

# Individual differences in first-pass fixation duration in reading are related to resting-state functional connectivity

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## ABSTRACT

Although there are considerable individual differences in eye movements during text reading, their neural correlates remain unclear. In this study, we investigated the relationship between the first-pass fixation duration (FPFD) in natural reading and resting-state functional connectivity (RSFC) in the brain. We defined the brain regions associated with early visual processing, word identification, attention shifts, and oculomotor control as seed regions. The results showed that individual FPFDs were positively correlated with individual RSFCs between the early visual network, visual word form area, and eye movement control/dorsal attention network. Our findings provide new evidence on the neural correlates of eye movements in text reading and indicate that individual differences in fixation time may shape the RSFC differences in the brain through the time-on-task effect and the mechanism of Hebbian learning.

## 1. Introduction

Eye movement is the most common and important behaviour during text reading. There are considerable individual differences in eye movements during text reading (Ashby, Rayner, & Clifton, 2005; Rayner, Li, Williams, Cave, & Well, 2007; Castelano & Henderson, 2008; Risse & Kliegl, 2011; Veldre & Andrews, 2014). Previous studies have indicated that such individual differences are related to multiple factors, such as reading fluency (Dahhan et al., 2014), age (Risse & Kliegl, 2011; Reichle et al., 2013), cultural background (Rayner et al., 2007), and the cognitive processes underlying text reading (Hyönä, Lorch, & Kaakinen, 2002; Lou, Liu, Kaakinen, & Li, 2017). However, little is known about the neural correlates of these individual differences.

One of the most frequently used eye-movement measures to reflect individual differences in reading is fixation duration (Andrews & Coppola, 1999; Henderson, Choi, & Luke, 2014; Henderson, Choi, Luke, & Schmidt, 2018; Henderson & Luke, 2014; Luke, Darowski, & Gale, 2018; Rayner et al., 2007). It has been found that the individual differences in average fixation durations in reading are stable across time, indicating that this measurement represents reliable underlying cognitive processes of individuals (Henderson & Luke, 2014). Here, we focused on the individual differences in average fixation duration during first-pass text

reading, called first-pass fixation duration (FPFD). During reading, readers usually make forward saccades while occasionally making regressive saccades. Forward saccades are used to acquire new visual information that warrants comprehension, and regressive saccades are usually associated with detection and correction of temporary comprehension errors (Rayner, 1998, 2009). In this study, we mainly focused on the processes during first-pass reading (best reflected by FPFD), but ignored the fixations associated with error detections (reflected by other fixations related to regressive saccades, such as second-pass fixation durations).

According to the current knowledge of eye movements in reading (Engbert, Nuthmann, Richter, & Kliegl, 2005; Findlay & Walker, 1999; Li & Pollatsek, 2020; Rayner, 1998; Reichle, Rayner, & Pollatsek, 2003; Reilly & Radach, 2006; Snell, van Leipsig, Grainger, & Meeter, 2018), the length of the FPFD is mainly associated with four underlying cognitive components. The first cognitive component is early visual processing, which deals with low-level visual information. This component is associated with the primary visual cortex and the extrastriate cortex located in the occipital lobe, which transmits information to both the word-recognition-related regions, located in the ventral temporal lobe, and the eye-movement control and dorsal attention network located in the frontal and parietal cortex (Ungerleider & Haxby, 1994).

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The second cognitive component is word identification. It has been proposed that the cognitive and neural processes of visual word identification include two steps. First, the orthographic representation of a word is activated, and second, the phonological and semantic representations of the word are activated (Jobard, Crivello, & Tzourio-Mazoyer, 2003). Since the FPDF mainly reflects the early stage of word identification (Inhoff, 1984; Rayner, 1998), it should be more closely related to the stage of accessing orthographical representation. According to a large body of neuroimaging and neuropsychological evidence, the orthographical representation of words is mainly supported by the visual word form area (VWFA) (Vigneau, Jobard, Mazoyer, & Tzourio-Mazoyer, 2005; Dehaene & Cohen, 2011). Neuroimaging studies have shown that the VWFA is more sensitive to word forms than to other visual stimuli (Dehaene et al., 2001; Dehaene et al., 2004; Xue, Chen, Jin, & Done, 2006; Szwed, Cohen, Qiao, & Dehaene, 2009; Ben-Shachar, Dougherty, Deutsch, & Wandell, 2011; Szwed et al., 2011). Neuropsychological studies have also shown that impairment of the VWFA damages the ability to process visual word forms (Starrfelt & Gerlach, 2007; Pflugshaupt et al., 2009). Therefore, the VWFA should be the primary brain region supporting this second cognitive component.

The last two components are attention shifts and oculomotor control. Distinguishing the neural correlates of these two components in neuroimaging studies is difficult because they are often closely related to each other within cognitive processes (Pierrot-Deseilligny, Milea, & Muri, 2004; Choi, Desai, & Henderson, 2014). It has been discovered that these two components are related to a brain network that includes the frontal eye field (FEF), supplementary eye field (SEF), and intraparietal sulcus (IPS) (Grosbras, Laird, & Paus, 2005; Geng & Mangun, 2009; Esterman et al., 2015), often referred to as the eye-movement control network (Pierrot-Deseilligny, Milea, & Müri, 2004; Grosbras et al., 2005) or the dorsal attention network (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Petersen & Posner, 2012). This network has been identified as one of the most robust large-scale brain networks (Yeo et al., 2011), and previous neuroimaging studies have indicated its connectivity to the early visual network and VWFA (Vogel, Miezin, Petersen, & Schlaggar, 2011; Yeo et al., 2011). Recently, Zhou, Liu, Su, Yan, and Shu (2019) found that the difficulty in word segmentation when reading Chinese could enhance the functional connectivity between the dorsal attention network and VWFA during text reading, indicating that the neural interaction between the dorsal attention network and VWFA may play an important role in text reading.

Only very few studies have investigated the neural correlates of the length of fixation durations in reading. Henderson et al. (2014) investigated whether and how the individual differences in fixation duration in reading are related to the morphology of the primary visual cortex. They found that, across subjects, greater grey matter surface area and volume in the primary visual cortex are associated with shorter and less variable fixation durations in reading. Henderson, Choi, Luke, and Desai (2015) investigated how variations in within-subject fixation duration during text reading are related to whole-brain level task-related activations. It was found that a large set of brain regions, including the calcarine sulcus, cuneus, medial superior frontal gyrus (including the SEF), lingual gyrus, superior temporal cortex, and precentral gyrus, showed a positive correlation between the length of fixation duration and strength of activation. These brain regions are largely consistent with the aforementioned speculated neural networks associated with FPDF. However, because this study focused on within-subject fixation differences rather than on individual differences, the results cannot directly indicate the neural correlates of individual differences in reading. Importantly, the two above-mentioned studies both focused on local neural measurements. Because the reading processes underlying fixation durations rely on co-operation between different brain systems, the length of fixation duration should also be related to the connectivity between these neural systems.

In the present study, we aimed to investigate whether and how individual differences in FPDF during Chinese text reading are related to

the resting-state functional connectivities (RSFCs) between the brain networks supporting visual processing, visual word recognition, and eye-movement control/attention. The fundamental mechanisms of eye movements in Chinese and English text reading have been found to be similar (Li, Bicknell, Liu, Wei, & Rayner, 2014). Therefore, although we proposed the cognitive and neural processes underlying FPDF mainly referencing studies on English reading, their relevant hypotheses should also be applicable to Chinese reading. RSFC refers to the statistical association of spontaneous blood oxygen level-dependent (BOLD) signal in discrete brain regions or networks. Animal research has indicated that RSFCs are spatiotemporally coupled to resting-state neural activity in excitatory neurons (Ma et al., 2016). Neuroimaging studies have found that individual differences in many types of behavioural and task-state neural measurements are related to RSFC data (Hampson, Driesen, Skudlarski, Gore, & Constable, 2006; Seeley et al., 2007; Song et al., 2008; Di Martino et al., 2009; Koyama et al., 2011; Shannon et al., 2011; Stevens & Spreng, 2014; Tavor et al., 2016). In the field of reading, several studies have reported correlations between individual differences in reading behaviours and RSFC (e.g., Koyama et al., 2011; Wang, Han, He, Liu, & Bi, 2012; Li et al., 2013; Doucet et al., 2015). For example, it has been found that the RSFC between the dorsal attention network and VWFA is related to reading fluency (the number of characters that one can read per minute) and lexical decision scores (Zhou, Xia, Bi, & Shu, 2015; Zhou, Wang, Xia, Bi, & Shu, 2016). Unlike the time measures associated with the completion of reading tasks, FPDF reflects ongoing cognitive processing and is strongly associated with dynamic cognitive components during reading (Reichle et al., 2003; Inhoff, Eiter, & Radach, 2005). Therefore, whether individual differences in FPDF are related to RSFC is an interesting and open question.

A further question is how FPDF may be related to RSFC. Both positive and negative correlations have been observed between the RSFC and processing/response time in the literature (for examples of positive correlations, see Gordon, Breeden, Bean, & Vaidya, 2014; Koyama et al., 2011; Wang et al., 2012; Wei et al., 2012; Zhou et al., 2016; for examples of negative correlations, see Koyama et al., 2011; Wang et al., 2012; Zhou et al., 2016). The theoretical explanation for these observed correlations varied across studies, depending on the specific brain areas and behavioural measurements involved. In this study, we proposed two alternative hypotheses for the relationship between FPDF and RSFC that would lead to the opposite predictions of our results. Hypothesis 1 is that a strong RSFC can facilitate or automatise the co-operation between brain areas, thus accelerating the related cognitive processes. In this case, a strong RSFC between our target brain regions/networks would result in a shorter FPDF, leading to a negative correlation between RSFC and FPDF across individuals (Seeley et al., 2007; Chen, Chou, Song, & Madden, 2009; Wei et al., 2012). Hypothesis 2 is that the length of FPDF would modulate the strength of brain activation in our target regions/networks and change the RSFCs between them. This hypothesis is mainly based on two previous findings. The first is the Hebbian-learning rule, which refers to the rule that the positive correlated activities of neurons leads to an increase in their connectivity and the negative correlated activities of neurons leads to a decrease in their connectivity (Hebb, 1949; Artola, Brocher, & Singer, 1990). In this regard, recent studies have demonstrated that changes in the RSFCs between brain regions also follow the Hebbian-learning rule (Harmelech, Preminger, Wertman, & Malach, 2013). Therefore, if one task evokes positive BOLD responses in two brain regions, then the performance of this task will lead to an increase in the RSFC between these two regions. The second finding is the time-on-task effect, which refers to the increase of the BOLD amplitude with longer processing time (Domagalik, Beldzik, Oginska, Marek, & Fafrowicz, 2014; Henderson et al., 2015; Yarkoni, Barch, Gray, Conturo, & Braver, 2009). This effect has been observed in extensive brain regions across a range of tasks (Yarkoni et al., 2009). With respect to eye movements, Domagalik et al. (2014) found that, during the spatial cueing task (Posner, 1980), a wide set of brain regions associated with eye-movement control and visual processing showed

positive trial-by-trial correlations between the BOLD signals and saccadic reaction times. Henderson et al. (2015) reported a similar finding in a text reading task where extensive brain regions associated with reading and eye-movement control showed positive fixation-by-fixation correlations between the BOLD signals and fixation durations. Based on these previous findings, long fixations should lead to stronger activation than short fixations in the target brain regions of the current study. Because the Hebbian-learning of RSFC should be sensitive to the strength of coactivation between brain areas, we speculated that the fixation durations may modulate the Hebbian-learning of RSFC in daily reading through the time-on-task effect, resulting in a positive correlation between RSFC and FPDF across individuals.

## 2. Materials and methods

### 2.1. Participants

Fifty-six healthy undergraduate and graduate students (29 females) with an average age of 22.7 years ( $SD = 2.36$  years) participated in this study. All participants had normal or corrected-to-normal vision. All were right-handed and native Chinese speakers. All participants reported no history of any psychiatric or neurological diseases, nor had any of them ever suffered a head injury. Prior to the experiment, each participant read and signed an informed consent form issued by the Institutional Review Board of the MRI Research Center of the Institute of Psychology of the Chinese Academy of Science (IPCAS).

### 2.2. MRI data acquisition

Structural and functional MRI data were collected using a GE Discovery MR750 3 T scanner at the MRI Research Center of the IPCAS. High-resolution T1-weighted structural images were obtained using the following parameters: repetition time = 6.652 ms, echo time = 2.928 ms, flip angle =  $12^\circ$ , inversion time = 450 ms, field of view =  $100 \times 100$  mm<sup>2</sup>, matrix size =  $256 \times 256$ , slice thickness = 1 mm, voxel size =  $1 \times 1 \times 1$  mm<sup>3</sup>, slice number = 192, and scanning time = 4 min 41 s. Resting-state fMRI data were acquired using the following parameters: repetition time = 2 s, echo time = 30 ms, flip angle =  $90^\circ$ , field of view =  $100 \times 100$  mm<sup>2</sup>, matrix size =  $64 \times 64$ , scanning time = 8 min, and number of time points = 240. All participants were required to focus on white cross fixation with a black background on the screen during the time of scanning. Since the MRI Research Center of the IPCAS had its own mandatory scanning parameters for the acquisition of resting-state fMRI data, the slice number was slightly changed during the performance of our study. It was 33 (voxel size =  $3.5 \times 3.5 \times 4.2$  mm<sup>3</sup>) for 29 of our participants and 35 (voxel size =  $3.4 \times 3.4 \times 4$  mm<sup>3</sup>) for 27 of our participants.

### 2.3. Eye movement data acquisition

After the MRI scanning, participants performed a self-paced reading task outside the scanner, during which their eye movements were recorded. The task was identical to that used in a previous study (Lou et al., 2017), in which participants read an article introducing dinosaurs (the materials are available from OSF: <https://osf.io/2ua9d/>). The article was separated into ten sections, with each section consisting of one or two paragraphs. The first section comprised a short introduction about dinosaurs, followed by eight sections that introduced one dinosaur species each. The last section had a short conclusion about dinosaurs. Each section was presented on a separate screen. Participants advanced to the next section by pressing a button on a gamepad and were not able to return to the previous sections. After reading the whole article, participants were asked to answer 24 questions about the contents of the article. All questions were mandatory and multiple choice. For each question, the participants had to choose one correct statement from a total of four.

Before the experiment, the eye tracker was calibrated for each participant. The participants were instructed to read the texts silently and were told that there were some questions after reading the whole article. The materials were presented on a 21-inch CRT monitor (Sony G520: resolution =  $1024 \times 768$  pixels, refresh rate = 150 Hz) connected to a Dell PC. Participants viewed the stimuli from approximately 58 cm from the monitor. At this viewing distance, each character subtended a visual angle of approximately  $0.7^\circ$ . They placed their chins on a chin rest to minimise head movements. The character strings were shown in Song 20-point font in white (RGB: 255, 255, 255) on a black background (RGB: 0, 0, 0). Participants read sentences binocularly, with only the right eye being monitored. Eye movements were recorded using an EyeLink 1000 eye tracking system with a sampling rate of 1,000 Hz.

### 2.4. Pre-processing and calculation of eye-movement measures

The eye-movement data were pre-processed using EyeDoctor 0.6.5. Fixations and saccades that contained blinking were removed. In addition, two kinds of fixations were removed: (1) fixations before or after saccades shifting from the end of the line to the start of the next line, and (2) fixations out of the scope of the text.

After pre-processing, the FPDF was calculated using the DPEEM package (Zhang, Li, & Lin, 2019) in R (R Core Team, 2018). Fixation was classified as a first-pass fixation if none of the text to the right (nor any of the lines below) of the fixated position had been fixated. Fifty-nine percent of the fixations were classified as first-pass fixations<sup>1</sup>. Then, fixations longer than 1000 ms and shorter than 80 ms were removed. In total, 1.25% of the first-pass fixations were removed. After that, each participant's mean FPDF was calculated and entered into the RSFC-behaviour correlation analyses (see below).

### 2.5. Data pre-processing for RSFC analyses

The fMRI data were pre-processed using the Statistical Parametric Mapping software (SPM12; <http://www.fil.ion.ucl.ac.uk/spm/>) and the advanced edition of DPARSF V4.3 (Yan & Zang, 2010) implemented in DPABI V3.0 (Yan, Wang, Zuo, & Zang, 2016). For each participant, the first ten volumes were discarded, after which slice timing and head motion correction were performed. The 3D T1 images of each participant were first co-registered to the mean images of the motion-corrected functional images and were then segmented (Ashburner & Friston, 2005). Next, a custom, study-specific template was generated by applying Diffeomorphic Anatomical Registrations Through Exponentiated Lie Algebra (DARTEL) (Ashburner, 2007). The motion-corrected functional images were spatially normalised into the Montreal Neurological Institute (MNI) space by applying the deformation field estimated in segmentation. The normalised images were spatially smoothed using a Gaussian kernel (full width at half maximum of 6 mm). Linear trends were removed to reduce the effects of low-frequency drifts. The effects of nuisance variables, including 24 rigid head motion parameters (Friston, Williams, Howard, Frackowiak, & Turner, 1996; Yan et al., 2013), white matter signal, and cerebrospinal fluid signal, were removed by linear regression from each voxel's time course. Since global signal removal remains a controversial pre-processing step for RSFC analyses, which has both advantages and disadvantages (Murphy & Fox, 2017), we conducted all analyses twice, once with global signal regression and again without it, and presented the two sets of results in parallel. Temporal band-pass filtering (0.01–0.1 Hz) was performed to reduce the effects of high-frequency noises.

<sup>1</sup> The remaining 41% were the regressive fixations (25%) and the forward fixations during the second-pass and third-pass reading, etc.

2.6. RSFC computation and RSFC-behaviour correlation analyses

The RSFC computation and RSFC-behaviour correlation analyses were performed using DPABI (Yan et al., 2016). The brain maps of the results were shown using the Brainnet Viewer software (Xia, Wang, &

He, 2013).

2.6.1. Defining the seed regions of interest (ROI)

For early visual processing, we used the Automated Anatomical Labelling (AAL) template (Tzourio-Mazoyer et al., 2002) to define the

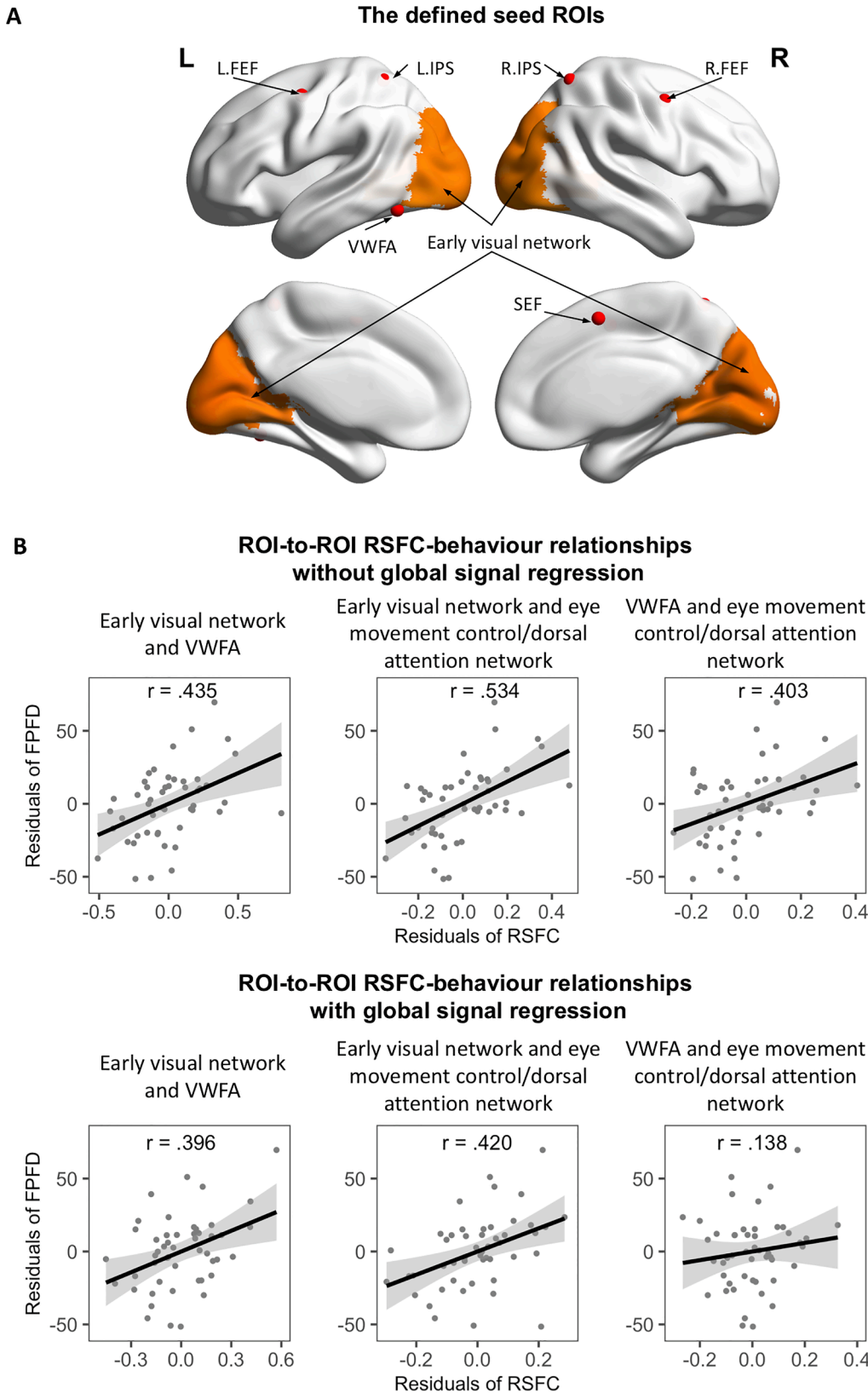


Fig. 1. Results of the main analysis of the RSFC-behaviour correlation. Panel A shows the location of the seed ROIs. Panel B shows the relationships between RSFCs and FPDF without (upper plot) and with (lower plot) global signal regression, respectively. In each of these two plots, the left subplot shows the effect of RSFC between the early visual network and VWFA, the middle subplot shows the effect of RSFC between the early visual network and the eye movement control/dorsal attention network, and the right subplot shows the effect of RSFC between the VWFA and the eye movement control/dorsal attention network. The partial correlation coefficients are labelled on each subplot. The shadow indicates the standard error.

seed ROI. All 12 regions of the occipital lobe, which include the bilateral calcarine, bilateral cuneus, bilateral lingual gyrus, bilateral superior occipital gyrus, bilateral middle occipital gyrus, and bilateral inferior occipital gyrus, were merged into one seed ROI.

The seed ROI of VWFA was defined based on a meta-analysis of 16 neuroimaging studies that reported 27 activation peaks in this area during word reading (Jobard et al., 2003). We used the mean coordinate of these peaks (MNI coordinate:  $-44, -58, -15$ ) reported by Jobard et al. (2003) to create a spherical seed ROI with a radius of 6 mm.

For oculomotor control and attention shift, seed ROIs were defined based on the results of a previous meta-analysis of 59 brain-imaging experiments on eye movements (Grosbras et al., 2005). Grosbras et al. (2005) revealed 15 brain regions associated with eye-movement control. We focused on the top five of these regions, which showed much higher activation likelihood estimation values than the other regions and are more frequently reported in the literature. These five regions are located in the left FEF, left IPS, right FEF, right IPS, and SEF. The Talairach coordinates reported by Grosbras et al. (2005) were converted into MNI coordinates using the advanced edition of DPARSF V4.3 (Yan & Zang, 2010; Lancaster et al., 2007), and spherical seed ROIs were created centred on the MNI coordinates with a radius of 6 mm (MNI coordinates: left FEF:  $-31, -2, 52$ ; right FEF:  $43, -2, 49$ ; SEF:  $0, 5, 53$ ; left IPS:  $-28, -50, 61$ ; right IPS:  $26, -57, 61$ ). In the main analyses, we combined these five seed ROIs into one super ROI because these five regions belong to the same eye-movement control/dorsal attention network and the RSFC-behaviour correlation patterns of the five individual seed ROIs were similar.

Therefore, for the RSFC analyses in the present study, we defined three seed ROIs corresponding to early visual processing, word identification, and oculomotor control/attention shifts. The locations of the defined ROIs are shown in Fig. 1A.

### 2.6.2. RSFC-behaviour correlation analysis

The main analysis of the RSFC-behaviour correlation was performed at the ROI-to-ROI level. For the RSFC calculation, each participant's mean time series for each seed ROI was calculated and correlated with each other. For the RSFC-behaviour correlation analyses, we used stepwise linear regression models in which four variables were set as the covariates to be controlled. The first was the slice number. Since there was a difference in the scanning parameters among the participants, a binary variable (0 for 33 slices and 1 for 35 slices) was set as a logical covariate to control for its effects. To control for the effects of head motion, we set a covariate to control its effects. We used the mean FD\_Jenkinson (Jenkinson, Bannister, Brady, & Smith, 2002) to represent the head motion because Yan et al. (2013) found that the mean FD\_Jenkinson could represent the effects of head motion better than other measures. The other three covariates were gender (a binary variable, 0 for females and 1 for males), age (a continuous variable), and task accuracy (a continuous variable).

Four stepwise linear regression models were built for different purposes using jamovi 1.1.7 (retrieved from <https://www.jamovi.org>). The first three models were built to estimate the proportion of the variances in FPFd that could be explained by each of the three RSFC measurements (i.e. the RSFC between one of the three ROI pairs). Therefore, each of the three models only included one of the three RSFCs as its regressor and the FPFd as the dependent variable. The fourth model was built to estimate the proportion of the variances in FPFd that could be explained by the three RSFC measurements jointly. Therefore, this model included all three RSFCs as regressors. For all four models, the slice number, age, gender, task accuracy, and head motion were set as covariates. For each model, the covariates were included in the first step, and the RSFC(s) was included in the second step. The proportion of the variances in FPFd that could be explained by the RSFC(s) was estimated using the  $\Delta R^2$  between the two steps.

We further conducted an analysis to examine the result patterns of the five individual ROIs of the eye-movement control/dorsal attention

network. Ten RSFCs between the five individual ROIs and the two target ROIs of the VWFA and early visual cortex were calculated. Ten stepwise linear regression models were then built, each of which included one of the ten RSFCs as its regressor and the FPFd as the dependent variable. The slice number, age, gender, task accuracy, and head motion were set as covariates.

To comprehensively show the RSFC-behaviour correlation patterns of our data, we conducted two supplementary analyses. In Supplementary Analysis 1, we used the same seed ROIs as in the main analysis and examined the correlations between FPFd and the ROI-to-voxel RSFCs at the whole-brain level. In Supplementary Analysis 2, we used the seven intrinsic large-scale brain networks (Yeo et al., 2011) as the seed ROIs to examine whether and how FPFd is correlated with the RSFCs between the intrinsic large-scale brain networks. Please see the Supplementary Online Materials for the detailed methods.

## 3. Results

### 3.1. Behaviour results

There were 24 questions to examine the participants' comprehension of the article, with a chance level of accuracy of 25%. To ensure that participants paid enough attention to the reading task before entering the RSFC-behaviour correlation analyses, we included in the analyses only the participants whose accuracy was significantly higher than the chance level (accuracy  $> 10/24$ , according to the exact binomial test). According to this criterion, 49 participants (25 females; age mean = 22.59,  $SD = 2.08$ , range = 19–27; accuracy mean = 65.86%,  $SD = 12.42\%$ , range = 46–96%; FPFd mean = 229 ms,  $SD = 26$ , range = 176–286 ms) were qualified for the RSFC-behaviour correlation analyses.

### 3.2. Results of the RSFC-behaviour correlation analyses

In the analysis without global signal regression, the mean RSFCs between the three pairs of ROIs across participants were as follows: the mean RSFC between the early visual network and VWFA was 0.529 ( $SD = 0.271$ , range = 0.046–1.289), the mean RSFC between the early visual network and eye-movement control/dorsal attention network was 0.357 ( $SD = 0.193$ , range = 0.011–0.886), and the mean RSFC between the VWFA and eye-movement control/dorsal attention network was 0.368 ( $SD = 0.156$ , range = 0.132–0.737).

In the analysis with global signal regression, the mean RSFCs between the three pairs of ROIs across participants were as follows: the mean RSFC between the early visual network and VWFA was 0.024 ( $SD = 0.213$ , range =  $-0.418$ –0.687), the mean RSFC between the early visual network and eye-movement control/dorsal attention network was  $-0.013$  ( $SD = 0.139$ , range =  $-0.342$ –0.237), the mean RSFC between the VWFA and eye-movement control/dorsal attention network was 0.103 ( $SD = 0.123$ , range =  $-0.198$ –0.392).

In the RSFC-behaviour correlation analyses using the RSFCs between the three seed ROIs, for each of the three models that include only one of the three RSFC measures, we reported the regression coefficient ( $b$ ), the standard error ( $SE$ ), and the  $t$ -value of the RSFC, which could reflect the relationship between the RSFC and the FPFd. Additionally, we reported the differences between the two steps in each model including the  $\Delta R^2$  and  $F$ -value, which could reflect the proportion of the variances in FPFd that could be explained by the RSFC. For the last model, which included all three RSFCs, we reported the  $\Delta R^2$  and  $F$ -value, which could reflect the proportion of variances in FPFd that could be explained by the three RSFCs jointly.

The results of the analyses using RSFC without global signal regression are shown in Table 1 and Fig. 1B (upper plot). The RSFCs between each pair of seed ROIs were all significantly correlated to the individual differences in FPFd and could significantly explain these differences (for the RSFC between the early visual network and VWFA,  $b$

**Table 1**  
Results of the main analysis of the RSFC-behaviour correlation.

Model (regressor of interest)	Regression coefficient (b)	Standard error (SE)	t	Variance explained ( $\Delta R^2$ )	F
Analysis without global signal regression					
Model 1 (RSFC between early visual network and VWFA)	42.062	13.426	3.133 <sup>**+</sup>	0.168	9.815 <sup>**</sup>
Model 2 (RSFC between early visual network and eye movement control/dorsal attention network)	76.282	19.143	3.985 <sup>***+</sup>	0.243	15.879 <sup>***</sup>
Model 3 (RSFC between VWFA and eye movement control/dorsal attention network)	68.737	24.064	2.856 <sup>**+</sup>	0.144	8.159 <sup>**</sup>
Model 4 (All three RSFCs)	–	–	–	0.265	5.672 <sup>**</sup>
Analysis with global signal regression					
Model 1 (RSFC between early visual network and VWFA)	47.385	16.950	2.796 <sup>**+</sup>	0.139	7.815 <sup>**</sup>
Model 2 (RSFC between early visual network and eye movement control/dorsal attention network)	79.530	26.495	3.002 <sup>**+</sup>	0.157	9.010 <sup>**</sup>
Model 3 (RSFC between VWFA and eye movement control/dorsal attention network)	29.595	32.820	0.902	0.017	0.813
Model 4 (All three RSFCs)	–	–	–	0.234	4.781 <sup>**</sup>

Note. \*  $p < .05$ ; \*\*  $p < .01$ ; \*\*\*  $p < .001$ ; +  $t$ -values surviving the Bonferroni correction in which the significance level is divided by the number of models, i.e.  $p < .017$ .

= 42.062,  $t = 3.133$ ,  $p = .003$ ; for the RSFC between early visual network and eye-movement control/dorsal attention network,  $b = 76.282$ ,  $t = 3.985$ ,  $p < .001$ ; for the RSFC between VWFA and eye-movement control/dorsal attention network,  $b = 68.737$ ,  $t = 2.856$ ,  $p = .007$ ; the significance of all three  $t$ -values survives the Bonferroni

correction in which the significance level is divided by the number of models, i.e.  $p < .017$ ). The three RSFCs together explained 26.5% of the variance in FPPD ( $F = 5.672$ ,  $p = .002$ ).

The results of the analyses using RSFC with global signal regression are shown in Table 1 and Fig. 1B (lower plot). The RSFCs between the early visual network and VWFA ( $b = 47.385$ ,  $t = 2.796$ ,  $p = .008$ ) and between the early visual network and eye-movement control/dorsal attention network ( $b = 79.530$ ,  $t = 3.002$ ,  $p = .005$ ) were significantly related to the individual differences in FPPD (the significance of both  $t$ -values survives the Bonferroni correction, i.e.  $p < .017$ ). The RSFC between the VWFA and eye-movement control/dorsal attention network did not show a significant relationship with individual differences in FPPD ( $t < 1$ ). The three RSFCs together explained 23.4% of the total variance in FPPD ( $F = 4.781$ ,  $p = .006$ ).

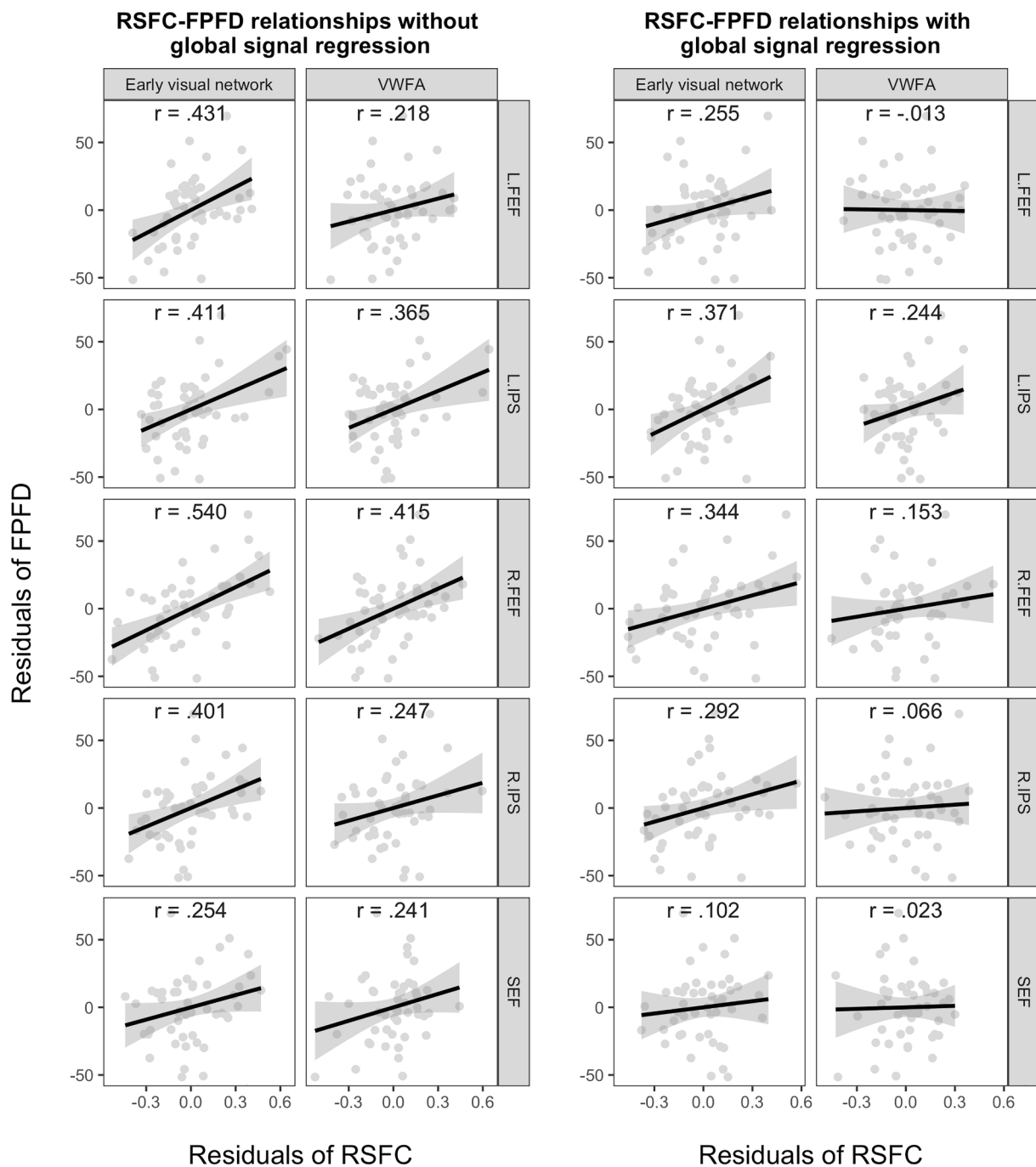
For the five individual ROIs of the eye-movement control/dorsal attention network, the RSFC-behaviour correlations are shown in Table 2 and Fig. 2. Although only a few of the RSFC-behaviour correlations were significant, nearly all of them were in the same positive direction, indicating that the merging of the five individual ROIs of the eye-movement control/dorsal attention network was an appropriate manipulation. For the results of the analysis without global signal

**Table 2**

The RSFC-FPPD relationships between the five individual ROIs of the eye movement control/dorsal attention network and the early visual network and VWFA.

Model (regressor of interest)	Regression coefficient (b)	Standard error (SE)	t
Analysis without global signal regression			
Model 1 (RSFC between L.FEF and early visual network)	56.905	18.356	3.100 <sup>**+</sup>
Model 2 (RSFC between R.FEF and early visual network)	53.172	12.781	4.160 <sup>***+</sup>
Model 3 (RSFC between SEF and early visual network)	30.219	17.729	1.704
Model 4 (RSFC between L.IPS and early visual network)	47.502	16.218	2.929 <sup>**+</sup>
Model 5 (RSFC between R.IPS and early visual network)	45.897	16.160	2.840 <sup>**</sup>
Model 6 (RSFC between L.FEF and VWFA)	28.297	19.519	1.450
Model 7 (RSFC between R.FEF and VWFA)	49.373	16.660	2.964 <sup>**+</sup>
Model 8 (RSFC between SEF and VWFA)	33.090	20.534	1.611
Model 9 (RSFC between L.IPS and VWFA)	45.606	17.939	2.542 <sup>*</sup>
Model 10 (RSFC between R.IPS and VWFA)	31.123	18.834	1.653
Analysis with global signal regression			
Model 1 (RSFC between L.FEF and early visual network)	34.084	19.878	1.715
Model 2 (RSFC between R.FEF and early visual network)	32.920	13.825	2.381 <sup>*</sup>
Model 3 (RSFC between SEF and early visual network)	15.159	22.667	0.669
Model 4 (RSFC between L.IPS and early visual network)	58.806	22.648	2.596 <sup>*</sup>
Model 5 (RSFC between R.IPS and early visual network)	33.776	17.067	1.979
Model 6 (RSFC between L.FEF and VWFA)	-1.919	22.156	-0.087
Model 7 (RSFC between R.FEF and VWFA)	19.800	19.731	1.004
Model 8 (RSFC between SEF and VWFA)	3.672	23.955	0.153
Model 9 (RSFC between L.IPS and VWFA)	41.571	25.461	1.633
Model 10 (RSFC between R.IPS and VWFA)	8.242	19.178	0.430

Note. \*  $p < .05$ ; \*\*  $p < .01$ ; \*\*\*  $p < .001$ ; +  $t$ -values surviving the Bonferroni correction in which the significance level is divided by the number of models, i.e.  $p < .005$ .



**Fig. 2.** Results of the analysis for the five individual ROIs of the eye movement control/dorsal attention network. The left panel shows the results without global signal regression, and the right panel shows the results with global signal regression. Each subplot of each panel shows the results of the model that included the RSFC between one of the five individual seed ROIs in the eye movement control/dorsal attention network (indicated by the panel's row labels), and one of the other two seed ROIs (indicated by the panel's column labels). The partial correlation coefficients are labelled on each subplot. The shadow indicates the standard error.

regression, significant RSFC-FPFD correlations were found between the left FEF and the early visual cortex ( $b = 56.905$ ,  $t = 3.100$ ,  $p = .003$ ), between the right FEF and the early visual cortex ( $b = 53.172$ ,  $t = 4.160$ ,  $p < .001$ ), between the left IPS and the early visual cortex ( $b = 47.502$ ,  $t = 2.929$ ,  $p = .005$ ), between the right IPS and the early visual cortex ( $b = 45.897$ ,  $t = 2.840$ ,  $p = .007$ ), between the right FEF and VWFA ( $b = 49.373$ ,  $t = 2.964$ ,  $p = .005$ ), and between the left IPS and the VWFA ( $b = 45.606$ ,  $t = 2.542$ ,  $p = .015$ ). For the results of the analysis with global signal regression, significant RSFC-FPFD correlations were found between the right FEF and the early visual cortex ( $b = 32.920$ ,  $t = 2.381$ ,  $p = .022$ ) and between the left IPS and the early visual cortex ( $b = 58.806$ ,

$t = 2.596$ ,  $p = .013$ ).

The results of the two supplementary analyses are detailed in the Supplementary Online Materials. To summarize, the findings of the supplementary analyses are similar to that of the main analysis. In Supplementary Analysis 1, for each seed ROI, the observed RSFC-FPFD correlations were mainly distributed inside or near the other two seed ROIs (see Table S1, Supplementary Fig. 1, and Supplementary Fig. 2), indicating the RSFCs between the three seed ROIs are the major RSFCs correlated with FPDF. In Supplementary Analysis 2, the RSFC between the visual network and the dorsal attention network was the only RSFC correlated with FPDF (see Table S2). Because the seed ROIs used in the

main analysis are all located within the visual network and the dorsal attention network, this finding is also convergent with the finding of the main analysis.

#### 4. Discussion and conclusions

We investigated whether and how individual differences in the FPPD in reading are related to RSFC in the human brain. We focused on the RSFCs between three target regions/networks, that is, the early visual network, the VWFA, and the eye-movement control/dorsal attention network. We found that the RSFCs between the three networks were all positively correlated with individual FPPD differences. These RSFCs can together explain about one quarter of the variance in the individual differences in FPPD, indicating a strong relationship between the RSFC and FPPD.

Our findings can be linked to a large body of previous research on the neurobiology of reading. In task-state neuroimaging studies, the involvement of the early visual network, the VWFA, and the eye-movement control/dorsal attention network in reading have been well indicated (Bolger, Perfetti, & Schneider, 2005; Choi et al., 2014; Choi & Henderson, 2015; Zhou et al., 2016). In resting-state neuroimaging studies, the RSFCs of these regions/networks have also been found to be related to several behavioural measurements of reading, such as reaction times of single characters (Wang et al., 2012), reading fluency (Zhou et al., 2015; Zhou et al., 2016), and lexical decision scores (Zhou et al., 2016). Our results provide a new aspect of evidence about how these regions/networks are related to reading behaviours. More importantly, our findings provide two novel insights into the brain-behaviour relationship in reading. First, our findings indicate that, as a behavioural measure strongly associated with online dynamic cognitive processes, individual differences in FPPD in reading were related to a relatively static functional property in the human brain: the RSFC. Second, the positive correlations between the length of the FPPD and the RSFCs between our seed regions/networks indicated that, for the brain areas of the reading network, and perhaps also for other areas where activation level is correlated with processing time, their RSFCs may be shaped by the processing time through the time-on-task effect and the mechanism of Hebbian learning.

In the present study, we mainly focused on a simplified neural model for the FPPD, which included only the most relevant brain regions related to FPPD. The complete neural model for the FPPD could be much more complex. For example, it has been found that the fixation duration during text reading can be affected by semantic processing (Yang, Staub, Li, Wang, & Rayner, 2012). Thus, the neural correlates of the FPPD may also include the semantic network. This speculation may be supported by a finding of our ROI-to-voxel whole brain analysis (Supplementary Analysis 1), which showed that the RSFC between the early visual network and a cluster in the left inferior temporal gyrus was related to the FPPD. This cluster is located between the VWFA and the left MTG, an area that is important for semantic processing (Wei et al., 2012). Therefore, this area may play a role in mapping orthographic representations to lexical semantic representations. To further explore the neural correlates of the FPPD outside our ROIs, we conducted a supplementary RSFC-behaviour correlation analysis (Supplementary Analysis 2), in which the 21 RSFCs between the 7 major brain networks were investigated. However, the results did not reveal any other brain networks related to FPPD, except for the visual and dorsal attention networks. Considering that the brain mechanisms that underlie eye movements and reading could be complex, the relationships between FPPD and the RSFC of other brain regions should be further explored in future studies.

Global signal regression is one of the most debated pre-processing options for RSFC analyses. On one hand, the global signal is associated with head motion, respiration, and cardiac rhythms so that global signal regression can reduce artefacts arising from these factors (Power et al., 2014). On the other hand, the global signal is also tightly coupled with

underlying neural activity (Schölvinck, Maier, Ye, Duyn, & Leopold, 2010), and global signal regression may introduce spurious anti-correlations between brain areas (Murphy & Fox, 2017). Our results have shown some impacts of global signal regression. For most of our results, the correlations between FPPD and RSFCs decrease with the global signal regression (see Tables 1, 2, and S1). The inter-subject variance of the FPPD that can be explained by the RSFCs also dropped from 26.5% to 23.4% when the global signal was regressed out from the RSFCs. However, our main finding, that the individual FPPD differences are positively correlated with the RSFCs between the main regions/networks related to FPPD, is stable across the results with and without global signal regression (Table 1 and Fig. 1). Therefore, the differences induced by global signal regression do not affect our main findings.

One important direction of reading research is to combine cognitive models of reading with neurobiological ones. In their influential paper introducing the E-Z Reader model, Reichle et al. (2003) inferred the underlying neural mechanisms of eye movements in reading based on their model and the relevant knowledge of neuroscience. Some of these inferred neural mechanisms have received support from neuroimaging studies (Henderson et al., 2014; Reichle, Tokowicz, Liu, & Perfetti, 2011). Recent studies have investigated individual differences in eye movements using the E-Z Reader model. For example, Reichle et al. (2013) tried to explain the differences in eye movements between adults and children by manipulating the parameters of the E-Z Reader model. Since the detailed neural mechanisms underlying eye movements during reading remain largely unknown, it remains difficult to integrate computational models such as the E-Z Reader model into the current RSFC study. However, these new advances are important for our understanding of individual differences in reading and should be considered in future studies of the neurobiology of reading.

The present study has several limitations. First, the sample size of our participants was small, which only allowed for investigating relatively simple relationships between behavioural and brain measurements. In future studies with a larger sample size, more complex brain-behaviour relationships are warranted. Second, we only used RSFC data to investigate the neural correlates of the FPPD. Since the FPPD is strongly associated with online dynamic cognitive processes, future studies should combine static brain measurements with dynamic task-related brain measurements, such as task fMRI and MEG data. Third, the task used in the present study had a high memory load, which required the participants to remember the whole article before answering the questions. The high memory load of the task may have impact on high-level cognitive processes. It may also result in the low accuracy of the participants' answers to the questions and the high regression probability (25%) in our data. To confirm that the low accuracy in our experiment was caused by the high memory load of the task, we asked 21 additional participants (undergraduate and graduate students) to complete an offline version of the same task. The participants were allowed to read the article again when they answered the questions so that the memory load became low. The accuracy dramatically improved (mean = 91.07%, SD = 4.80%, range = 79.17–95.83%), indicating that the high memory load was the main cause for the low accuracy of the original task. Because the FPPD is assumed to reflect the early stage of word processing, the impacts of the memory load and high-level cognitive processes on FPPD should be small. However, such impacts should be further examined in future studies. Fourth, previous studies of individual differences in reading have investigated many eye-movement measures other than FPPD, including global measures such as saccade sizes (Andrews & Coppola, 1999; Rayner et al., 2007), word-level measures such as first fixation durations and gazed durations on words (Payne, Federmeier, & Stine-Morrow, in press), and sentence-level measures such as forward fixation time and regression path reading time of sentences (Lou et al., 2017). Some studies focused on the mean value of the measures (e.g. Andrews & Coppola, 1999; Rayner et al., 2007), while others have focused on intra-individual variability and skew of the measures (e.g. Henderson et al., 2018). These measures may reflect



different aspects of text reading, and their neural correlates should be investigated in future studies. Finally, to explain the positive correlation between PFPD and RSFC, we speculated that individual differences in processing time may shape the RSFC in the brain through Hebbian learning. This hypothesis requires further justification through longitudinal studies that systematically investigate the relationship between individual differences in processing time and the changes in RSFC.

In conclusion, we found that individual differences in the PFPD in reading are positively related to the RSFCs between three regions/networks, including the early visual network, VWFA, and eye-movement control/dorsal attention network. Our results provide new evidence on the neural correlates of eye movements in text reading and indicate that individual differences in fixation time may shape the RSFC differences in the brain through the time-on-task effect and the mechanism of Hebbian learning.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bandl.2020.104893>.

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