripts by efficiently suppressing attractive auditory information at the highly familiar stage. In this case, activation in the incongruent condition will be suppressed and weaker than the congruent condition. This interpretation is in line with our findings that brain activation in the congruent condition was associated with oral reading in typical readers, whereas incongruent condition was related to oral reading in dyslexia. The alternative explanation is also associated with development but assumes that individuals with dyslexia process pinyin differently from typical controls. In general, typical readers shift from assembled to addressed phonology with reading experience (Mei et al., 2014). Pinyin is assembled in nature. But since there are only ∼400 syllables, it can be expected that typical readers in upper elementary grades who are highly familiar with it could achieve the addressed phonology. Given that children learn Chinese characters as holistic syllable-level units, children who read pinyin with the same addressed phonology may benefit more. In this case, the differential brain-behavior correlations probably reflect the assembled phonology adopted by dyslexic children in processing pinyin-sound pairs. Although this explanation is appealing, conclusions cannot be made without further examination. To date, research on the developmental trajectory of pinyin reading is still lacking. More studies on preliterate and emerging readers with a longitudinal design are needed.

Nonetheless, these findings indicate impaired automatic grapho-phonological mapping in dyslexia from the perspective of individual differences. This anomaly could be underpinned by the altered recruitment of cortical areas such as the left OTC and bilateral STC. As alphabetic languages, learning to read in Chinese requires establishing links between visual forms and linguistic representations (Perfetti and Harris, 2013). Chinese children rely on phonological mediation in reading comprehension at the earliest stages and later gradually shift to rapid grapho-semantic processing with a large amount of practice (Zhou et al., 2018). In this case, deficits in grapho-phonological mapping and corresponding neural basis can impede the development of the ventral pathway for rapid character/word recognition and result in reading problems. Recruiting preliterate children and conducting longitudinal neuroimaging research are necessary to further examine the causal relationship (Nash et al., 2017).

Limitations and Future Directions

This study has several limitations, and caution should be taken when interpreting the results. First, since we adopted a passive audiovisual integration paradigm here, we could not directly measure the involvement of semantics in print-sound processing. Second, we administered the pinyin experiment ahead of the character experiment to reduce the possible prime effect of characters on processing visually presented pinyin stimuli. This may influence brain activation to speech sounds in the character experiment because the same auditory stimuli were used. Third, to have sufficient statistical power, we used the liberal criteria to assess imaging data quality and exclude participants with poor quality data accordingly. Forth, while the overall pattern indicates that children in both groups maintained their attention throughout the experiment, the dyslexia group performed significantly worse. We controlled performance IQ in all the analyses to deal with this issue. The results demonstrated that the main findings of brain-behavior relationships are robust. At last, we did not have enough cases for looking into different subtypes of dyslexia. In the future, studies using multiple experimental designs related to print-sound integration should be conducted with a larger sample size, where a counterbalance design for estimating the order effect, much stricter criteria for controlling MRI data quality, strategies for well-matching on in-scanner performance between groups, and dividing dyslexia into subtypes can be applied.

CONCLUSION

The present study explored the impaired audiovisual integration of character-sound associations and pinyin-sound associations in Chinese children with dyslexia at the neurofunctional level. The results revealed that dyslexia manifested an atypical relationship between silent reading comprehension and the neural integration of character-sounds in the left IFC and between oral reading fluency and the neural integration of pinyin-sounds in the left OTC and bilateral STC, providing possible neural substrates underpinning inefficient grapho-semantic mapping and grapho-phonological mapping, respectively. Importantly, the current findings also imply that Chinese children with dyslexia may process pinyin—the alphabetic coding system representing the pronunciations of characters—in a lagged or deviated way, which can further impede the development of the direct route for rapid character/word recognition and semantic access.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Institutional Review Board of the State Key Laboratory of Cognitive Neuroscience and Learning. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

ZX, HS, and XL: conceptualization, funding acquisition, and supervision. ZX, TY, XC, HL, and XZ: investigation. ZX: formal analysis, data curation, and writing–original draft preparation. ZX, TY, XC, FH, HL, XZ, HS, and XL: writing–review and editing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.748644/full#supplementary-material

Supplementary Figure 1 | The summary of demographic and behavioral measures is shown as boxplots, with the box indicating the IQR. The whiskers show the range of values within 1.5 × IQR and a horizontal line indicating the median. Individual data are shown as dots. The color coding is indicated in the legend below to the plot. Data visualization was performed with PlotsOfData (https://huygens.science.uva.nl/PlotsOfData/). IQR, interquartile range.

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Letter-Like Shape Recognition in Preschool Children: Does Graphomotor Knowledge Contribute?

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Based on evidence that learning new characters through handwriting leads to better recognition than learning through typing, some authors proposed that the graphic motor plans acquired through handwriting contribute to recognition. More recently two alternative explanations have been put forward. First, the advantage of handwriting could be due to the perceptual variability that it provides during learning. Second, a recent study suggests that detailed visual analysis might be the source of the advantage of handwriting over typing. Indeed, in that study, handwriting and composition –a method requiring a detailed visual analysis but no specific graphomotor activity– led to equivalent recognition accuracy, both higher than typing. The aim of the present study was to assess whether the contribution of detailed visual analysis is observed in preschool children and to test the variability hypothesis. To that purpose, three groups of preschool children learned new symbols either by handwriting, typing, or composition. After learning, children performed first a four-alternative recognition task and then a categorization task. The same pattern of results as the one observed in adults emerged in the four-alternative recognition task, confirming the importance of the detailed visual analysis in letter-like shape learning. In addition, results failed to reveal any difference across learning methods in the categorization task. The latter results provide no evidence for the variability hypothesis which would predict better categorization after handwriting than after typing or composition.

Keywords: letter representation, letter recognition, letter categorization, handwriting, graphic motor programs, visual analysis, perceptual variability

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INTRODUCTION

New technologies are pervasive in our everyday life and computers are increasingly used at school (Wollscheid et al., 2016). The possibility of typewriting replacing handwriting from the very outset of literacy acquisition thus raises the question of its impact on reading development and on written language perception. Indeed, handwriting requires to reproduce a visual form by the execution of a sequence of fine movements that completely define the shape of the letter. This activity thus incurs very precise processing in terms of both visual and motor activity. By contrast, typewriting consists in a simple keypress based on the visual matching between two graphic forms. Interestingly, recent data suggest that simple visual exposure—even if massive—is not sufficient to yield a representation sufficiently detailed to lead to successful recognition. Wong et al. (2018) examined knowledge about the shape of the "looptail" *g* allograph that is used in most print materials. They observed that skilled adult readers failed on simple tasks such as drawing the letter *g* or identifying it among distractors. Even more surprisingly, despite extensive visual exposure to the looptail *g* allograph, many skilled readers failed to simply recall its existence as an alternate form of the lowercase letter g. The authors suggested that the absence of writing experience with the looptail *g* might be the source of its ensuing underspecified shape representation. These observations question the type of experience required to construct detailed and accurate shape representations of letters, with clear educational implications.

Indeed, letter recognition ability is an important predictor of subsequent reading skills (Näslund and Schneider, 1996; Scanlon and Vellutino, 1996; O'Connor and Jenkins, 1999; Lonigan et al., 2000; Foulin, 2005). Moreover, most current models of word recognition assume that letter recognition is an essential step in the flow of processing leading to word identification (McClelland and Rumelhart, 1981; Coltheart et al., 2001; Dehaene et al., 2005; Perry et al., 2007).

Longcamp and colleagues directly assessed the impact of typewriting on the construction of letter representation. They conducted behavioral studies that compared recognition performance observed after handwriting and after typewriting (Longcamp et al., 2005b, 2006, 2008). For both preschool children and adults, learning new characters through handwriting led to better recognition and orientation discrimination than learning through typewriting (see Seyll et al., 2020 for similar results). According to Longcamp et al. (2006), the advantage of handwriting is due to the contribution of the graphic motor programs—i.e., mental descriptions of the sequence of fine movements required to write the letter (van Galen, 1991; see Palmis et al., 2017, for a review)—constructed in memory through writing experience. More precisely, "the detection of a match or a mismatch between the perceived shape and the memorized motor program might contribute to the mirror–normal recognition processes and therefore explain the behavioral facilitation for the characters learned by handwriting" (Longcamp et al., 2006, p. 653). This process would be particularly helpful for letters that are ambiguous for the visual system such as mirror letters (e.g., b-d or p-q).

This interpretation thus assumes that joint reading and writing activities would gradually lead to a multimodal network of letter representation linking both the visual and the graphic motor codes (see for reviews Longcamp et al., 2010, 2016; James, 2017). In this embodied cognition perspective, one single sensory modality is sufficient to activate the entire distributed network which was engaged when the object was initially stored in memory (Wilson, 2002; Barsalou et al., 2003; Barsalou, 2008; Sullivan, 2018). The multimodal account of letter representation is supported by neuroimaging studies showing that the visual perception of letters activates precisely the same premotor area which is engaged during writing (Longcamp et al., 2003, 2005a; James and Gauthier, 2006). This premotor activation would reflect the automatic activation of the graphic motor program necessary to produce the perceived letter (Longcamp et al., 2003, 2005a).

Recently, however, several additional explanations of the advantage of handwriting over typing have been proposed. James and Engelhardt (2012; see also Li and James, 2016; James, 2017) proposed that handwriting would lead to broader and more abstract letter representations than other learning methods because it entails perceptual variability during learning. According to this hypothesis, facing varying exemplars would help identify the critical invariants and ignore irrelevant changes. The importance of perceptual variability during learning is not a new hypothesis. Indeed, according to several studies, comparison would play a critical role in the categorization of novel objects (e.g., Gentner and Namy, 1999; Namy and Gentner, 2002; Graham et al., 2010; Twomey et al., 2014). Some studies even suggested that the greater the variability among exemplars during learning, the better the generalization to new category instances (Posner and Keele, 1968; Perry et al., 2010). Handwriting is particular because in that case, the brain, the body, and the environment interact in a circular way (Li and James, 2016). The efferent motor commands sent by the brain for producing a given letter lead to variable outputs—i.e., the handwritten productions—which in turn constitute variable environmental inputs for the visual system and reshape the letter category boundaries. In contrast to handwriting, typing does not provide such variability since it exposes the learner to one single and invariant prototypical exemplar of each character, at both output and input levels.

Indeed, a recent behavioral study shows that variability improves the learning of letters by revealing that 5-year-old children were better at letter categorization when they were exposed to multiple exemplars of the letters during learning than when they were exposed to one single exemplar, whatever the learning modality—free handwriting, tracing, or viewing (Li and James, 2016). However, the advantage of perceptual variability arose whether the learning modality involved graphomotor activity or not. Moreover, it emerged whether the exemplars were self-produced, produced by another child, or simply typed. Hence, those results suggest that it is not the graphomotor activity *per se* that is the key factor explaining the facilitating effect but rather the perceptual variability that handwriting produces during learning.

A third interpretation has been proposed by Seyll et al. (2020). They suggested that the role of one component process, namely, the detailed visual analysis involved in handwriting, might have been underestimated in the advantage of handwriting over typing. More precisely, they assessed whether the detailed visual analysis required by handwriting but not by typing might contribute to the advantage of the former. To that purpose, they introduced a third learning method—called composition—requiring a detailed visual analysis but suppressing the graphomotor activity. During composition, participants received the set of elementary visual features used to construct the symbols and they were asked to reproduce the target symbol by selecting the appropriate features and assembling them together (as with a jigsaw puzzle).

After learning, participants performed two recognition tests, a four-alternative forced-choice (4AFC) test and an old/new test. Distractors used in the 4AFC were visually close to the target symbol (e.g., mirror-reversed symbol and symbol with one feature mislocated). Distractors used in the old/new recognition test consisted exclusively in the mirror-images of the learned symbols (as in Longcamp et al., 2006, 2008). The results failed to reveal any clear advantage of handwriting over composition, both leading to better recognition than typing, thus suggesting a significant contribution of the detailed visual analysis in the advantage of handwriting over typing.

We recently discovered that a similar hypothesis had already been proposed and put to the test by Courrieu and De Falco (1989).[1] They examined perceptual discrimination of Roman letters before and after learning. The learning conditions varied according to two orthogonally manipulated factors, analysis of target letters into segments, and dynamic tracing of the letters. In the analysis condition, which is very similar to our composition condition, preschool children received the target letter broken down into three segments on separate pieces of paper, and they had to recombine the pieces to reproduce the model. In the tracing condition, the children had to draw the target letter by following a trace on the worksheet. They improved significantly more from pre- to post-test when the learning involved analysis of letters into segments than when it did not, thus supporting the detailed visual analysis hypothesis, but the results failed to reveal any clear beneficial effect of tracing. However, tracing is known to be less effective than free copying (Naka, 1998). According to Naka (1998), the disadvantage of tracing over free copying might be due to the fact that, in contrast to handwriting, tracing does not require to generate and hold the image of the shape into memory. However, it is also likely that tracing does engage the graphomotor system to a lesser extent than free copying and does not lead to the storage of a graphomotor plan robust enough to facilitate discrimination. Nevertheless, given Naka's (1998) results, our choice of free copying provides a more appropriate test of the role of graphomotor knowledge.

The purpose of the present study was twofold. First, it aimed at further investigating the role of the detailed visual analysis inherent to handwriting by assessing whether the results observed with adults by Seyll et al. (2020) were generalizable to preschool children. To that purpose, children learned new symbols through handwriting, through typing, or through composition. After learning, they performed a 4AFC recognition task (as in Seyll et al., 2020). At the onset of reading acquisition, the visual system has to develop specific adaptations in order to effectively discriminate one letter from another. Indeed, learning to read impacts certain natural properties of the visual system. One such property is mirror-image generalization, or *mirror-invariance*, the natural process of generalization across mirror images (Bornstein et al., 1978; Biederman and Cooper, 1991; Dehaene et al., 2010). In contrast to literate adults, prereaders have not yet overcome mirror-invariance and often apply it to graphic shapes (Gibson et al., 1962; Cornell, 1985; Fernandes et al., 2016). As suggested by Longcamp et al., 2006, handwriting might be particularly helpful in overcoming mirror-invariance during literacy acquisition. If the graphic motor programs constructed through handwriting are the source of its advantage (*graphomotor hypothesis*), one might expect better recognition performance after handwriting than after typing and composition, both leading to equivalent recognition levels. In contrast, if the source of the handwriting advantage is the detailed visual analysis required by copying (*visual analysis hypothesis*), handwriting and composition should lead to equivalent recognition performance, both better than typing. Of course, the two hypotheses are not exclusive. If both graphic motor programs and detailed visual analysis contribute to the handwriting advantage (*mixed hypothesis*), handwriting should lead to more accurate recognition than composition, itself better than typing.

The absence of a clear advantage of handwriting over composition in Seyll et al. (2020) does not allow one to conclude that handwriting and composition would lead to equivalent performance in any recognition situation. Based on Li and James (2016) suggestion, it seemed plausible that despite equivalent recognition performance, handwriting would induce larger and richer representational categories as it is the only method that provides a diversity of exemplars during learning in the present experiment. It is worth noting that the 4AFC and Old/New tests may not be adequate to assess the richness of representations. The second purpose of the present study was to assess whether handwriting would improve categorization, as proposed by Li and James (2016). To this end, we also administered a categorization task like the one used by Li and James (2016). If perceptual variability improves the richness of letter representations, handwriting should affect categories and lead to better categorization performance than both other learning methods.

MATERIALS AND METHODS

Participants

Sixty-nine French-speaking kindergarteners (5 years 3 months to 6 years 3 months) took part in the experiment. There were 35 girls and 34 boys, and four left-handed participants. All were attending kindergarten in three different schools and had no known neurological diseases or psychological disorders. Participants were randomly assigned to one of the three groups. One group learned the symbols by handwriting, the second group by typing, and the third group by composition. Data from eight participants were discarded because they did not complete all the tests. There were 20 remaining participants in the handwriting group (*mean age* = 68.1 months; *SD* = 3.68), 22 in the typing group (*mean age* = 68.5 months; *SD* = 2.92), and 19 in the composition group (*mean age* = 69.5 months; *SD* = 3.61). Written informed consent was provided by the parents. The study was approved by the local ethics committee.

Stimuli

The method description is largely similar to Seyll et al. (2020) as the method is almost identical. Stimuli were symbols created

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[1] We thank the Editor for pointing us to that reference.

from a set of six elementary features (**Figure 1A**). All possible symbols combining three features were generated, and we choose eight symbols in this library (**Figure 1B**). Stimuli were simpler than those used in Seyll et al. (2020). First, symbols were simplified in terms of the number of features. Indeed, whereas symbols used in Seyll et al. (2020) were composed of three, four, or five features, those used in the present study were all composed of three features. Then, only two elementary curves were used instead of four. Symbols used in the present study are referred to as ”letter-like shapes” because they share the main characteristics with letters. They are the result of a combination of graphic elementary features, they can be handwritten, and the elementary features can be isolated.

Procedure

Three sessions were held 1 week apart. The learning phase was distributed over the first two sessions. The 4AFC task was administered immediately after the second learning session and again at the beginning of the third session. The categorization task was administered during the third session immediately after the 4AFC task. Before the first learning session, participants performed visuo-spatial and graphomotor tests—i.e., the visual perception and the motor coordination subtests of the VMI, respectively (Beery and Beery, 2004). All sessions took place in a quiet room at school and participants were tested individually.

In order to promote engagement, the tasks were embedded in a treasure hunt context. A little boy was displayed on the tablet screen and children were invited to help him to find a treasure. They were then explained that this little boy is living in a very distant country and that to help him, they would have to learn the letters used in his country. Moreover, to introduce the three sessions, children were shown a three-part totem and explained that each session would be rewarded by a part of it. Once the totem was completed, they could reach the treasure.

Stimulus presentation and response recording were programmed in Python using PsychoPy libraries. Stimuli were displayed on a Wacom Cintiq 13HDT tablet.

Learning Phase

All participants were asked to memorize eight unfamiliar symbols. In each learning session, there were three blocks each involving one random presentation of the eight symbols. Participants could take a break between blocks if needed. Before training, they received three practice trials with simple geometric shapes (a semicircle, a square, and a triangle). Feedback was given after each practice trial but not during learning.

The target symbol was horizontally centered on the tablet screen (as can be seen in **Figure 2**, its vertical position varied as a function of the learning method) and was displayed in black in a white 37-mm-wide area against a gray background. It stayed visible on the screen during the whole trial and the transition to the next trial was triggered by the participant. No constraint was imposed on production speed.

Handwriting Method

The target was centrally displayed during the entire trial (**Figure 2A**). At the start of each trial, participants were given a 100 × 100 mm sheet, and had to copy one symbol per sheet within a square of 35 × 35 mm. Once the copy was done, the experimenter took the sheet back and hid it from view. No constraint was imposed on stroke direction or order. To trigger the next trial, participants clicked on the “next” button displayed in the lower-right corner of the screen. Response times from target onset until the “next” button press were recorded.

Typing Method

The screen was divided into three portions: the target symbol was displayed in the upper portion, the virtual keyboard in the middle portion, and the response area in the lower portion (**Figure 2B**). The virtual keyboard was composed of eight 17-mm-wide keys, corresponding to the eight target symbols. The position of the keys varied randomly across trials in order to promote an active visual research. The response area was of the same size and color as the target area. Those three portions were displayed during the entire trial. Participants had to find the key corresponding to the target symbol and click with the stylus on it. Responses triggered the apparition of the selected symbol in the response area for 1 s before the start of the next trial. Accuracy and response times from target onset until the key press were recorded. It should be noted that the typing method used in the present experiment is different from a typical typing task given that the position of the keys varied randomly across trials. In what follows, however, we will refer to it as “typing method” for the sake of clarity.

Composition Method

The screen was divided into three portions: the target symbol was displayed in the upper portion, the set of individual features in the middle portion, and the response area in the lower portion (**Figure 2C**). The middle section was composed of six features displayed in 20-mm-wide squares. The position of the features was kept constant across trials and across participants. The response area was of the same size and color as the target area. Those three portions were displayed during the entire trial. Participants had to compose the target symbol by selecting features in the features area and dragging them in the appropriate position in the response area. No constraint was imposed on stroke order. To trigger the next trial, participants clicked on the “next” button displayed in the lower-right corner of the screen. Productions and response times from target onset until “next” button press were recorded.

Recognition Task

Participants performed the 4AFC recognition task immediately after training (Immediate Test) and again 6–8 days later (Delayed Test). Each trial consisted of the presentation of four symbols: the learned symbol plus three distractors, i.e., the mirror image of the symbol (mirror symbol), the learned symbol with a feature displaced (transformed symbol), and the mirror image of the transformed symbol (mirror transformed symbol) (**Figure 3**). The four symbols were randomly displayed upper left, upper right, lower left, and lower right. The learned symbol could not occur more than twice in a row at the same position. Participants had to select the learned symbol by clicking on it with the stylus.

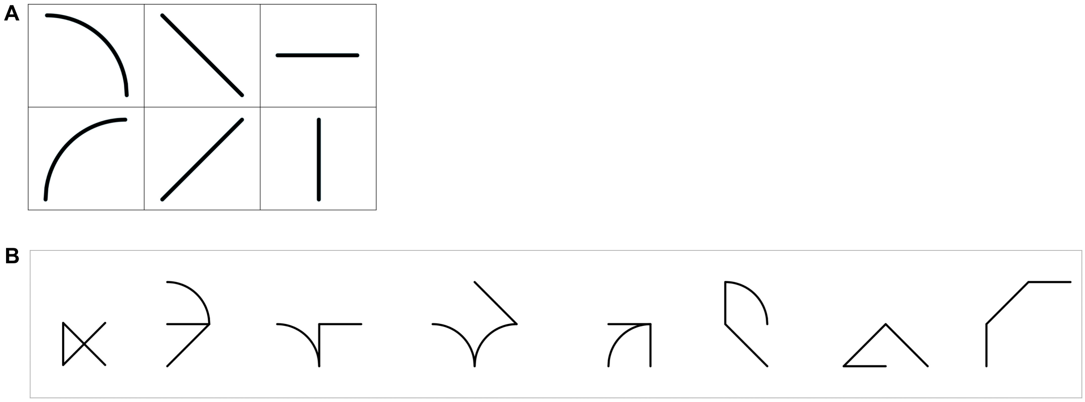

FIGURE 1 | (A) The six elementary features used to construct the symbol library. **(B)** The eight symbols to be learned.

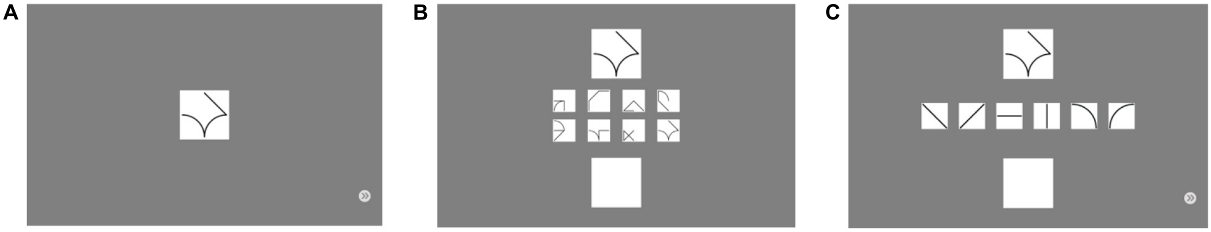

FIGURE 2 | One example of trial display for each learning method: **(A)** handwriting, **(B)** typing, and **(C)** composition.

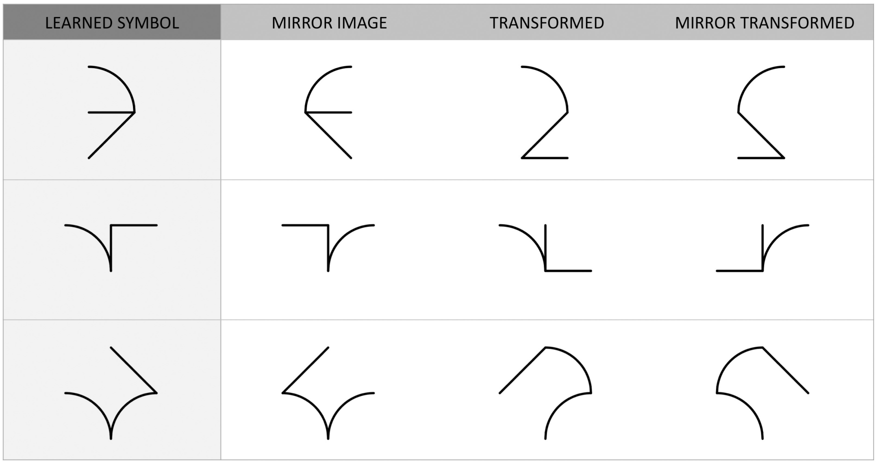

FIGURE 3 | Examples of trials in the 4AFC recognition task.

As for the learning phase, symbols were displayed in black in a white 37-mm-wide area against a gray background. There were two blocks each involving the random presentation of the eight symbols and their distractors. Participants could take a break between blocks.

Each trial started with a centered fixation cross for 300 ms, followed by a 200 ms gray screen. Then the four choices were displayed until the response. The intertrial interval was 500 ms. The main dependent measure was accuracy. Response speed was not emphasized, although response times from target onset were also recorded.

Categorization Task

During the categorization task, children were required to sort 32 handwritten exemplars into categories corresponding to four of the learned symbols. Eight exemplars of each symbol were used. They were handwritten productions created by children of the same age range in a previous study (**Figure 4**). The exemplars

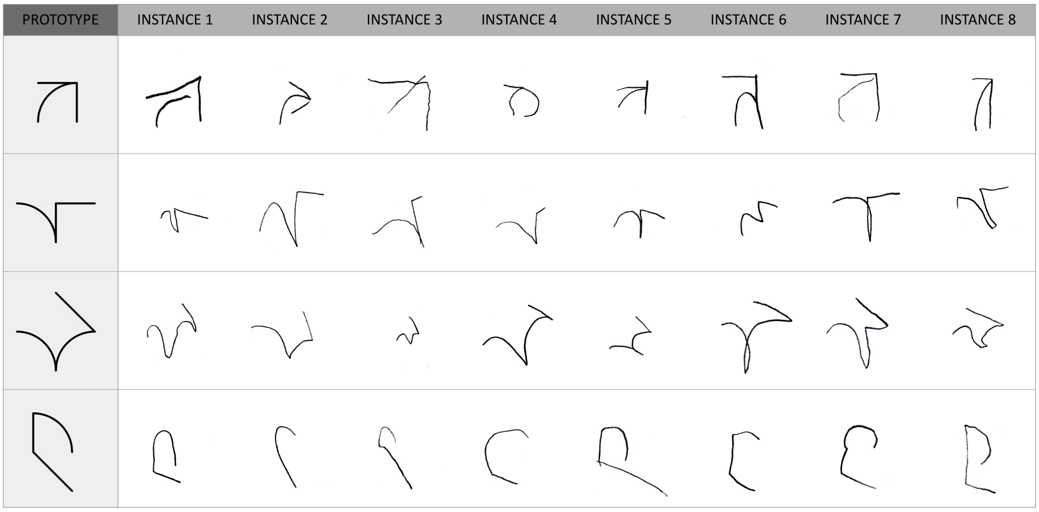

FIGURE 4 | The 32 handwritten productions used as experimental stimuli in the categorization task.

were displayed in black against a white background. Categories were instantiated by five house pictures displayed next to each other on the top of the screen. Four houses were assigned to the learned symbols, and one house was dedicated to the unlearned, new symbols. Across participants, the position of the four symbol-houses was randomized, but the "new symbols" house was fixed to the right. For a given participant, the position of the five houses remained constant. There were four blocks, each involving the random presentation of eight stimuli (two instances of each symbol). Participants could take a break between blocks.

Each trial started with the presentation of a new handwritten instance centered in the lower part of the screen. The five categories and the symbol instance remained visible during the entire trial (see **Figure 5** for one example of trial). To select the category corresponding to the handwritten symbol, children had to click with the stylus on the corresponding house. This action triggered the instance's move to the selected house. The trial finished by the instance's entrance in the selected house and a short blast. If the child did not identify the symbol as belonging to any of the four symbol categories, he could select the "new symbols" category. The main dependent measure was accuracy. Response speed was not emphasized, although response times were also recorded.

Before the test, participants performed 10 practice trials with four simple geometric shapes categories (a circle, a heart, a square, and a triangle). Oral feedback was given after each practice trial but not during the test.

RESULTS

All data files are available at https://osf.io/a2893/. In frequentist analyses, handwriting was systematically contrasted to typing on the one hand and to composition on the other hand (as in Seyll et al., 2020). For both tasks, accuracy was analyzed in terms of proportion of correct responses. As no emphasis was put on response times, they were not further analyzed. Response times on correct trials were around 5,100 ms for both tasks, and they were similar for all learning methods.

4AFC Recognition Task

Shapiro–Wilk normality tests on percentages of correct responses indicated no significant deviation from normality. Correct response rates (see **Table 1**) were submitted to an ANOVA with learning method (handwriting, composition, typing) as a between-subject factor and time of test as a within-subject factor (immediate, delayed). Mean percentages of correct responses are plotted in **Figure 6A**. The main effect of learning method was significant, $F(2,58) = 15.006$, $p < 0.001$, $\eta_p{}^2 = 0.341$. *A priori* contrasts revealed a significantly higher proportion of correct responses after handwriting ($M = 76.1\%$, $SD = 13.5$) than after typing ($M = 60.0\%$, $SD = 9.03$), $t = 4.525$, $p < 0.001$, but no significant difference between proportion of correct responses

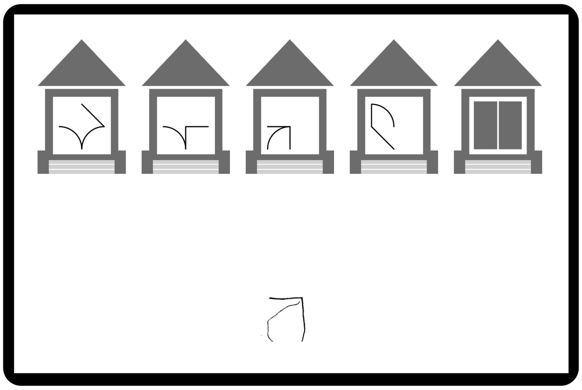

FIGURE 5 | Categorization task: example of display.

TABLE 1 | Performance for both recognition tasks across learning methods.

		Composition	Handwriting	Typing
4AFC task				
Immediate test				
	Mean percent correct responses	78.0%	79.7%	65.6%
	Standard deviation	14.6%	16.3%	13.9%
Delayed test				
	Mean percent correct responses	78.0%	73.4%	55.4%
	Standard deviation	11.9%	15.6%	13.4%
Mirror errors				
	Mean percent mirror errors	20.9%	23.7%	35.1%
	Standard deviation	11.4%	13.3%	10.4%
Categorization task				
	Mean percent correct responses	71.1%	73.3%	68.2%
	Standard deviation	15.8%	14.4%	18.4%
	Mean percent "New" errors	24.0%	22.5%	26.0%
	Standard deviation	18.6%	15.3%	21.9%

following handwriting and composition (M = 78.0%, SD = 11.5), t = 0.380, p = 0.705. The main effect of time of test was significant, $F(1,58) = 6.200$, $p = 0.016$, $\eta_p^2 = 0.097$, reflecting a higher rate of correct responses immediately after learning (M = 74.1%, SD = 16.0) than 1 week later (M = 68.3%, SD = 16.8). The interaction was not significant, $F(2,58) = 1.816$, $p = 0.17$, $\eta_p^2 = 0.059$. To assess evidence in favor of an absence of difference between the handwriting and composition conditions, we additionally ran a Bayesian repeated-measures ANOVA, which produced concordant indications. Overall, the best model included time of test and learning method ($BF_{10} \sim 10{,}000$). *Post hoc* comparisons provided decisive evidence of differences between typing and both other conditions (Kass and Raftery, 1995, respectively, $BF_{10} \sim 50{,}000$ for composition and $BF_{10} \sim 2{,}500$ for handwriting) and substantial evidence in favor of an absence of difference between composition and handwriting ($BF_{10} \sim 0.254$).

Error types are plotted in **Figure 6B**. On average, participants selected the mirror-image of the learned symbol on 26.9% of trials, the transformed symbol on 1.1% of trials, and the mirror transformed symbol on 1.0% of trials. A Shapiro–Wilk test on the rate of mirror-image choices indicated no significant deviation from normality. An ANOVA performed on the rate of mirror-image choices revealed a significant difference between learning methods, $F(2,58) = 8.561$, $p < 0.001$, $\eta_p^2 = 0.228$. A significantly higher proportion of mirror-symbol choices was observed after typing (M = 35.1%, SD = 10.4) than after handwriting (M = 23.7%, SD = 13.3), $t = 3.144$, $p < 0.001$, but there was no significant difference between handwriting and composition (M = 20.9%, SD = 11.4), $t = 0.734$, $p = 0.466$. The Bayesian ANOVA provided strong evidence in favor of an effect of learning method, $BF_{10} \sim 58$. *Post hoc* tests again indicated differences between typing and both other conditions ($BF_{10} \sim 11$ and 136, respectively, for handwriting and composition), and weak evidence in favor of the absence of difference between composition and handwriting ($BF_{10} \sim 0.377$).

Categorization Task

Shapiro–Wilk normality tests on percentages of correct responses indicated significant deviations from normality in two of the three groups. Hence, scores were submitted to a non-parametric ANOVA with learning method (handwriting, composition, and typing) as a between-subject factor. The Kruskal–Wallis test was non-significant [$H(2) = 0.863$, $p = 0.65$]. A Bayesian ANOVA similarly provided substantial evidence in favor of the null ($BF_{10} \sim 0.195$). Mean percentages of correct responses and error rates are reported in **Table 1**.

On average, participants selected an erroneous category on 5.0% of trials and the "new symbols" category on 24.2% of trials. Shapiro–Wilk normality tests on rates "new symbols" choices indicated significant deviations from normality in two of the three groups. A non-parametric ANOVA performed on the rate of "new symbols" choices revealed no significant difference between learning methods, $H(2) = 0.226$, $p = 0.89$. The Bayesian ANOVA produced substantial evidence in favor of the null ($BF_{10} \sim 0.15$).

DISCUSSION

The changing habits introduced by the increasing use of digital devices in everyday life and at school raises the question of their impact on literacy acquisition. Indeed, one might wonder whether the reduced usage of handwriting at the very outset of reading acquisition has an impact on letter recognition, an essential step in word identification (McClelland and Rumelhart, 1981; Coltheart et al., 2001; Dehaene et al., 2005; Perry et al., 2007) generally considered as predictive of subsequent reading skills (Näslund and Schneider, 1996; Scanlon and Vellutino, 1996; O'Connor and Jenkins, 1999; Lonigan et al., 2000; Foulin, 2005).

A negative impact of keyboard use during letter learning has already been demonstrated. Indeed, multiple behavioral studies showed that handwriting is a more effective learning method and leads to better recognition and mirror discrimination than typing (Longcamp et al., 2005b, 2006, 2008; Seyll et al., 2020). Several interpretations of this finding have been proposed. First, the motor knowledge acquired through handwriting could contribute to recognition. Second, the perceptual variability entailed by handwriting could be the source of its advantage (James, 2017). Third, Seyll et al. (2020) argued that the detailed visual analysis required by handwriting might be a significant factor accounting for the advantage of handwriting over typing.

The first aim of the present study was to assess whether the results observed with adults by Seyll et al. (2020) were generalizable to preschool children. To that purpose, children learned new graphic shapes through handwriting, through typing, or through composition, and performed a 4AFC recognition task after learning. The second aim was to assess whether handwriting would lead to better categorization than typing and composition. To that purpose, we added a

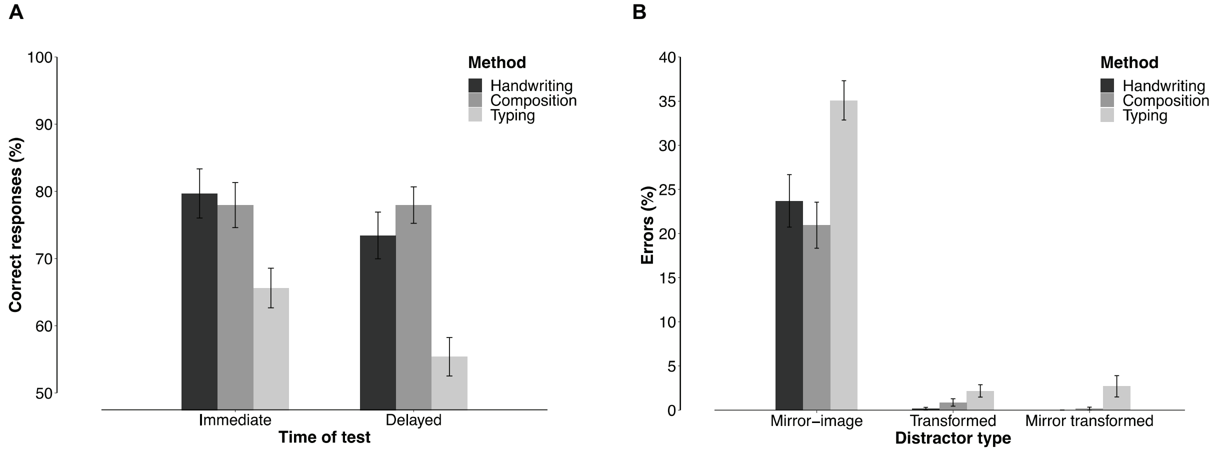

FIGURE 6 | (A) Mean percentage of correct responses for the immediate and delayed 4AFC test across learning methods. **(B)** Errors produced across the three learning methods. Error bars depict standard errors.

categorization task like the one used by Li and James (2016) at the end of the last session.

Recognition performance in the 4AFC task confirmed and corroborated the results observed in adults (Seyll et al., 2020), that is, higher recognition rates after handwriting and composition than after typing, with the two former leading to equivalent performance. Such a pattern is consistent with the idea that the detailed visual analysis plays an important role in letter-like shape learning and provides no evidence that the graphic motor programs, as such, contribute to letter recognition. Moreover, the present findings are in line with most current models of word recognition, which assume that letter recognition is a visual process based on elementary features extraction (McClelland and Rumelhart, 1981; Coltheart et al., 2001; Perry et al., 2007; Grainger et al., 2008). Indeed, the composition learning method used in the present study can be linked to the latter models because it precisely involves a visual focus on elementary features during learning.

Regarding the second issue, correct categorization rates failed to reveal any significant difference across the three learning methods. Moreover, if handwriting leads to richer and larger categories, new test exemplars should be less frequently rejected and a lower proportion of “new symbols” choices should be observed after handwriting than after typing and composition. However, as for the main analyses, the percentage of “new symbols” choices failed to reveal any significant difference across learning methods. Our results thus provide no evidence to confirm the variability hypothesis.

Mirror discrimination is essential for efficient reading. The present findings replicate the detrimental impact of typing on mirror-normal discrimination observed in previous studies (Longcamp et al., 2005b, 2006, 2008; Seyll et al., 2020). Mirror-image errors are common at the onset of reading acquisition and dramatically decrease in the course of reading acquisition, between 5 and 7 years of age (Gibson et al., 1962; Nelson and Peoples, 1975; Fernandes et al., 2016). Several studies suggest that reversal errors are more frequent in children with developmental dyslexia during the first years of schooling (Wechsler and Hagin, 1964; Liberman et al., 1971; Wolff and Melngailis, 1996), and a recent study suggest that dyslexic children do not automatize mirror discrimination (Fernandes and Leite, 2017). There is thus cause for concern about a possible exacerbation of this weakness with the introduction of keyboarding at school. Dyslexic children might be more impacted by learning through typing than typically developing children and the predominant use of typing at school might constitute an additional risk factor for them.

In sum, the present findings clearly confirm that the detailed visual analysis is important in letter-like shape learning. It would yield detailed, accurate, and distinctive representations which support easy discrimination and identification. Under such a view, the association between letter perception and motor activation should be interpreted as a consequence of the learning experience and not as a necessary condition for encoding and recognition. Neither the present nor our previous studies (Seyll et al., 2020, 2021) showed an advantage for handwriting over composition and the Bayesian inference tests supported the null hypothesis. Even if it is too early to completely discard a possible contribution of graphic motor programs to letter recognition, our findings challenge the supporters of the graphomotor hypothesis to provide further evidence, over and above the influence of detailed analysis.

Regarding the potential implications of our conclusions for educational issues, it should be noted that the present learning situation differs in several ways from the usual school settings: the learning task was strictly visual and did not involve associations between graphic shapes and letter names or sounds, and the artificial symbols used here differ from real letters. Further studies using more ecological conditions and stimuli would be relevant to confirm the present findings.

While the present results provide no evidence in favor of a contribution of graphic motor programs and handwriting *per se*, it should, however, be noted that in the classroom, handwriting training and copy exercises may constitute the most natural way to promote such detailed visual analysis for most kids. Yet, handwriting might not constitute a suitable learning method for children with poor fine motor skills. Indeed, several studies revealed that poor fine motor skills are associated with poor reading skills (e.g., Grissmer et al., 2010; Cameron et al., 2012; Suggate et al., 2018, 2019). With normal adults, Seyll and Content (2020) showed that disturbing the graphomotor activity during symbol learning affects subsequent recognition and mirror-normal discrimination. The advantage of composition over typing observed in the present study might be exploited with children suffering from severe fine motor skills deficits. Indeed, it is plausible that children with poor fine motor skills would benefit from composition learning, as did the children of the present study. Further studies would be necessary to determine whether this is indeed the case.

DATA AVAILABILITY STATEMENT

All data files are available at https://osf.io/a2893/.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Comité d'Éthique de la Faculté des Sciences Psychologiques et de l'Éducation, ULB. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

Both authors designed the experiment, analyzed the data and wrote the manuscript.

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