Separable Roles for Attentional Control Sub-Systems in Reading Tasks: A Combined Behavioral and fMRI Study

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Attentional control is important both for learning to read and for performing difficult reading tasks. A previous study invoked 2 mechanisms to explain reaction time (RT) differences between reading tasks with variable attentional demands. The present study combined behavioral and neuroimaging measures to test the hypotheses that there are 2 mechanisms of interaction between attentional control and reading; that these mechanisms are dissociable both behaviorally and neuro-anatomically; and that the 2 mechanisms involve functionally separable control systems. First, RT evidence was found in support of the 2-mechanism model, corroborating the previous study. Next, 2 sets of brain regions were identified as showing functional magnetic resonance imaging blood oxygen level-dependent activity that maps onto the 2-mechanism distinction. One set included bilateral Cingulo-opercular regions and mostly right-lateralized Dorsal Attention regions (CO/DA+). This CO/DA+ region set showed response properties consistent with a role in reporting which processing pathway (phonological or lexical) was biased for a particular trial. A second set was composed primarily of left-lateralized Frontal-parietal (FP) regions. Its signal properties were consistent with a role in response checking. These results demonstrate how the subcomponents of attentional control interact with subcomponents of reading processes in healthy young adults.

Keywords: dual route, lexicality, orthography, phonology, regularity

The cultural development of reading is one of humankind's most revelatory accomplishments. Despite its importance in modern life, fluent reading is something that many people take for granted, perhaps because it, like many other learned skills, is achieved with a remarkable degree of automaticity across many contexts (e.g., Neely 1977; Schneider and Shiffrin 1977). Fluid and automatic reading is certainly not taken for granted by the 5–10% (or more) of the population that suffers from dyslexia, or impaired reading despite normal intelligence and adequate instruction (Siegel 2006). The link between attention and reading ability is underscored by the observation that dyslexia co-occurs with attention deficit hyperactivity disorder (ADHD) more frequently than would be expected by chance, with comorbidity estimated at 18–45% (August and Garfinkel 1990; Willcutt and Pennington 2000; Germano et al. 2010; Willcutt et al. 2010). Additionally, deficits in visual attention span may contribute to dyslexia independently of phonological processing skills (for reviews, see Valdois et al. 2004; Vidyasagar and Pammer 2010).

Automatic processes tend to be fast; relatively effortless; proceeding to some degree obligatorily; and incompletely accessible to conscious awareness (Logan 1997; but see also Stanovich 1990). Descriptors such as fast and obligatory indeed describe aspects of skilled reading in typical adult subjects, evidenced prominently by an entire literature exploring variants of the classic Stroop effect (Stroop 1935; Tanenhaus et al. 1980; Dennis and Newstead 1981; see MacLeod 1991 for a review). Automatic access to various word codes during reading tasks is also exemplified by the intrusion of orthographic information during tasks emphasizing phonology (e.g., Perfetti 1992; Booth et al. 1999, 2008) or by the observation that word meanings can be extracted from brief stimulus presentations, even if the meanings cannot be reported explicitly (Luck et al. 1996). Evidence that reading task variants are prone to interference from irrelevant processing features underlies one of the critical questions in the reading literature and, indeed, a primary motivation for the current study: If one of the features of skilled reading is automaticity, can experienced readers nonetheless exert selective attentional control over the component processes of reading? If so, how is such attentional control achieved?

One study suggested that 2 distinct mechanisms must be invoked to explain fully the reaction time (RT) differences between a simple reading task and an effortful (attention-requiring) reading task (Balota et al. 2000). Balota, Law and Zevin compared a speeded naming (read) task versus a novel regularize task, using a dual route framework. In contrast to the read task, the regularize task required subjects to pronounce words based exclusively on spelling-to-sound principles, pronouncing "pint" (/pajnt/) to sound like "lint" (/lInt/). The authors reasoned that if skilled readers can direct attentional control *completely* to *frequency-independent* grapheme-to-phoneme conversion to regularize words, then the typically observed main effects of lexicality and word frequency (suggestive of lexical route activation) should be reduced in the regularize task as compared with the read task.

Several key findings were reported by Balota et al. (2000). First, and not surprisingly, subjects performed the regularize task more slowly than the read task. Secondly, participants showed greater slowing to regularize words than pseudo-words, losing completely the speed advantage for words they showed in the read task. The reliable interaction of task by lexicality suggested that skilled readers had trouble completely inhibiting lexical (whole-word) processing for words, despite task instructions. Lastly, the usual word frequency effect (high frequency words are pronounced more quickly than low frequency words) *reversed* in the regularize task for regular, but not irregular words, producing a significant interaction of task, frequency, and regularity. This final observation was

interpreted as evidence of the need for more than one mechanism of attentional control for skilled reading.

Specifically, Balota and colleagues suggested that lexical route suppression and a subsequent "verification procedure" are *both* important mechanisms of interaction between reading processing and attention during the regularize task. The verification procedure, or response checking, can accommodate the word frequency effect reversal for regular words if, on some portion of the high frequency regular word trials, an additional time penalty is incurred because the participant second-guesses the (normal) pronunciation, subconsciously thinking the pronunciation should sound "funny."

The discussion in the Balota et al. (2000) study of a 2-mechanism interaction between reading and attentional control—pathway control in the form of lexical route suppression, plus response checking—was framed within a dual route model. According to dual route reading theory, visually presented words are processed along 2 distinct routes, the phonological and the lexical (e.g., Coltheart et al. 1993, 2001). The phonological route concatenates grapheme-to-phoneme mappings in a serial manner (Forster and Davis 1991) that is independent of word frequency and word regularity. Pseudowords can only be completely decoded via the phonological route. The lexical route, on the other hand, involves accessing whole-word representations of stimuli that have been learned through repeated exposure (e.g., Visser and Besner 2001), thus resolving more quickly for words that are more frequently encountered (Frederiksen and Kroll 1976), and without regard to word regularity (Coltheart et al. 2001). Word regularity determines whether the outputs of the 2 routes converge (regular words) or not (irregular words), a distinction that cannot be made until the "full reading process" occurs, that is, after route computation (Taylor et al. 2013). Prior to response articulation, "phoneme recognition" occurs (Pritchard et al. 2012), that is, a response is selected from between the 2 possibilities generated by the routes.

Dual route models are computationally capable of accommodating the types of shifts in response time and accuracy due to top-down attentional control that Balota and colleagues noted in their regularize paradigm (Rastle and Coltheart 1999), even if such "strategy" effects have not been a focal point of investigation with regard to the models (see Reynolds and Besner 2006 for a more detailed discussion). For example, when people read lists composed mainly of pseudowords, they make more regularization errors and show delayed RTs for exception (~irregular) words (Baluch and Derek 1991; Monsell et al. 1992; Rastle and Coltheart 1999; Zevin and Balota 2000). Context-dependent performance differences, including those arising from list composition manipulations, have often been interpreted as evidence for what is referred to as the pathway control hypothesis (e.g., Monsell et al. 1992; Pugh and Rexer 1994; Rastle and Coltheart 1999; Zevin and Balota 2000; Reynolds and Besner 2005; but see Lupker et al. 1997; Jared 1997 for conceptual frameworks other than pathway control). Attentional effects have also been noted at the response checking stage. For example, compared with naming tasks, lexical decision tasks show greater effects of whole-word variables like frequency (Balota and Chumbley 1985, 1990; Balota et al. 2004; but see Monsell et al. 1989 for an interpretation not invoking pathway control). In total, ample evidence suggests not only that there are indeed situations in which reading requires attentional control, but also that there are likely multiple loci (Vogel et al.

2005) at which attention may influence reading (including pathway control and response checking).

Just as reading involves several component processes that might serve as points of interaction with attention control, attentional control itself is achieved through the dynamic interaction of several brain systems (Dosenbach et al. 2008; Petersen and Posner 2012). Dissociation of attentional control systems is demonstrable through converging methods, including behavior (Fan et al. 2002), task based functional magnetic resonance imaging (fMRI) (e.g., Corbetta and Shulman 2002; Dosenbach et al. 2006; Spreng et al. 2010), functional connectivity MRI (e.g., Dosenbach et al. 2007; Seeley et al. 2007; Vincent et al. 2008; Power et al. 2011; Yeo et al. 2011) and lesion data (e.g., Nomura et al. 2010). The imaging and lesion data together suggest distinct patterns of activity and consistent network relationships between sets of regions subserving attentional control, for example, Cingulo-opercular (CO), Frontal-parietal (FP) and Dorsal attention networks.

Figure 1 depicts a unified model, combining aspects of the dual route theory and principles expressed by Petersen and Posner (2012), of how attentional control may interact with reading processing in skilled adult readers. The model proposes 2 points of interaction. An early point of interaction involves setting the bias to emphasize processing along either the lexical or the phonological route in a task- and stimulus-dependent manner ("pathway control"). The second point of interaction entails the selection and verification of the response from between the 2 route outputs ("response checking"). The model accounts for the primary behavioral effects reported by Balota et al. (2000) (a task-dependent lexicality effect and an impact of word regularity on the task reversal of the word frequency effect), while also constraining novel predictions regarding how control-related brain regions may interact with reading-related brain regions, as revealed by fMRI.

Specifically, the 2-mechanism model predicts that there will be at least 2 different kinds of reading-related control signals, anatomically segregated from one another and from data-processing systems (Posner and Petersen 1990). We considered, from first principles, that reading-related attentional control signals would most likely be observed in regions of the brain that have previously been shown to be important for attentional control generally. For example, CO control regions, thought to be important for parameter setting and maintenance of task mode (especially with regard to their task-sustained responses) (Dosenbach et al. 2007), may play a role in reflecting or reporting the pathway control required for a particular task/stimulus combination. Regions of the FP control network may subserve response checking, consistent with their previously ascribed role in supporting moment-to-moment "adaptive control" (Dosenbach et al. 2007, 2008). Brain regions belonging to other attentional control networks might additionally/alternatively be involved in the proposed model. For example, resting state functional connectivity fMRI (rs-fcMRI) work from our laboratory has demonstrated a privileged functional relationship between regions in the Dorsal attention system and reading-related regions including the putative Visual Word Form Area (VWFA) (Vogel et al. 2012; see also Zhao et al. 2011).

Despite the fundamental connection between attention and reading, the regularize paradigm used by Balota et al. (2000) has remained little studied over the last decade, particularly in terms of neuroimaging studies (but see Gold et al. 2005). The present study employed a comparison of a read task versus a
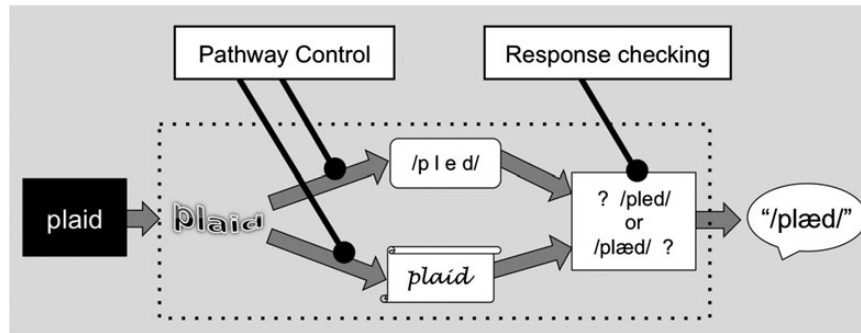
Figure 1. Schematic depicting 2 proposed mechanisms of interaction between attentional control systems and reading processing. Following presentation of a visual word stimulus (i.e., plaid) and basic perceptual processing, activation automatically proceeds along 2 processing routes. The phonological route is shown on top (/p l e d/) and the lexical route is depicted on the bottom (*plaid*). Following route processing, a single response is selected and prepared for articulation (? /pled/ or /plæd/ ?), a step that has been labeled "phoneme recognition" (see Pritchard et al. 2012, Fig. 1, for an updated dual route schematic). Finally, an overt response is articulated. Pathway control refers to the proposed site of early interaction between an attentional control system(s) and reading processing, reflecting the biasing of processing along one of 2 routes, depending on task demands and stimulus features. Response checking refers to a later interaction between an attentional control system(s) and reading processing, to ensure the appropriate response is selected from potentially competing alternatives.

regularize task in 2 independent samples of healthy young adults, referred to henceforth as the Behavioral cohort/study and the fMRI cohort/study. We tested the hypotheses that there are 2 distinct mechanisms of interaction between attentional control and reading processes (i.e., by replicating the behavioral observations of Balota and colleagues), and that the 2 mechanisms involve functionally and neuroanatomically separable attentional control systems.

In brief, several blood oxygen level–dependent (BOLD) fMRI response properties were predicted to distinguish candidate brain regions involved in pathway control from candidate regions involved in response checking. Of particular interest were the general response properties characterizing a region (relatively rapid vs. relatively protracted); the difference between words and pseudowords in each task for each region; the difference between regular and irregular words in each task for each region; and the anatomical locations of the regions that are most functionally similar to the candidate regions. The predictions are outlined in detail in Table 2, but can be summarized as deriving from the fact that regions involved in pathway control signal should show properties suggesting the reporting of a bias signal, whereas regions important for response checking should show properties consistent with the accumulation of information for the purpose of choosing between 2 possible responses. Of note, hierarchical clustering of event-related timecourses was employed (e.g., Ploran et al., 2007; Church et al., 2011), in conjunction with statistical testing, to identify and characterize candidate regions.

Materials and Methods: General

The methods common to both the behavioral and neuroimaging studies are described first, followed by the methods unique to each study.

Participants

Participants were recruited from the Washington University (St. Louis, MO, USA) community, and were excluded from eligibility for any of the following: neurologic and/or psychiatric diagnoses; history of dyslexia or reading difficulty; and current use of psychotropic medications. Functional magnetic resonance imaging study participants were additionally screened for MRI contraindications (e.g., metal implants, pregnancy, cardiac pacemakers). All study protocols were approved by the Washington University Human Studies Committee. Participants provided written informed consent and were compensated for their time.

Thirty-two right-handed, native and monolingual English speakers (ages 22–28 years; 15 male) were enrolled in the Behavioral study. All 32 participants provided behavioral data meeting the task accuracy criterion (>65%) for inclusion.

35 participants (19 male) ages 21–28 years were enrolled in the fMRI study. Two participants did not complete the imaging session due to personal reasons, and one participant performed the task too slowly to render separable hemodynamic responses for each stimulus. The final imaging data set thus included data from 32 subjects (31 with usable RT data).

Neuropsychological tests were administered to each participant. Test results established that all participants were reading at or above the 25th percentile with IQ estimates at or above the mean. Most participants were significantly above average in terms of both reading level and IQ; see Supplementary Material 0 for more complete information regarding neuropsychological testing.

Stimuli

The Behavioral study included 636 stimuli, comprising 252 pseudowords (pronounceable, nonsense letter strings) and 384 words. The words included 96 of each of 4 combinations of regularity (regular or irregular) × frequency (high or low) and length (short or long). Short items were 3–5 letters (mainly 1 syllable) and long items were 6–8 letters (mainly 2 syllables).

For brevity, only the statistical analyses of the Behavioral cohort's RTs for the short items ($n = 318$) are presented in the Results. Table 1 provides a summary of the important lexical properties of the Behavioral study short stimuli included in the primary analyses. Supplementary Material 1 provides additional information about the stimuli, including a complete list of the short stimuli used in both studies; Supplementary Material 2 provides additional information about the long stimuli used in the Behavioral study.

The fMRI cohort performed the tasks on short stimuli only ($n = 320$ total), with the majority ($n = 272$) of the stimuli overlapping with the short items used in the Behavioral cohort.

Stimuli were matched, as much as possible, across the conditions of interest for lexical properties that were *not* explicitly

Table 1

Mean values of lexical properties across 5 short stimulus types: Behavioral study

Stimulus type[a]	Number of letters (SD)	Number of syllables (SD)	Number of orthographic neighbors[b] (SD)	Number of phonological neighbors[b] (SD)	SFI[c] (SD)
High frequency regular words	4.25 (0.64)	1.00 (0.00)	8.15 (4.89)	15.81 (9.35)	59.51 (5.12)
Low frequency regular words	4.25 (0.64)	1.00 (0.00)	7.46 (5.09)	15.52 (9.91)	46.49 (3.87)
High frequency irregular words	4.33 (0.56)	1.00 (0.00)	6.23 (4.01)	15.52 (9.09)	61.50 (5.96)
Low frequency irregular words	4.29 (0.65)	1.04 (0.20)	5.65 (5.03)	15.27 (10.91)	46.55 (3.60)
Pseudowords	4.29 (0.62)	1.00 (0.00)	5.34 (4.48)	—	—

[a]For all word stimulus types, $n = 48$; for pseudowords, $n = 126$.
[b]Orthographic neighbors and phonological neighbors calculated using the English Lexicon Project database (http://elexicon.wustl.edu, Last accessed 11/9/13; Balota et al. 2007).
[c]SFI is from Zeno et al. (1995).

Table 2

Predicted BOLD fMRI effects for regions reflecting pathway control and response checking

Prediction		Pathway control		Response checking	
		Reporting a bias signal		Accumulating information	
General response properties		A relatively brief response, reflecting a bias signal		A relatively protracted response, reflecting the accumulation of information	
Lexicality effect		Overall smaller BOLD responses "Opposite … and more equal"		Overall larger BOLD responses "Opposite … and unequal"	
	Read task	pseudowords > words	Small difference	pseudowords > words	Small difference
	Regularize task	words > pseudowords	Small difference	words > pseudowords	Large difference
Regularity effect	Both tasks	irregular > regular	Small difference	irregular > regular	Large difference
Neighbors on the dendrogram		Visual regions and spatial attention regions		Regions associated with speech planning and articulation	

manipulated. The acoustic properties of the onset phoneme were also chosen so as not to vary systematically by stimulus type (Spieler and Balota 1997). For both the Behavioral and fMRI studies, stimuli were randomly intermixed within task runs, and each participant performed either the read task or the regularize task on each stimulus.

Word frequency ratings were based on the Zeno et al. (1995) Standard frequency index (SFI); stimuli sampled an SFI continuum from 40.0 to 75.0 relatively evenly (unit = log-transformation of a weighted frequency per million). A word was deemed regular (rather than irregular) if its rime (e.g., –at in cat) followed typical spelling-to-sound correspondences (n.b., there is no fixed set of spelling-to-sound rules in English). Pseudowords were created *de novo*, using onset (e.g., /k/ in cat) and rime (e.g., /æt/ in cat) graphemes that tend to be both consistent and regular (i.e., unambiguously pronounced).

The stimuli were divided into fixed lists: 6 lists of 106 items each for the Behavioral study, and 10 lists of 32 items each for the fMRI study. Stimulus types were equally distributed across the lists, and the list ordering and list task assignment were counterbalanced across participants.

Task Instructions, Response Collection and Accuracy Scoring

For the regularize task, subjects were instructed to "sound out" items (real words and nonsense words) as though reading them for the first time, using whatever strategies they normally use when encountering new items. Participants were given 13 demonstration trials as well as 73 self-paced practice trials, with feedback, for the regularize task. In the fMRI study, the practice session occurred prior to the start of scanning, out of the scanner. None of the practice items appeared as stimuli in the experimental runs.

Accuracy of pronunciation was coded by a single rater. For the regularize task, a pronunciation of a regular word (e.g.,

"hike") was correct if it corresponded to the standard dictionary pronunciation. An irregular word was correct if its pronunciation obeyed any of several potentially phonologically legitimate alternative spelling-to-sound mappings of its rime (e.g., pronouncing "have" as /hev/). For both tasks, pseudowords were considered correct if their pronunciations followed standard orthographic-phonological mapping conventions, or rhymed with similarly spelled real words (e.g., /krot/ for "crote").

Responses were recorded so that RTs could be extracted offline. Raw sound files were recorded for each run for each participant, using a Sony MP3 Digital Voice Recorder (ICD-UX70 1GB USB) in the Behavioral study, and Cool Edit 2000 software for the fMRI study (Syntrillium). Recorded files were normalized, noise-reduced and purged for artifacts (e.g., coughs, throat clearings) using Audacity (http://audacity.sourceforge.net/).

For the Behavioral study, RTs were calculated from cleaned files using an in-house Matlab program (Matlab 7.80; R2009a; The MathWorks, Natick, MA, USA) (Nelles et al. 2003). Reaction times were also spot-checked manually using Audacity. Trial-by-trial RTs for the fMRI study were calculated *manually* by a single rater, using Audacity, because some of the participants' responses coincided with the scanner noise. To account for possible individual differences in general processing speed, trial-by-trial RTs for both studies were z-score transformed (Faust et al. 1999). The mean and standard deviation (SD) were calculated for each participant across all correct trials of both tasks, excluding raw RTs < 200 ms or >3 SD above that individual's mean as probable outliers (on average, fewer than 1.5% of trials). Only correct trials were included in the RT and BOLD analyses.

Repeated-measures analyses of variance (ANOVAs) were planned at the subject-level to examine effects of categorically defined variables, including task, lexicality, and regularity. Correlation analyses were computed to examine the effect of frequency, a continuous variable. Additional analyses at the

item-level in the Behavioral study confirmed that the pattern of results was not driven by the particular selection of stimuli (data not shown). Appropriate post hoc analyses were used to clarify the results of the planned comparisons.

Following Balota et al. (2000), the interaction analyses of the RT data including frequency and lexicality were computed using only regular words and pseudowords. Since both regular words and pseudowords generate the same pronunciations for the 2 tasks, their task comparison is free of potentially confounding articulatory effects.

Materials and Methods: Behavioral Study

Task Structure

For the Behavioral study, 3 consecutive runs of the regularize task were followed by 3 runs of the read task ("Pronounce these items normally"). Each run included 106 items and lasted 6 min, 10 s. Pilot testing suggested that the fixed regularize/read ordering was most effective for establishing and maintaining task mode.

Stimuli were displayed on a black background in lowercase white letters at font size 56, subtending 2.1°–5.0° of visual angle horizontally and 0.7°–1.1° vertically. Each stimulus appeared alone, and in the middle of the screen, for 2500 ms (see Supplementary Fig. 1). Participants could respond as soon as the stimulus appeared and up until the next stimulus appeared. A white fixation crosshair appeared in the middle of the screen for 1 s between stimuli, to encourage visual fixation on the screen.

Apparatus

Stimuli were controlled using Psyscope × B53 (Cohen et al. 1993) on a Power Macintosh G3, and were displayed on a 16 in Sony CRT computer monitor. A standing microphone was placed 2–3 cm away from the participant's mouth, and transmitted spoken responses to the Sony MP3 Digital Voice Recorder.

Materials and Methods: fMRI Study

Task Structure

Following standard localizer and anatomical scan acquisition (described below), each participant performed 5 runs each of the 2 tasks, in the following sequence: 2 runs of regularize, 2 runs of read, 2 runs of regularize, 2 runs of read, and finally one run each of regularize and read. This quasi-alternating run order contrasts with the blocking order utilized in the Behavioral study, and was employed in order to balance the conflicting objectives of minimizing task-switching versus safeguarding against losing an entire task (e.g., as a block of runs) due to subject movement, equipment failure, etc. Each run included 32 items and lasted 5 min, 21 s. Trials were jittered with an intertrial interval of 1, 2, or 3 frames. The scan time required for the task runs averaged 75 min.

Stimulus Presentation

To discourage movement and provide a landmark for head position during scanning, participants were fitted with an individualized, thermoplastic mask that was attached to the head coil. A mirror was also placed on top of the head coil, allowing visualization of an LCD projection screen near the caudal end of the tube. Stimuli were projected onto the screen from the adjacent control room, using Psyscope × B53 (Cohen et al. 1993) on a Macintosh iMac. Stimuli were displayed on a black background in lowercase white letters at font size 56, subtending 2.1°–4.9° of visual angle horizontally and 0.7°–1.05° vertically. Each stimulus appeared alone, and in the middle of the screen, beginning at 1350 ms after the onset of an image acquisition frame (see Supplementary Figs 1 and 2). The stimulus remained on the screen for 1550 ms. This timing was chosen, based on pilot studies, in order to maximize the likelihood that vocal responses would occur within the 1000 ms gap in scanning that occurred after each TR. During the 1–3 frames (jittered) between trials, a white fixation crosshair appeared in the middle of the screen. Participants could respond as soon as the stimulus appeared and up until the next stimulus appeared (i.e., within 6–12 s). Participants were instructed to maintain visual fixation on the crosshair for the duration of the run. Participants were fitted with an MRI-compatible headset and microphone, with the microphone positioned 1–2 cm away from the mouth.

Image Collection

Images were acquired using a Siemens 3T Trio scanner (Erlangen, Germany) and a Siemens 12-channel Matrix head coil. A single high-resolution structural scan was acquired using a sagittal magnetization-prepared rapid gradient echo (MP-RAGE) sequence (slice time echo = 3.08 ms, TR = 2.4 s, inversion time = 1 s, flip angle = 8°, 176 slices, 1 × 1 × 1 mm voxels). Functional runs were acquired parallel to the anterior–posterior commissure plane using an asymmetric spin-echo echo-planar pulse sequence (TR = 2.0 s plus a 1.0 s delay, total TR = 3.0 s; T2* evolution time 27 ms; flip angle 90°). Thirty-two contiguous interleaved 4 mm axial slices, with 4 × 4 mm in-plane resolution, allowed for total brain coverage. Magnetization steady state was assumed after 12 s, so that functional data acquisition began with the fifth MR frame. As mentioned, the pulse sequence used here included a 1 s delay after each TR to facilitate the collection and monitoring of participants' overt responses.

Image Preprocessing

Despite the requirement for overt vocal responses, in-scanner movement was relatively low. Frame-by-frame movement correction data from the rotation and translation in the x, y, and z planes was computed for each participant for each run, and no runs had overall movement >1.00 mm RMS. Average per-run movement was 0.24 mm RMS.

Automated image preprocessing included the following procedures: 1) removal of a single pixel spike caused by signal offset, 2) correction of odd versus even slice intensity differences due to interleaved slice acquisition, 3) debanding, 4) quantification of and correction for movement within- and across- runs, via realignment of slices into scanner space using rigid-body rotation and translation, 5) correction for magnetic field distortions using subject-acquired field maps, and (6) within-run normalization of signal intensity to a whole-brain mode of 1000.

Preprocessed functional BOLD data from each participant were next registered to a common atlas using 12-parameter affine warping of the individual's MP-RAGE to the target. The target atlas was based on Talairach and Tournoux (1988), and was created in-house by mutually coregistering the anatomy of

12 healthy young adults and 12 healthy school-age children (Brown et al. 2005) (for the purposes of reporting, all coordinates from these data have been converted to MNI space. Coordinates from other studies are reported in the original space used by the authors, along with an MNI conversion (http://www.sdmproject.com/utilities/?show=Coordinates, Last accessed 11/9/13)). Previous work from our laboratory has systematically validated the use of combined child/adult reference atlases (e.g., Burgund et al. 2002; Kang et al. 2003). Furthermore, we have obtained excellent data fits using combined child/adult atlases both for functional analyses comparing age groups (e.g., Schlaggar et al. 2002; Brown et al., 2005) and for functional analyses examining groups of a single age cohort (e.g., Ihnen et al. 2009, Vogel et al. 2012, Lessov-Schlaggar et al. 2013, Vogel et al. 2013). As part of the atlas transform, the data were resampled on an isotropic 2 mm grid.

Next was performed a set of preprocessing steps that have been shown to be useful (Power et al. 2013) for minimizing motion-related noise in the BOLD signal in resting state MRI analyses (e.g., Fox et al. 2009; Power et al. 2012; Satterthwaite et al. 2013), versions of which have been implemented in task based fMRI data (Zhao et al. 2011). The complete sequence included demeaning and detrending each run followed by across-run regression of the following: 1) 6 parameters obtained by rigid body head motion correction, 2) the whole-brain signal averaged across the entire brain, 3) ventricular signal averaged from ventricular ROIs, and 4) white matter signal averaged from white matter ROIs. The first derivatives of these regressors were also used, yielding a total of 18 regressors.

Supplementary Material 3c describes further the motivation for applying this final preprocessing step and additional details about the methodology, and also explains that the fundamental results were similar when analyses were recomputed using data that did not undergo this step.

Scope of Imaging Analysis: Primary Effects (Task and Lexicality) and Secondary Effects (Regularity)

The hypothesis of a 2-mechanism interaction between attentional control sub-systems and reading processing implies testable predictions regarding task, lexicality, and regularity (description of predictions, along with Table 2, to follow). Region selection was thus driven by identifying, from whole-brain analyses, regions showing 1) an interaction of task by timecourse, and/or 2) an interaction of task by lexicality by time. Effects of regularity were then explored in secondary analyses using the task- and task × lexicality-sensitive regions.

Effects of task and lexicality were prioritized for region definition (rather than effects of regularity) because they showed the largest and most reliable behavioral effects, and because they could be computed using the full stimulus set (i.e., words and pseudowords), therefore being more likely to detect even small effects. Figure 2 depicts schematically the critical pieces of the analysis stream for the fMRI study, the steps of which are next described.

Image Analysis: Region Identification

GLM Modeling

Statistical analyses of the preprocessed BOLD data were computed at the voxel level using a general linear model (GLM) (Ollinger et al. 2001). The GLM design incorporated time as an 8-level factor, with the 8 levels corresponding to successive MR frames following presentation of the stimulus. Two levels of task (read or regularize) and 2 levels each of lexicality and regularity (the latter applicable to words only) were also included as factors in the design matrix. Frequency was not treated in the imaging analyses. Events of interest included only correct trials; errors were modeled separately in the GLM and were ignored here. No assumptions were made about the shape of the hemodynamic response function (HRF). Time-courses for all analyses were entered into ANOVAs using random effects models. GLM modeling and a portion of the subsequent analyses were conducted using in-house software programmed in the Interactive Data Language (IDL) (Research Systems, Inc. Boulder, CO). Additional statistical analyses were conducted using SPSS 16.0.1 (SPSS Inc., 2007) and Matlab (Matlab 7.80; R2009a; The MathWorks, Natick).

Voxelwise Image Generation

Task × Timecourse

First, a 2 task (read vs. regularize) by 8 timepoints (timecourse) voxel-wise whole-brain rmANOVA was computed to identify regions whose BOLD timecourses showed a differential deflection from baseline (positive or negative), that depended on which task the participant was performing.

Lexicality × Task × Timecourse

Next, a 2 lexicality (all words vs. pseudowords) by 2 task (read vs. regularize) by 8 timepoints (timecourse) voxel-wise whole-brain rmANOVA was computed to identify regions showing differential BOLD timecourse activity for the 2 tasks that *also* depended on whether the stimulus in a particular trial was a word or a pseudoword.

Thresholding and Peak Identification

The voxel-wise analyses described above produced images containing voxels showing a task × timecourse interaction or a lexicality × task × timecourse interaction. These 2 images were corrected for false positives, based on Monte Carlo simulation, using a criterion of 24 contiguous voxels with a $z > 3.5$ (Forman et al. 1995; McAvoy et al. 2001). Regions were then extracted from each of the 2 images using an in-house peak-finding algorithm courtesy of Avi Snyder. Activity peaks were identified within the Monte Carlo-corrected images by applying a smoothing kernel of 4 mm kernel and requiring that adjacent peaks be no closer than 10 mm apart.

Timecourse Extraction

The task × timecourse and lexicality × task × timecourse rmA-NOVAs described above were recomputed, this time using the regions identified by the peak definition as ROIs, in order to derive the timecourses of activity for each ROI in each participant, for every level of every factor in the design. Average time-courses of the BOLD % signal change at each of 8 timepoints were then computed and visualized for the various conditions.

Creation of Primary Region Pool

Finally, regions from the 2 whole-brain images described ((task × timecourse) and (lexicality × task × timecourse)) were pooled into a single set of possible ROIs. Region sets were combined in order to cast as wide a net as possible in identifying regions that may contribute to the 2 most reliable features
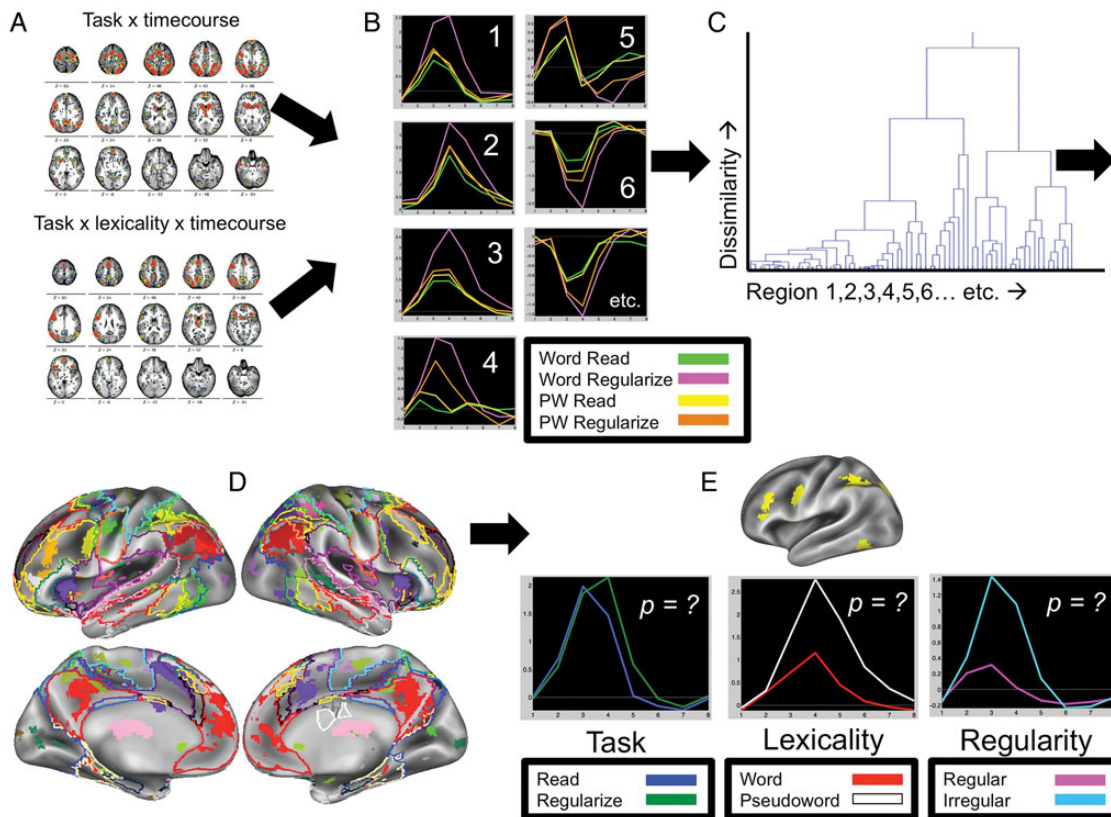
Figure 2. Schematic depicting the targeted analysis stream for the fMRI study. First (*A*), whole-brain ANOVAs identified individual regions showing (task × timecourse) and (task × lexicality × timecourse) effects. Next (*B*), the timecourses of the regions showing the 2 effects of interest were computed. Then (*C*), concatenated timecourses were used to cluster the regions using a UPGMA algorithm. Clusters were mapped (*D*) to the cortical surface for visualization, along with putative community borders. For each cluster (*E*), effects of task, lexicality and regularity (each with respect to timecourse) were interrogated, by computing rmANOVAs treating regions as "subjects" and clusters as the grouping variable. The results of the rmANOVAs were used to test the predictions outlined in Table 2.

of the behavior (the task effect, and the modulation of the task effect by lexicality); also there was considerable overlap between the images. Overlapping regions and regions with biologically implausible timecourses were excluded from the ROI pool as described in Supplementary Material 4.

Hierarchical Clustering of Identified Regions

The 2-mechanism model depicted in Figure 1 predicts that 2 different types of attentional control signals interact with reading processing regions in the read/regularize task paradigm. The primary objective of the imaging analyses was therefore to test the hypothesis that subsets of attentional control-related regions from the overall pool (perhaps including members of systems such as the FP, CO, Dorsal attention, etc.) would segregate into 2 distinct sets based on response properties, suggesting dissociable contributions to the tasks. All the regions in the final pool of task- and task × lexicality-sensitive regions were therefore segregated, based on BOLD responses, using hierarchical clustering.

Creation of Dendrogram and Visualization of Region Clusters

One advantage of not using as assumed HRF when estimating an fMRI BOLD response is that information in the HRF shape —including time to rise, width of peak, and time to return to baseline—may provide information about the underlying neural activity that is not rendered by statistical testing of

effects of interest. In particular, it is possible to identify sets of brain regions that are functionally related for a particular task by querying for similarity in the regions' BOLD HRFs, for example, via hierarchical clustering. Hierarchical clustering entails making choices, including where to threshold the dendrogram, that are generally informed by a priori predictions about the structure of the underlying data, rather than being prescribed quantitatively (e.g., Ploran et al. 2007; Church et al. 2011).

Hierarchical clustering was computed in Matlab (Matlab 7.80; R2009a; The MathWorks, Natick). To focus on the rise and peak of the hemodynamic response, the first 6 timepoints (i.e., 18 s) of each average timecourse were isolated, for each of 4 conditions (2 lexicality × 2 task), for each region. (Thus timecourses for the regions originally identified in the task × timecourse image had to be re-extracted from a task × lexicality × timecourse rmANOVA.) The timecourses for each of the 4 conditions were concatenated for each region, creating a matrix of 24 columns (6 timepoints for each of 4 conditions) with as many rows as there were regions. The UPGMA (Unweighted Pair Group with Arithmetic Mean) method was used to generate clustering assignments between the regions represented in the matrix (e.g., Ploran et al. 2007; Church et al. 2011).

The dendrogram resulting from the UPGMA clustering was examined by plotting the observed clusters, at various similarity $(1 - r)$ thresholds, on the surface of the brain, using Caret software (Van Essen et al. 2001). Given our a priori interest in

attentional control regions, the 2 clusters that appeared to fall into attentional control-related network boundaries (i.e., putative attentional control clusters) were carried forward into subsequent analyses.

Predictions of fMRI Analysis: Pathway Control and Response Checking

Several predictions regarding the BOLD activity patterns for regions involved in pathway control and response checking guided the remaining analyses. The predictions, described below and outlined in Table 2, are designed to test 1) whether or not the region sets identified using hierarchical clustering show different functional properties and 2) whether or not the roles of the region sets map onto the model schematized in Figure 1.

Regions subserving top-down pathway control may show BOLD signals consistent with a read-out as to whether a participant was directing attention to lexical or phonological processing in the context of a particular task and stimulus. If pathway control is akin to parameter setting (in that it is required for every task regardless of difficulty (Meiran 1996)), regions supporting pathway control might be expected to show responses that are generally less variable across the 2 tasks in terms of peak % BOLD change (i.e., smaller differences between the 2 levels of many variables). Such reporting signals may also be predicted to be relatively rapid to rise and rapid to fall. For example, the effects of lexicality (words vs. pseudowords) for the 2 tasks might be small, relatively transient, of roughly equivalent magnitudes and in opposite directions for the 2 tasks. The "opposite and equal" prediction for the lexicality effect reflects that each task requires a bias signal, but that those bias signals are different. That is, skilled readers presented with familiar words presumably emphasize the lexical pathway during the read task, and the phonological pathway during the regularize task. Also, regions reflecting pathway control should show minimal effects of word regularity, consistent with the dual route postulate that both regular and irregular words are processed along both pathways essentially obligatorily (Coltheart et al. 2001).

Unlike pathway control, presumably necessary for any task variant, response checking is likely *more* critical for the task requiring overriding the usual stimulus–response mapping, regularize. If response checking matters more for regularize than for read, then regions involved in response checking should show generally larger effects of task than the early actors, both as a main effect and as interactions with other variables. Thus, response checking regions should show lexicality effects that are "opposite and unequal" (specifically, larger in the regularize task, where the response checking assumes a larger importance). Similarly, the effect of regularity at response checking regions should be larger for the regularize task than the read task (in addition to being larger overall in response checking regions compared with pathway control regions; see above). It is also likely that regions showing signals associated with response checking will show a more protracted timecourse of response than will regions that reflect pathway control, owing to the time required to complete a decision-making process.

To test this set of predictions, timecourses from each region in each UPGMA-generated cluster were extracted and entered into statistical analyses as described below.

Plotting Average Timecourses for Each Control-Related Cluster

Average Lexicality × Task Timecourses Plotted

Timecourses (extracted as described above) were averaged, across all regions of each of 2 putative attentional control clusters, for each of the 4 conditions originally leveraged to compute the clustering (lexicality (2) × task (2)). Because these lexicality × task timecourses comprised the very data that entered into the clustering, clusters are expected, by definition, to show different patterns across these timecourses.

Regularity × Task Timecourses Extracted, and Average Timecourses Plotted

Timecourses were next extracted for all regions in the final set by computing a rmANOVA over 2 regularity (regular vs. irregular) by 2 task (read vs. regularize) by 8 timepoints (timecourse). As for task × lexicality, average timecourses across all regions of the 2 putative attentional control clusters were then plotted for each of 4 combinations of regularity (2) × task (2).

Quantification of Differences Between Region Clusters

To test quantitatively the imaging predictions, several rmANOVAs were next computed in which each *region* from each cluster was treated as "a subject" and each regions' *cluster assignment* was treated as a grouping variable. Two omnibus rmANOVAs were computed, one that included as within-"subject" variables lexicality (2) × task (2) × timecourse (8), and a second that included regularity (2) × task (2) × timecourse (8). Follow-up planned comparisons additionally assessed for separate effects of cluster membership on lexicality (2) × timecourse (8) for each task; and regularity (2) × timecourse (8) for each task. This targeted set of analyses (all of which featured cluster as the grouping variable) allowed for the identification of which of the many possible effects of lexicality, task, and regularity best characterizes the functional segregation of the 2 putative attentional control clusters, and in particular whether those differences map onto the hypothesized 2-mechanism model shown in Figure 1.

The rmANOVAs conducted using cluster as a grouping variable were not all equally unbiased. Specifically, the regions were originally defined as showing reliable effects of either task × timecourse or lexicality × task × timecourse, and the resulting clustering was computed using the concatenated timecourses from the 4 conditions of task (2) × lexicality (2). Therefore, the omnibus lexicality × task × timecourse × cluster ANOVA is *biased* towards a reliable result, although statistical significance is not a *necessary* consequence of the analysis. It is conceivable that timecourse differences causing 2 sets of regions to segregate in cluster space are not large enough and/or reliable enough to result in a statistically significant 4-way interaction. Importantly, the post hoc tests (e.g., examining the effect of lexicality for the read task only) are unbiased, since they consider only portions of the original data used to define the clusters. Our interpretations emphasize the results of the post hoc tests.

In contrast to the lexicality analyses, the rmANOVAs using regularity as a factor are completely unbiased, as the regions were defined blind to regularity. The statistical reliability of the omnibus rmANOVA and all of the post hoc tests involving regularity can therefore be assessed without caveats related to bias.

Results

Key Results From Balota et al.'s Behavioral Analysis Were Replicated

The behavioral data measured both outside and inside the scanner confirmed the generalizability of the key Balota et al. (2000) findings, driving a principled investigation of the associated neural activity in the fMRI study. Participants in the scanner were slower than the Behavioral study participants to perform both tasks, by ~350 ms, but the pattern of results was quite similar across the 2 cohorts.

RT analyses were conducted on zRT data (Faust et al. 1999) at the subject level; analyses on raw RTs yielded similar results. Table 3 shows the mean raw RT and accuracy rates for both the behavioral and imaging cohorts for both tasks, for various stimulus types; as described in the Methods, analyses focus on the Behavioral cohort (but see Supplementary Material 2 for the more complete treatment of the behavioral results, including the long items from the Behavioral cohort and the short items from the Imaging cohort).

Participants Were Slower to Regularize Than to Read

There was a significant main effect of task, driven by slower performance on the regularize than the read task (mean RTs of 1170 ms vs. 733 ms; rmANOVA $F_{1,31} = 348.45$, $P < 0.001$; see Supplementary Fig. 3A).

Direction of Lexicality Effect Depended on Task

There was a significant interaction of task and lexicality (regular words vs. pseudowords) ($F_{1,31} = 109.12$, $P < 0.001$; see Supplementary Fig. 3B). This interaction was driven by a positive effect of lexicality in the read task (+101 ms; $F_{1,31} = 37.61$, $P < 0.001$), and a negative lexicality effect in the regularize task (−145 ms; $F_{1,31} = 60.26$, $P < 0.001$). That is, participants were *faster* to *read* regular words than pseudowords but *slower* to *regularize* words than pseudowords.

Task and lexicality interacted significantly for the comparison of irregular words versus pseudowords as well ($F > 70$), showing a very similar pattern as that observed for regular words, that is, a positive lexicality effect for read and a negative lexicality effect for regularize.

Correlation Analyses at the Item-Level Suggested That Regularity Modulated the Word Frequency Effect for the Regularize Task

Unlike the original Balota et al. study, the current study coded and treated frequency as a continuous variable, as SFI (the Zeno et al. 1995 frequency measure) was sampled relatively evenly across a range. Hence correlation analyses, rather than repeated-measures ANOVAs, were used to assess the modulation of the effect of frequency by regularity in the 2 tasks. In order to maximize the power to detect what was potentially a weak effect, item-level correlation analyses were computed using all 384 word stimuli (rather than just the short words) ($n = 192$ each of regular and irregular words). Each item was entered into 2 bivariate correlations, one for each task (read and regularize). The correlations between frequency and group-average zRT for each task were computed separately for regular and irregular words. As shown in Supplementary Figure 4, frequency facilitated read zRT for both regular ($R = −0.176$; $p = 0.015$) and irregular words ($R = −0.312$; $P < 0.001$), as expected. Critically, frequency also significantly *inhibited* regularize task zRT for regular words ($R = 0.242$; $P = 0.001$), while the effect for irregular words was null ($R = −0.046$; $p = 0.524$). (When the correlations were recomputed using only the short words from the Behavioral cohort, the patterns of facilitation and inhibition remained the same. For the critical effect of inhibition of regularize RT for regular words, reliability was decreased to *near* statistical significance ($P = 0.051$), but the Pearson's R was very similar ($R = 0.200$), and the slope of the linear fit was comparable. Also, the effect of frequency on irregular words in the regularize task was still null when computed using the smaller stimulus set ($R = −0.062$; $P = 0.550$).) The regular versus irregular distinction revealed by the correlation results, while not a direct test of difference, is nonetheless consistent with Balota et al.'s 3-way interaction of task × frequency × regularity, further motivating the exploration of the 2-mechanism hypothesis with the imaging data.

Supplementary Material 5 and Supplementary Figure 5 present an additional post hoc correlation analysis, conducted at the subject-level rather than the item-level, that provides further evidence in support of the 2-mechanism account.

fMRI Revealed Substantial and Reliable Involvement of Attentional Control-Related Brain Regions

Task x Timecourse

Many regions of the brain, in both the right and left hemispheres, showed differential activity across time that depended on task. Figure 3 depicts the statistical image of the interaction of task by timecourse. Although activations were widespread, the focus here is on regions involved in attentional control in relation to reading-related processing.

Figure 3 shows prominent involvement of regions in the CO control system (purple arrows), including bilateral anterior insula/frontal operculum (aI/FO) and dorsal anterior cingulate cortex/medial superior frontal cortex (dACC/msFC); FP control system (yellow arrows), including left dorsolateral prefrontal cortex and left intraparietal sulcus (IPS); and Dorsal attention

Table 3

Mean Raw Reaction Times (ms) and Accuracy Rates, with SD (short items)

|	Read task				Regularize task			
	Behavioral study		fMRI study		Behavioral study		fMRI study	
Stimulus type	RT M (SD)	Acc M (SD)	RT M (SD)	Acc M (SD)	RT M (SD)	Acc M (SD)	RT M (SD)	Acc M (SD)
High frequency, regular	672 (119)	1.00 (0.000)	965 (184)	0.999 (0.007)	1242 (295)	0.989 (0.025)	1556 (580)	0.988 (0.021)
Low frequency, regular	691 (129)	0.999 (0.007)	982 (182)	1.000 (0.000)	1209 (295)	0.991 (0.028)	1517 (596)	0.988 (0.019)
High frequency, irregular	706 (125)	0.995 (0.013)	994 (179)	0.984 (0.028)	1252 (290)	0.856 (.122)	1554 (597)	0.912 (0.080)
Low frequency, irregular	739 (129)	0.970 (0.041)	1046 (230)	0.956 (0.055)	1246 (251)	0.845 (.100)	1577 (596)	0.899 (0.083)
Pseudo-words	783 (175)	0.990 (0.016)	1094 (262)	0.992 (0.016)	1081 (277)	0.990 (0.022)	1342 (546)	0.993 (0.013)
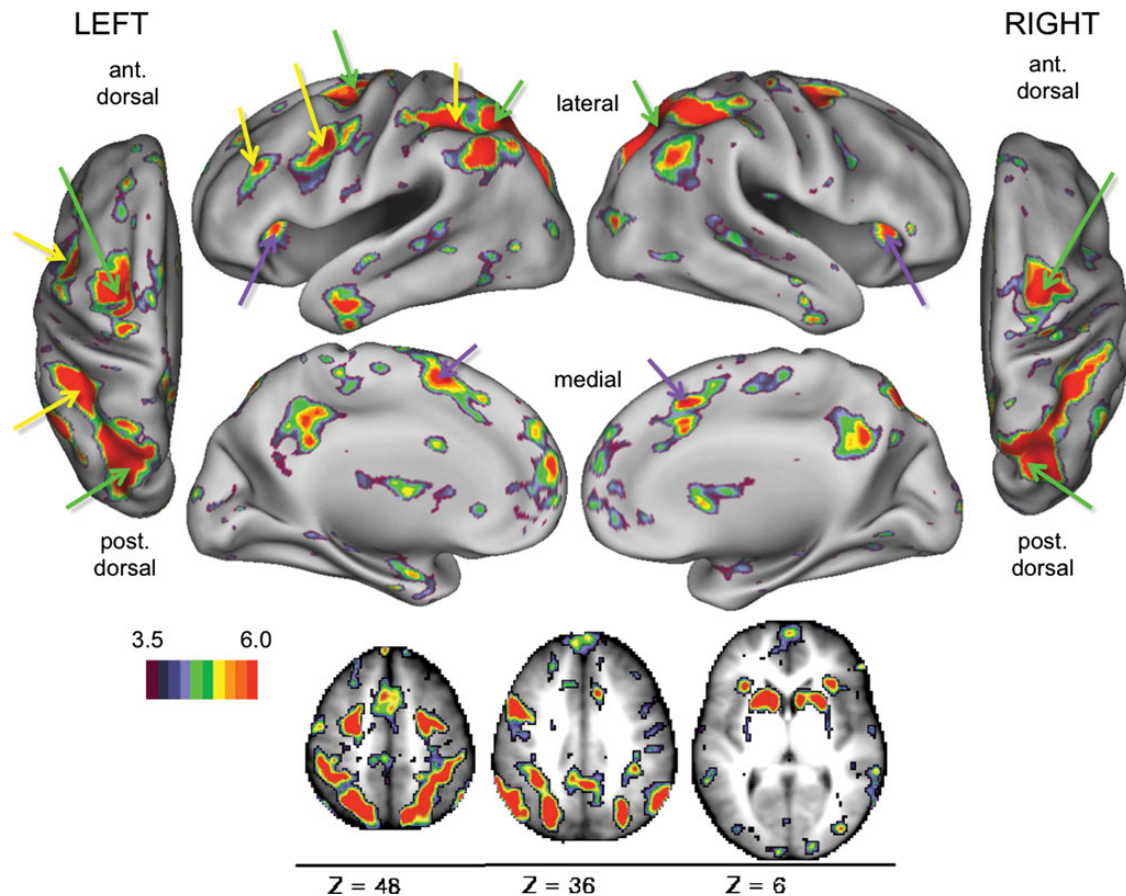
Figure 3. Statistical image of the voxelwise rmANOVA for the effect of task by timecourse. Color scale corresponds to a *z*-score range of 3.5–6.0. Functional data were displayed on an inflated cortical surface using Caret software (http://www.nitrc.org/projects/caret/ Last accessed 11/9/13; Van Essen et al. 2001); 3 transverse slices in functional acquisition space are also shown. Colored arrows highlight attentional control-related regions belonging to the Cingulo-opercular system (purple), Dorsal attention system (green) and FP system (yellow).

system (green arrows), including bilateral Frontal eye field (FEF). Reliable activations were also obtained in regions typically reported in studies of single word reading, including left Angular gyrus (AG) and in a region in left fusiform gyrus near the putative Visual word form area (pVWFA). Activations in bilateral Inferior frontal gyrus *pars opercularis* (IFG*po*) wrap under the lip of the gyrus inferiorly and are difficult to visualize in this image.

Task × Lexicality × Timecourse

Many brain regions, spanning both hemispheres, showed significant BOLD activity changes across time that depended both on lexicality and task (see Fig. 4). The task × lexicality × timecourse image appears similar to the task × timecourse image (compare Figs 3 and 4). Prominent activations are seen in regions belonging to the 3 attentional control systems highlighted in the task × timecourse image in Figure 3: bilateral CO (purple arrows); left-hemisphere FP (yellow arrows); and bilateral Dorsal attention (green arrows).

Region Selection: Peak-Finding, Timecourse Extraction, Pruning for non-Biologic Timecourses and Removal of Presumptive Duplicates

The automated peak-finding algorithm identified 72 regions of interest (ROIs) in the lexicality × task × timecourse image, and 144 regions in the task × timecourse image, for a total of 216 possible ROIs. After removal of overlaps as well as regions

with non-biologic timecourses (procedure described in Supplementary Material 4), 156 regions remained in the final pool (see Supplementary Table 1 for complete region set).

Hierarchical Clustering Revealed 2 Dissociable Attentional Control-Related Clusters

UPGMA hierarchical clustering of the final set of 156 regions produced a dendrogram with relatively high fidelity to the underlying structure (cophenetic $R = 0.82$; see Fig. 5). At a similarity threshold of $(1 − r) = 0.15$, 2 candidate clusters of particular interest were identified, each composed primarily of regions falling within the boundaries of networks related to attentional control, as well as putative reading-related regions (see Fig. 6).

The cluster shown in purple in Figure 6 includes several regions of the CO control system bilaterally, as well as a handful of mostly (but not entirely) right-lateralized dorsal attention system regions (referred to as CO/DA+; see Supplementary Fig. 6 for the image including the network borders). The cluster projected in yellow in Figure 6 is entirely left-lateralized, and includes almost exclusively regions that fall into the FP control network (abbreviated FP; again, see Supplementary Fig. 6).

Guided by the predictions outlined in Table 2, we now address whether each of the following meaningfully distinguishes the 2 candidate attentional control clusters, CO/DA+ and
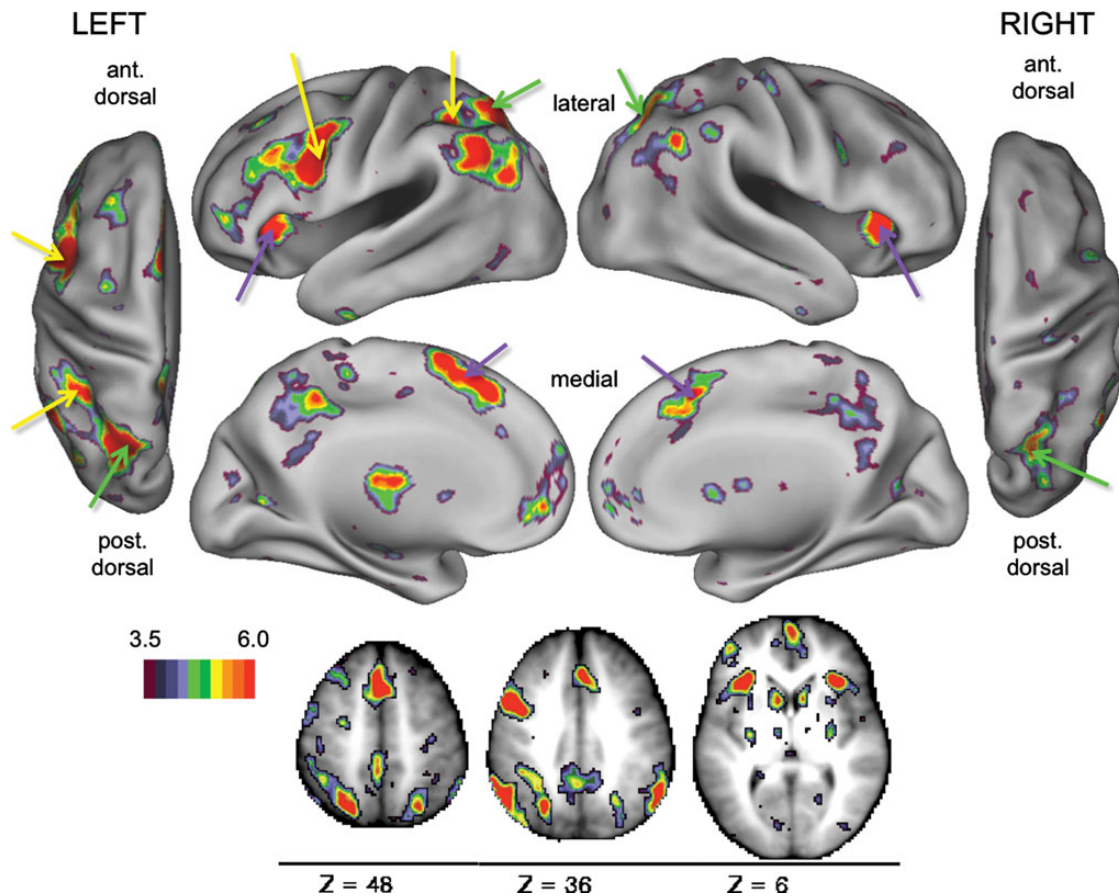
Figure 4. Statistical image of the voxelwise rmANOVA for the effect of task by lexicality by timecourse. Color scale corresponds to a *z*-score range of 3.5–6.0. Functional data were displayed on an inflated cortical surface using Caret software (Van Essen et al. 2001); 3 transverse slices in functional acquisition space are also shown. As in Figure 3, colored arrows highlight attentional control-related regions belonging to the Cingulo-opercular system (purple), Dorsal attention system (green) and FP system (yellow).
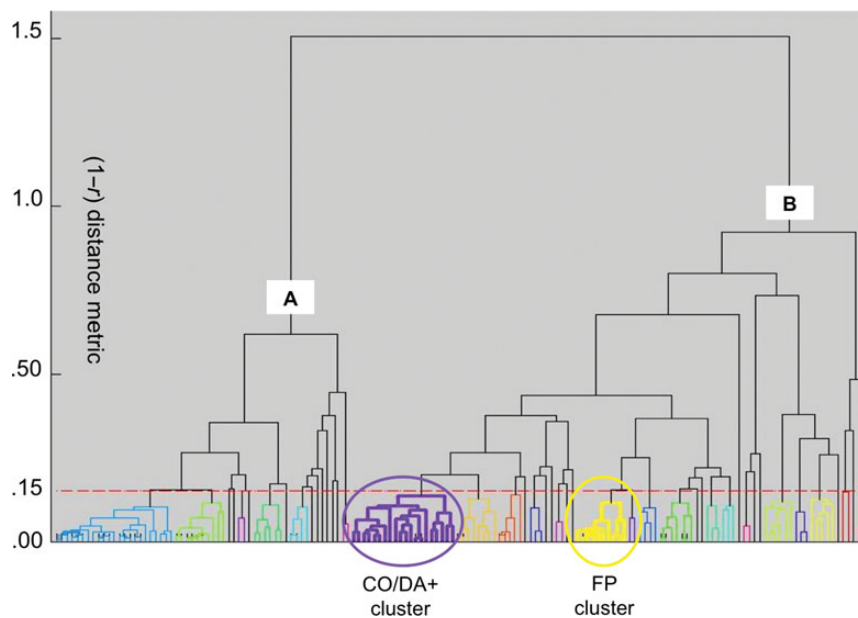
Figure 5. Dendrogram resulting from the hierarchical clustering of 156 regions computed using a UPGMA method in Matlab (cophenetic $R = 0.82$). Highlighted are the 2 clusters identified as being comprised chiefly of control-related regions: a CO/Dorsal attention + (CO/DA+) cluster (purple), including 20 regions, and a FP cluster (yellow), including 10 regions. Red horizontal line indicates clustering threshold of $(1 - r) = 0.15$. *A* and *B* mark the left and right sides of the dendrogram (see Supplemental Table 1).

LEFT
ant. dorsal
lateral
post. dorsal

RIGHT
ant. dorsal
medial
post. dorsal

■ Cingulo-opercular / Dorsal attention + (CO/DA+) cluster

■ Left Frontal-parietal (FP) cluster
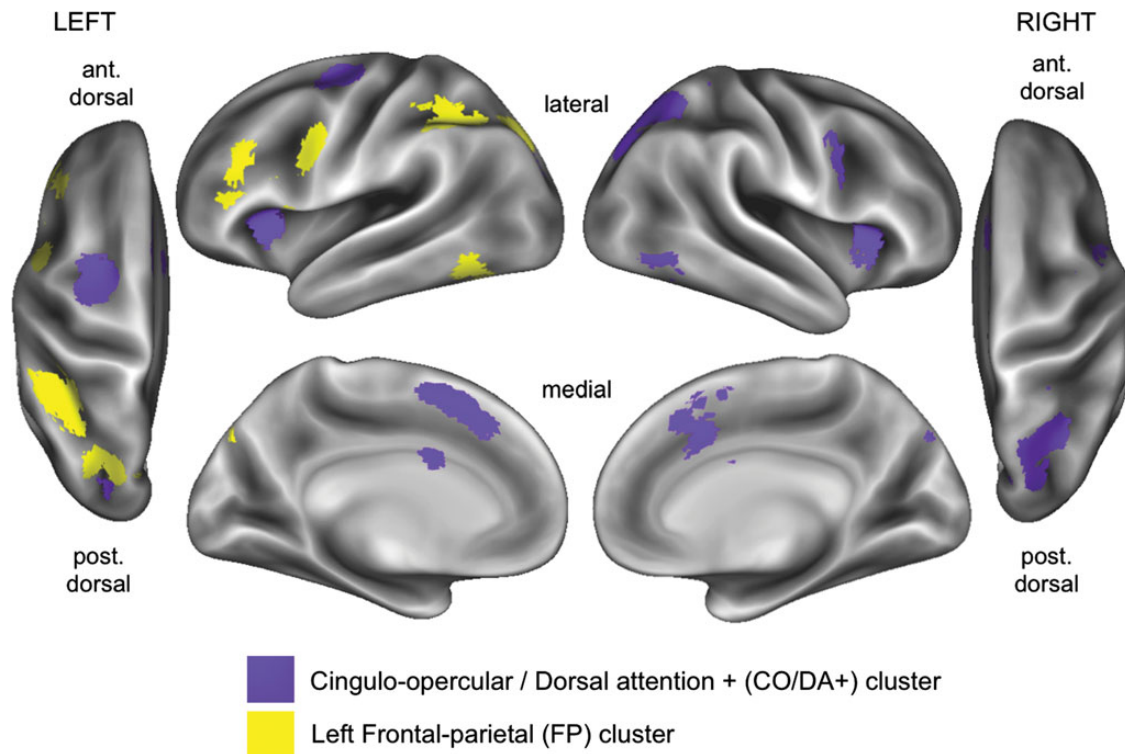
Figure 6. Surface projection of the CO/DA+ cluster, shown in purple (*n* = 20 regions), and the FP cluster, shown in yellow (*n* = 10 regions), defined from the clustering depicted in Figure 5. Clusters projected using Caret software (Van Essen et al. 2001).

FP, from one another, and/or supports a role for the cluster(s) in pathway control and response checking: 1) general HRF features, 2) statistical interactions of variables of interest, and 3) nearest neighbors on the dendrogram.

Magnitude, Timing and HRF Shape Differences Between the Clusters

General featural differences in the BOLD fMRI responses to the 2 tasks may be useful for distinguishing regions likely to act in pathway control from regions likely to be important for response checking. Such featural differences are shown in Figure 7, which depicts separate timecourses for each cluster, for each task, for each of the 3 main stimulus types (pseudowords, regular words, and irregular words).

First, the overall magnitude of % BOLD signal change across the entire timecourse tended to be lower in the CO/DA+ regions than the FP regions, supporting a role for the CO/DA+ regions in reading out a bias signal (relatively rapid), and a role for the FP regions in accumulating information over time in order to make a decision (relatively protracted). Relatedly, in terms of time-to-peak, the CO/DA+ regions tended to peak at timepoint 2 or 3 for both tasks, whereas the FP regions almost uniformly peaked later, at timepoint 4. The shapes of the timecourses also differed notably between the 2 clusters. Specifically, not only did the CO/DA+ regions peak earlier than the FP regions, but the BOLD responses of the CO/DA+ regions also returned to baseline more rapidly than did the FP regions, that is, the CO/DA+ regions showed relatively narrow HRFs, while the FP regions showed relatively wide, extended HRFs.

Statistical Tests of Differences Between the Clusters

Omnibus rmANOVAs and planned post hoc rmANOVAs were computed in order to determine which of various task- and

stimulus- combinations distinguished the 2 cluster sets from one another quantitatively (please refer again to Table 2). For the analyses, each region from the CO/DA+ and FP clusters was treated as a "subject," and cluster assignment was treated as the grouping variable. Note that the timecourses depict all 8 timepoints in the timecourse, even though only the first 6 frames were used to compute the clustering (see explanation above). The post hoc analyses likewise used all 8 timepoints of the timecourses.

Sensitivity to Lexicality

First, we consider the effect of lexicality, stratified by task, in the 2 attentional control clusters of interest. First, the omnibus ANOVA confirmed that cluster membership reliably modulated the interaction of lexicality × task × timecourse ($P = .004$, Greenhouse–Geisser corrected). Of interest is the difference in the patterns reflected by the 2 clusters, given the predictions outlined in Table 2, that is, the results of the post hocs. Figure 8 depicts the timecourses averaged over each set of regions separately for words and pseudowords for each task. Both sets of regions showed a significant difference between the BOLD response to words and the BOLD response to pseudowords, for the read and regularize tasks considered separately.

In particular, the CO/DA+ cluster showed lexicality effects for each task that were of roughly equal magnitude for read and regularize, but in opposite directions in the 2 tasks (pseudowords > words for read task; words > pseudowords for regularize task; "opposite and more equal"). The FP cluster showed lexicality effects for the 2 tasks that were, like the CO/DA+ cluster, in opposite directions for the 2 tasks, but, in contrast to the CO/DA+ cluster, of appreciably different magnitudes in the 2 tasks ("opposite and unequal"). The gray ovals
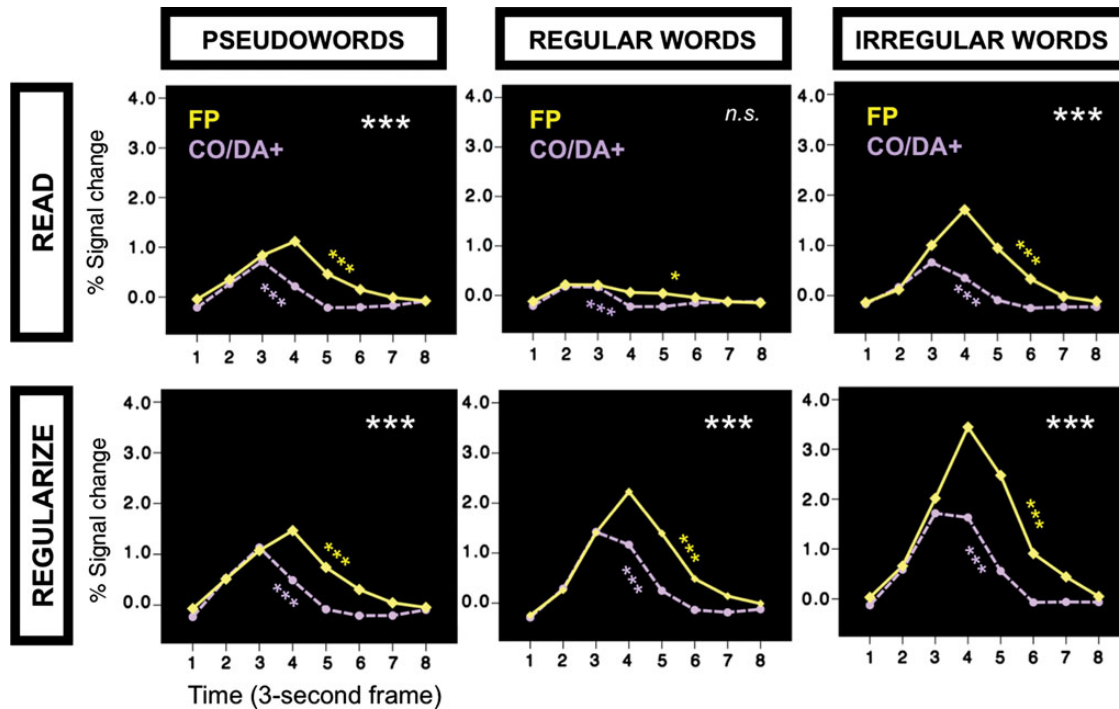
Figure 7. Average BOLD timecourses for each of the 2 attentional control clusters, for each task, separately for pseudowords, regular words, and irregular words. Each MR frame was 3 s. Asterisks indicate a significant interaction (rmANOVA: $*P \leq 0.05$; $***P \leq 0.001$). For all 6 conditions except for regular words in the read task, the FP cluster (yellow) showed a significantly larger % BOLD signal change, across time, than the CO/DA+ cluster (light purple), as indicated by the white asterisks. Each main effect of timecourse was significantly different from baseline, as indicated by the yellow and light purple asterisks.

spanning each column highlight the distinct patterns observed in the 2 clusters.

Additionally, the asterisks spanning each row highlight that there was a statistically different effect of lexicality in the 2 clusters for each task, considered separately. For the read task, the word > pseudoword difference was larger in the CO/DA+ than the FP regions; for the regularize task, the pseudoword > word effect was larger in the FP than the CO/DA+ regions. It is important to highlight the former observation (the statistically larger lexicality effect for the read task in the CO/DA+ cluster as compared with the FP cluster), given the larger overall magnitudes of the BOLD signals in the FP cluster, and the potential concern that interaction effects will be biased towards being larger in the regions with the larger overall signals.

The timecourses of the individual regions of both clusters generally recapitulated the patterns of task and lexicality described at the group level (i.e., the group average timecourses were not driven by outliers within each cluster).

Sensitivity to Regularity

Next, and again referring to the predictions outlined in Table 2, the effect of regularity by task was considered. As above with regard to lexicality, the omnibus rmANOVA confirmed that cluster membership reliably modulated the 3-way interaction of regularity × task × timecourse ($P \leq .001$). Figure 9 depicts the cluster-average BOLD response to irregular than to regular words, for both read and regularize. As suggested quite clearly by Figure 9, the 4-way interaction was driven by a larger difference in the BOLD response to irregular versus regular words for the FP regions than the CO/DA+ regions, for both tasks (both $P < 0.001$).

As with the effects of lexicality and task, the timecourses of the individual regions of both clusters generally recapitulated the patterns of regularity and task described at the group level (i.e., the group average timecourses were not driven by outliers within each cluster).

Cluster "neighbors" for CO/DA+ versus FP

Although the analyses described here have focused on the 2 attentional control clusters of interest, many other brain regions were identified in the whole-brain ANOVAs and are therefore represented in the dendrogram. Because proximity in cluster space suggests similarity in terms of functional response, it is useful to know which regions sit most proximally to the clusters of interest in the dendrogram (see Table 2). CO/DA+ regions were nearest on the dendrogram to bilateral middle occipital (visual) regions and additional Dorsal attention regions, including medial superior frontal regions. FP regions were, instead, closest to regions including parts of bilateral inferior frontal gyrus, *pars opercularis* (IFGpo), bilateral cerebellum and bilateral mouth somatomotor, as well as right superior temporal sulcus. See Supplementary Figs. 7 and 8 for more detailed renderings of the clustering relationships within each region set, as well as the anatomical locations of the closest dendrogram neighbors of each.

Supplemental Imaging Analyses

Finally, several analyses were conducted to ensure that the observed imaging effects were not driven by potential confounds. See Supplementary Materials 3a–c for information about RT regression, motion censoring, and an alternate preprocessing method.
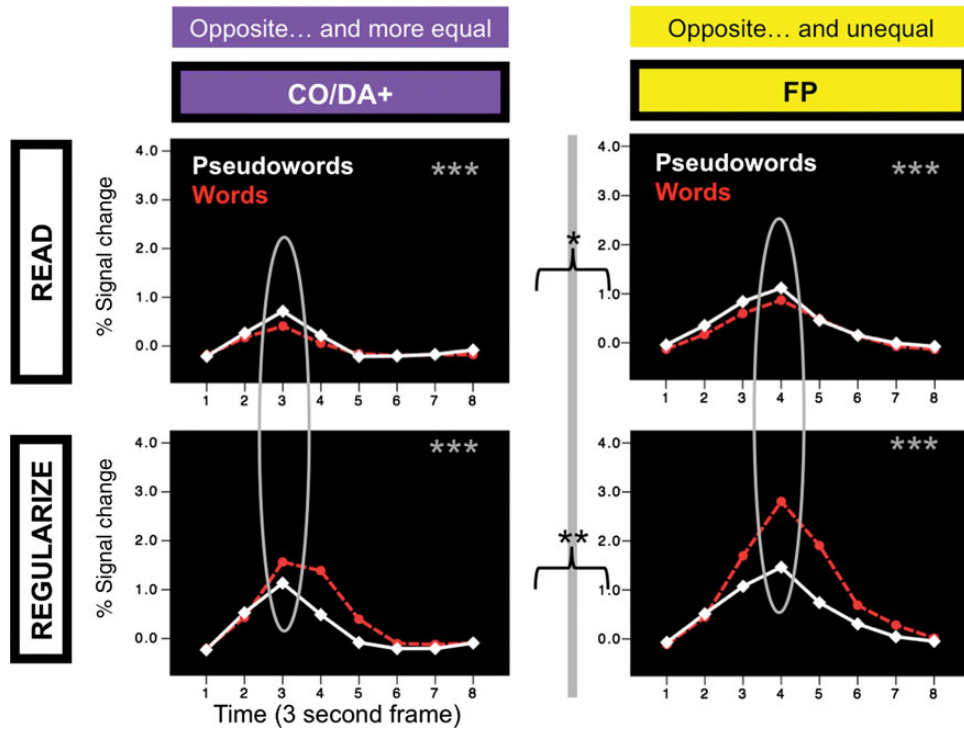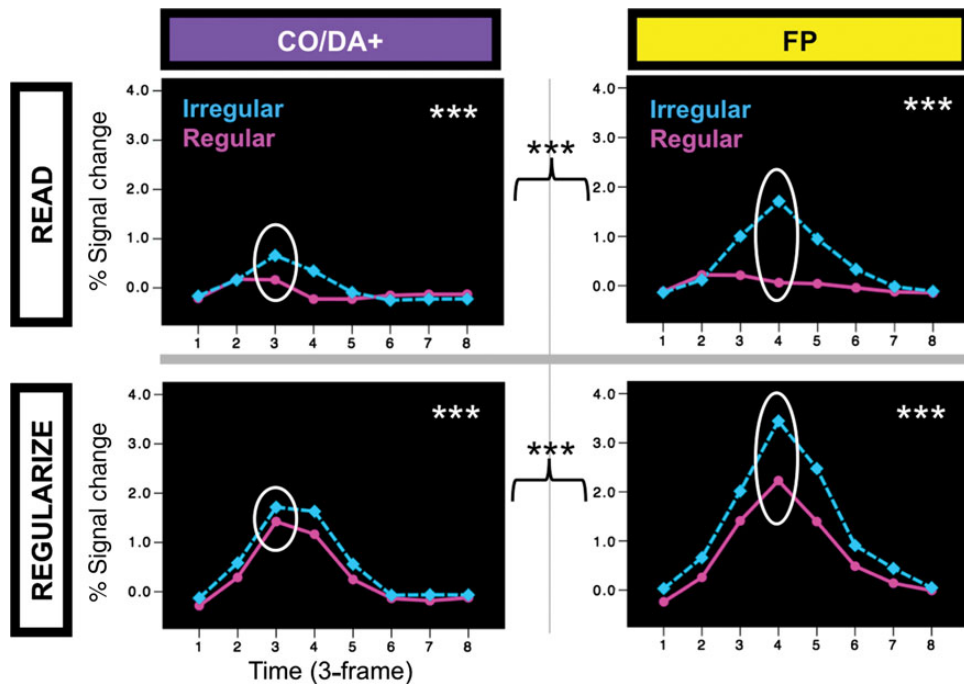
Figure 8. Average BOLD timecourses for each of the 2 attentional control clusters, for each of 4 combinations of lexicality and task. The top panel shows that the lexicality effect for the read task was significantly larger in the CO/DA+ regions than the FP regions (i.e., a significant interaction of lexicality × timecourse × cluster, for read). The bottom panel shows that the (reversed) lexicality effect for the regularize task was significantly larger in the FP regions than the CO/DA+ regions (i.e., a significant interaction of lexicality × timecourse × cluster, for regularize). The gray ovals highlight the pattern of lexicality effects observed in the 2 tasks in each cluster: opposite and "more equal" in the CO/DA+ regions, and opposite and unequal in the FP regions. Asterisks indicate significant interactions (rmANOVA: *$P < 0.05$; **$P \leq 0.005$, ***$P \leq 0.001$).

Figure 9. Average BOLD timecourses for each of the 2 attentional control clusters, for each of 4 combinations of regularity and task. For both tasks (i.e., top and bottom panels), the regularity effect was significantly larger in the FP regions than the CO/DA+ regions (i.e., a significant interaction of regularity × timecourse × cluster, for each task separately). The ovals highlight the larger peak regularity difference for each task. Asterisks indicate a significant interaction (rmANOVA: ***$P \leq 0.001$).

Discussion and Future Directions

As discussed in the Introduction, a previous behavioral study invoked *2 mechanisms* to explain reaction time (RT) differences between a read and a regularize task (Balota et al. 2000), suggesting that attention may interact with reading processing in more than one way. The regularize task, like many other paradigms used in cognitive neuroscience and psychology, represents a somewhat artificial construct, in that highly literate young adults do not typically focus on "sounding out" words that they already know how to read. However, even if the attentional control brought to bear on the regularize task in young adults is not exactly apropos to the kind of skilled reading that adults do on a regular basis, it is nonetheless a useful way to consider the interaction of reading processes and attentional control systems because 1) effortful sounding out of words is quite relevant to development, that is, these adults presumably used these mechanisms when they were learning to read and, relatedly, 2) it is parsimonious to assume that the way control systems interact with reading processes during the regularize task in adults, though the task is somewhat artificial, is simply one approach to revealing the underlying interaction between reading and attentional control that may be relevant generally for situations in which reading becomes effortful for adults (e.g., reading under conditions of distraction, when there are many new words, complex prose, etc.).

In the present report, both RT analyses (the Behavioral and fMRI cohorts) and imaging analyses (fMRI cohort) converge with the suggestion by Balota and colleagues of a 2-mechanism interaction of attentional control and reading (2000), further specifying the nature of that 2-mechanism interaction. A set of regions including members of the CO control system and Dorsal attention system showed response properties consistent with a role in reporting a processing bias signal, reflecting pathway control. A set of regions including members of a left-lateralized FP control system showed response properties consistent with a role in response checking. The implications of the behavioral results are briefly discussed first, followed by a more detailed consideration of the imaging findings, the novel observations.

First, a large and reliable interaction of task x lexicality was observed behaviorally, such that words, compared with pseudowords, were faster to be read but slower to be regularized. The 2-mechanism model depicted in Figure 1 suggests that attentional control interacts with reading processes at 2 loci that are relevant for word regularizing, which may explain why the task slowdown for words was so large. That is, the large RT cost associated with "wordness" may derive from 2 sources during the regularize task: difficulty biasing the phonological pathway, then the checking of the word's pronunciation before a response is articulated.

Additionally, correlation analyses treating frequency as a continuous variable revealed differences between the effect of frequency on regularize task performance for regular as compared with irregular words, As Balota and colleagues originally remarked regarding their observation of a significant 3-way interaction of task, frequency and regularity, the modulation of the task-induced WFE reversal by regularity provides compelling evidence for a mechanism other than pathway control to account fully for the results (Balota et al. 2000). Together, the behavioral results 1) nicely replicate the basic findings of Balota et al. (2000) and 2) solidly motivated the imaging investigation of the 2-mechanism model of attentional control and reading processing.

The imaging data corroborated the 2-mechanism model quite nicely. Two putative sets of attentional control regions were identified, from among all the regions showing significant effects of (task × timecourse) or (lexicality × task × timecourse), as likely candidates for the 2-mechanism model proposed in Figure 1. Specifically, the 2 region sets identified showed distinguishable patterns of BOLD activity with regard to task, lexicality and–though it was not used to define the regions originally–regularity. The anatomical locations of the 2 clusters' respective neighbors in the dendrogram further supported the BOLD evidence for separable roles (see Supplementary Figs. 5 and 6). One cluster included 20 regions, mainly from bilateral CO network and largely right-hemisphere Dorsal attention system (CO/DA+). The CO/DA+ cluster showed BOLD signals consistent with a role in biasing processing along one route, depending on task demands (pathway control). The second cluster included 10 exclusively left-lateralized regions, almost all of which form part of the FP control network. The FP cluster showed BOLD signals consistent with a role in response verification after route processing has completed (response checking), particularly during a more difficult reading task variant.

Several observations, based on the predictions in Table 2 and summarized in Figure 10, confirmed functionally separable roles for the CO/DA+ and FP clusters and mapped those roles on the 2-mechanism model. We next discuss those key observations, beginning with the CO/DA+ cluster.

CO/DA+ Cluster Response Properties

CO/DA+ regions showed lexicality effects for the 2 tasks that were roughly "opposite and more equal," with the trial-by-trial BOLD magnitudes possibly reflecting the pathway control signal relevant to a particular trial. Specifically, the CO/DA+ signals may reflect the extent to which the processing pathway most required for a task block (i.e., lexical or phonological) was successfully biased for a particular item (i.e., word or pseudoword). In this way, the signals observed in the CO/DA+ are consistent with a neural read-out of the attentional mechanism postulated by the pathway control hypothesis (as in Baluch and Derek 1991; Monsell et al. 1992; Rastle and Coltheart 1999; Zevin and Balota 2000).

The comparable magnitudes (and opposite directions) of the lexicality effects in the 2 tasks CO/DA+ regions were predicted by the assumption that for each task, one of the 2 routes is likely to be more heavily weighted. The regularize task clearly requires selective attention to the phonological pathway output. Less obvious is that the read task, even for mixed lists (here, ~40% pseudowords), probably involves a default biasing of the lexical pathway, at least in skilled adults. In the CO/DA+ regions, the positive lexicality effect for the read task was not only equal (and opposite) to the lexicality effect for the regularize task, but it (the positive lexicality effect in read) was *larger* than the comparable effect in the FP regions. This latter observation is consistent with the intuitive notion that for skilled adults performing normal reading, neither words nor pseudowords should require significant response checking (hence the popular notion of automaticity in reading, referenced in the Introduction).
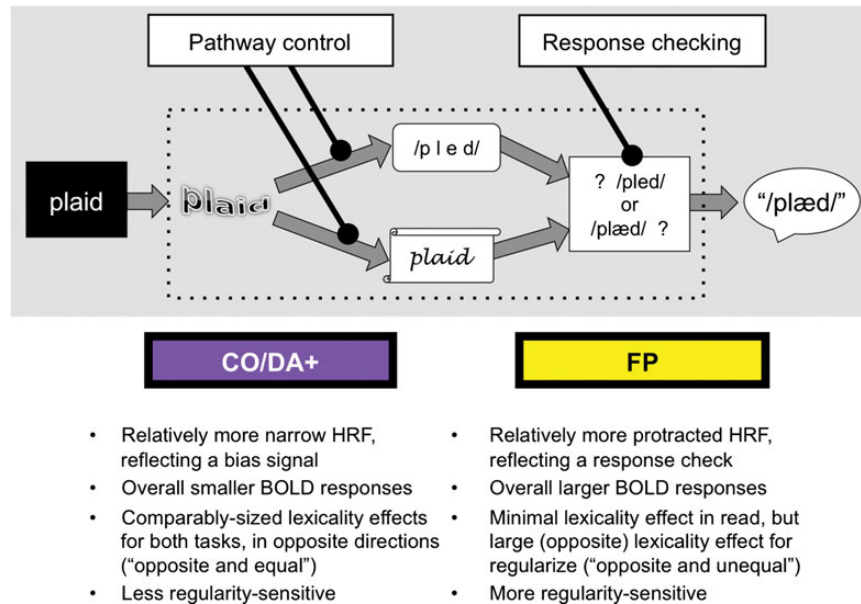
Figure 10. Summary schematic, based on Figure 1, depicting the 2 proposed mechanisms of interaction between attention and reading, along with descriptions of the region sets whose BOLD activity maps onto the distinction. A cluster of CO/Dorsal attention regions (CO/DA+) shows activity consistent with a role in reflecting pathway control, while a cluster of FP regions shows activity consistent with a role in response checking. Compare the response properties to the predictions outlined in Table 2.

Pathway control may be less disposable than response checking; no matter what the task variant, some signal is likely required to set the input–output parameters for task completion (Meiran 1996). Regions in bilateral aI/fO and dACC have been hypothesized to form the "core" of the task-set system (Dosenbach et al. 2006), although their precise functional ascription remains elusive (Posner and Petersen 1990; Dehaene et al. 1994; Bush et al. 2000; MacDonald et al. 2000; Botvinick et al. 2004; Brown and Braver 2005). Because the most consistent attentional control-related characterization of the core CO regions pertains to their involvement in sustained, task set-maintenance (and this event-related study design did not measure the task-related sustained signal), the exact specification of the role of the *trial-by-trial* BOLD signals observed here entails some amount of speculation. Nonetheless, the importance of the core CO regions, bilateral aI/fO and dACC, in shaping task performance is underscored by the observation that they tend to be among the most commonly activated regions across all kinds of neuroimaging studies (Nelson et al. 2010). It is also interesting that neuroimaging studies of the Stroop effect have noted strong and reliable activations in the dACC in relation to word–color interference (e.g., Pardo et al. 1990; Bench et al. 1993; Carter et al. 1995; Peterson et al. 1999; see also Bush et al. 1998 for a related, though not identical, phenomenon).

Signals reporting pathway control ought not to reflect appreciably the effect of word regularity, since both regular and irregular words are thought to generate activations along both pathways obligatorily (Coltheart et al. 2001). Indeed, CO/DA+ regions showed smaller effects of regularity than FP regions, considering both the read task and the regularize task. Note, however, that the CO/DA+ regions *did* show some sensitivity to regularity; in each task separately, irregular words produced significantly larger activations than regular words. Given that regions in the CO network simultaneously carry several types of processing signals (Neta et al. unpublished data), perhaps the relatively small effects of regularity observed

in the CO/DA+ regions reflect an orthogonal response property, such as time-on-task. The important point is that the effects of regularity are much more pronounced in the FP regions than the CO/DA+ regions.

In addition to CO regions, the CO/DA+ cluster includes several regions of the Dorsal attention system, a set of brain regions implicated in the allocation of top-down attentional control to specific portions of visual space (e.g., Corbetta and Shulman 2002). Resting-state functional connectivity (rs-fcMRI) work from our own laboratory has specifically suggested that Dorsal attention system regions are more closely functionally coupled to a region in left ventral occipital temporal cortex than are classic reading processing regions (Vogel et al. 2012), underscoring the relatedness of the type of processing performed by Dorsal attention system regions and the type of processing required for orthographic analysis. Our finding of a close functional relationship between CO regions and Dorsal attention regions as part of a single cluster is consistent with other work suggesting that the Dorsal attention system may flexibly modulate its coupling with other networks, depending on task demands (Spreng et al. 2010). Possibly the regions in the CO/DA+ cluster work together to read out the pathway control signals during the read/regularize tasks through a combination of each network's unique processing capabilities. It would be worthwhile to investigate whether for *other* reading task variants—perhaps a task in which serial, left-to-right attention to phonological decoding were not a critical component, as it is in regularize—would result in the reporting of pathway control signals by CO regions working less closely with or independently from Dorsal attention system regions. It would likewise be of interest to ask whether the CO and Dorsal attention system regions shown here to be jointly engaged in pathway control in highly skilled readers are similarly functionally coupled in dyslexic readers to achieve pathway control, given the data mentioned earlier suggesting spatial attention deficits as contributory to the pathology of impaired reading.

FP Cluster Response Properties

Consistent with a role in response checking, FP regions showed unequal regularity effects in the 2 tasks—in both cases irregular > regular words—with the effect being larger in the regularize as compared with the read task. The larger impact of regularity in the regularize task may reflect the discrepancy between the relative ease of response checking for normal reading (even for irregular words, as previously discussed) versus the increased need for response checking for the regularize task. Indeed, regions in dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex (PPC)—possibly overlapping with some of the members of the FP cluster in the present results—have been hypothesized in other contexts to mediate dynamic stimulus–response mappings (Huettel et al. 2005), perhaps encompassing the kind of computation required to generate /pInt/ (like "lint") in response to seeing "pint." Relatedly, individual FP regions in both inferior prefrontal cortex (IPC) and dorsolateral prefrontal cortex (dlPFC) have been implicated in various attention-related processes (Norman and Shallice 1986) including response retrieval (Wagner et al. 2001), response checking (Thompson-Schill et al. 1997), and the maintenance of stimulus-response mappings (MacDonald et al. 2000). FP regions in posterior parietal cortex (PPC) have been noted for their importance in facilitating decision-making in support of task demands (Platt and Glimcher 1999; Rushworth et al. 2001; Bunge et al. 2002). All of these functional ascriptions are consistent with a role for left FP regions in selecting and verifying the appropriate response from between the 2 route computations.

Parallel to the argument for unequal regularity effects, FP regions showed lexicality effects that were "opposite and unequal," in contrast to those observed in CO/DA+ regions ("opposite and equal"). In other words, the effect of lexicality was larger in FP regions for the task requiring the non-practiced response checking (regularize). Also, the negative lexicality effect in the FP regions for regularize was larger than the corresponding effect in the CO/DA+ regions.

The relatively larger negative lexicality effect (words > pseudowords) for regularize observed in the FP region set suggests that the FP regions may actually perform *more* of the processing associated with the regularize task, compared with the CO/DA+ regions. One additional hint of the primacy of the FP regions in directing attentional control during reading is that the effects in the FP cluster seemed slightly more robust to particular analysis choices, including RT regression, than are the effects in the CO/DA+ cluster (see Supplementary Materials 3a and c). Large and robust task-sensitive responses in the FP regions may reflect the extra-lexical, domain general nature of the processing in those regions, as characterized, for example, in one dlPFC region (Tal -50, +23, +27; MNI -53, +26, +30) in a previous study (Fiebach et al. 2007).

Magnitude, Timing and HRF Shape Differences Between the Clusters

Bolstering the hypothesis that the processing performed by the FP regions is particularly critical to the attentional control of reading is the set of general observations about the features of the clusters' BOLD responses. Specifically, the CO/DA+ and FP clusters differed in terms of overall BOLD magnitude, time-to-peak and width of the HRF. Compared with the CO/DA + cluster, the FP cluster (both in aggregate and in terms of the individual regions) showed responses that were slower to rise, higher to peak and slower to fall. Because of the sluggishness of the BOLD response and the timescale over which the data are collected, presumptive timing differences observed using standard event-related fMRI should be considered speculative. However, the relatively large, relatively wide HRFs of the FP regions are internally consistent with the argument articulated above, that the FP regions perform something of a *primary* role in the trial-by-trial attentional control required for the read and regularize tasks. It is also intriguing to consider the possibility that the wide HRFs seen in the FP regions reflect the linear summation of more than one BOLD response within a single trial (Boynton et al. 1996), that is, an even more complex role for the FP regions in coordinating the attentional control of reading than that which is suggested by the model in Figure 10.

A final general observation about the 2 clusters is that the FP cluster includes only regions in the left hemisphere, whereas the CO/DA+ cluster includes regions that span the right hemisphere, left hemisphere and midline. We did not predict that the task-related attentional control signals would segregate into 2 clusters with such a dramatic difference in hemispheric lateralization, and it is unclear what the left-hemisphere exclusivity of the FP cluster means in the context of read and regularize. Of course, it has long been posited that language relies primarily on left hemisphere structures, but indeed this and most other imaging studies in the recent literature show that brain activity related to reading and language tasks is very much dependent on right-hemisphere regions as well (e.g., Jobard et al. 2003; Taylor et al. 2013; Price 2012). Future studies could interrogate possible task differences in the extent to which FP and other attentional control networks are engaged either bilaterally or relatively unilaterally, and what such differences may mean in terms of information processing.

Both sets' Neighbors in the Dendrogram

The profiles of the clustering neighbors of the CO/DA+ and FP region sets strengthened their respective proposed roles. The CO/DA+ regions showed neighborhood relationships consistent with a more intimate interaction with the earlier stages of visual word recognition, that is, a role in pathway control. For example, they appeared close to bilateral middle occipital (visual) regions and some additional Dorsal attention regions (medial and superior frontal) in the clustering dendrogram. The most proximal neighbors to the FP regions were left and right Inferior frontal gyrus *pars opercularis* IFG*po*. A region in left IFG*po* has been consistently implicated in preparing the articulatory response during reading (e.g., Jobard et al. 2003; Taylor et al. 2013). Regions in bilateral cerebellum as well as bilateral mouth somatomotor cortex were also relatively close to the FP regions, as were regions in bilateral superior temporal gyrus. This clustering similarity suggests a tighter functional link between FP regions (compared with the CO/DA+ cluster) and regions important for speech articulation (Price 2012), corroborating a role for the FP cluster in response checking in the proposed model.

Contextualizing These Results in the Literature

Despite very different analysis approaches, there is some convergence between the results of the present study and the findings of the only extant neuroimaging analysis of the regularize task of which we are aware (Gold et al. 2005). Briefly, Gold

and colleagues concluded that "reading"-related activity, in left frontal regions in particular, is modulated in important ways not only by the kind of processing required (e.g., sound-based vs. meaning-based vs. orthography-based) but by the extent to which that processing requires attentional control, a conclusion supported by the present results as well.

Some studies have employed paradigms requiring a conscious reallocation of attention more similar to the task comparison introduced by Balota et al. (2000) and replicated here. For example, some electrophysiological data suggest that different task instructions can modulate word identification as shown, for example, by an enhanced N200 response during an orthographic, as compared with semantic and phonological, task (Ruz and Nobre 2008b), and by distinguishable patterns of preparatory brain activity in anticipation of different task requirements (Ruz and Nobre 2008a). The greater spatial resolution of PET and fMRI have also rendered informative observations, but many of these analyses have focused on reading-related and primary sensory regions (e.g., Roskies et al. 2001; McDermott et al. 2003; Dietz et al. 2005; Yoncheva et al. 2010; Twomey et al. 2011; Perrone-Bertolotti et al. 2012). The tendency for previous investigations to emphasize effects of controlled attention *in* the processing regions, rather than focusing on the control signals themselves, may reflect the greater transparency of the predictions of the dual route and other models with regard to *processing* regions as compared with *attentional control* regions (for a recent meta-analysis, see Taylor et al. 2013).

The present results add to the body of literature on the attentional control of reading by focusing explicitly on the contributions of signals from previously described control-related regions, using targeted behavioral results to test neuroimaging hypotheses. Specifically, we examined whether and how task instructions requiring a novel stimulus-response mapping for an otherwise automatically generated output (i.e., the *conscious* reallocation of selective attention) modulates both behavior and brain activity. Our data suggest that skilled adult readers *can* strategically direct attention to one component of reading, phonological processing, but with much effort (in terms of slow RTs). Critically, both the behavioral and the imaging data are best accounted for by a model in which 2 distinct attentional control processes interact with reading processes, both to report the bias signal associated with pathway control (CO/DA+ regions) and to ensure that the correct response is selected (FP regions).

The observations of the current study could provide a framework for future investigations of dyslexia, since dyslexia is disproportionately comorbid with ADHD (Willcutt and Pennington 2000; Germano et al. 2010; Willcutt et al. 2010), and thus far, few studies have explicitly examined whether brain activity in attentional control-related regions may help explain the pathophysiology of this most prevalent learning disorder (but see Eden et al. 1996a; Eden et al. 1996b; Demb et al. 1998; Bosse et al. 2007; Vidyasagar and Pammer 2010; Peyrin et al. 2012; Koyama et al. 2013 for some related findings). Future studies could also include extending the analyses described here to a population of non-impaired, school-age, beginning readers, to investigate how reading skill modulates both task performance and attentional control region recruitment. For example, it is likely that children will show smaller RT task x lexicality interactions than adults, and possibly also smaller effects of regularity on the task-induced WFE change. It would also be interesting to investigate in children whether regions in the CO and Dorsal attention systems would show functional similarity to each other, and functional dissimilarity from left FP regions, as was observed here in adults. If a CO/DA+ versus FP or some other distinction were observed in children, one follow-up question would be whether evidence could be found for a differential timecourse of development for these 2 sub-systems and their point of interaction with reading processing regions.

Supplementary Material

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Notes

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