



## Possible roles for fronto-striatal circuits in reading disorder



Roeland Hancock<sup>a,\*</sup>, Fabio Richlan<sup>b</sup>, Fumiko Hoeft<sup>a,c,d</sup>

<sup>a</sup> Department of Psychiatry and Weill Institute for Neurosciences, University of California, San Francisco, Box 0984, San Francisco, CA 94143, United States

<sup>b</sup> Centre for Cognitive Neuroscience, University of Salzburg, Salzburg, Austria

<sup>c</sup> Haskins Laboratories, 300 George St #900, New Haven, CT 06511, United States

<sup>d</sup> Department of Neuropsychiatry, Keio University School of Medicine, 35 Shinanomachi Shinjuku, Tokyo, 160-8582 Japan

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### ABSTRACT

Several studies have reported hyperactivation in frontal and striatal regions in individuals with reading disorder (RD) during reading-related tasks. Hyperactivation in these regions is typically interpreted as a form of neural compensation related to articulatory processing. Fronto-striatal hyperactivation in RD could however, also arise from fundamental impairment in reading related processes, such as phonological processing and implicit sequence learning relevant to early language acquisition. We review current evidence for the compensation hypothesis in RD and apply large-scale reverse inference to investigate anatomical overlap between hyperactivation regions and neural systems for articulation, phonological processing, implicit sequence learning. We found anatomical convergence between hyperactivation regions and regions supporting articulation, consistent with the proposed compensatory role of these regions, and low convergence with phonological and implicit sequence learning regions. Although the application of large-scale reverse inference to decode function in a clinical population should be interpreted cautiously, our findings suggest future lines of research that may clarify the functional significance of hyperactivation in RD.

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\* Corresponding author at: 401 Parnassus Ave, San Francisco, CA 94143, United States.

E-mail address: [Roeland.Hancock@ucsf.edu](mailto:Roeland.Hancock@ucsf.edu) (R. Hancock).

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## 1. Introduction

Reading disorder (RD, also known as developmental dyslexia or reading disability) is a developmental disorder typically associated with phonological processing difficulty and impaired development of fluent reading (Shaywitz and Shaywitz, 2005). Quantitative meta-analyses of neuroimaging studies comparing RD and typical readers have identified decreased task-related blood oxygen level dependent (BOLD) signal in occipito-temporal and temporoparietal brain regions within RD (Linkersdörfer et al., 2012; Maisog et al., 2008; Richlan et al., 2009), consistent with the role of these regions in phonological (Vigneau et al., 2006) and orthographic processing (e.g., Cohen and Dehaene, 2004; Price and Devlin, 2011). Temporo-parietal reductions in grey matter volume in RD adults (Richlan et al., 2013) and in at-risk pre-readers (Black et al., 2012; Raschle et al., 2011) along with evidence that candidate RD alleles modulate cortical morphology and activation in left temporo-parietal (Meda et al., 2008; Pinel et al., 2012) and occipito-temporal regions (Cope et al., 2012; Meda et al., 2008) suggest that the primary neurodevelopmental origin of RD lies in posterior brain systems. While most studies thus far have focused primarily on dysfunction in temporo-parietal and occipito-temporal regions, meta-analyses also support increased activation in RD relative to controls in several fronto-striatal regions, including the bilateral striatum (including caudate and putamen) and globus pallidus, thalamus, left inferior frontal gyrus (IFG), left insula and left precentral gyrus (Maisog et al., 2008; Richlan et al., 2009, 2011). The fronto-striatal hyperactivation patterns seen in RD have often been interpreted as reflecting compensation engaged to reduce the impact of a primary phonological processing deficits arising from the temporo-parietal region (e.g., Richlan et al., 2009) although the cognitive and neurobiological mechanisms that could lead to compensation are poorly understood.

Regions of altered activation between RD and typical readers are frequently interpreted in terms of the hypothesized primary phonological or orthographic deficits that characterize RD, or as compensation for impairments in these processes. However, differences in activation are found in many regions that may support a broader array of cognitive functions, e.g., the inferior frontal gyrus (IFG), basal ganglia and thalamus and precentral gyrus. We apply a new method for interpreting RD activation differences, based on large-scale automated meta-analysis (Yarkoni et al., 2011; see §2), to evaluate support for these interpretations. In particular, we consider the evidence for interpreting hyperactivation as neural compensation, alongside alternative interpretations. Notably, we consider whether hyperactivation could be attributable to impaired phonological representations or reflect abnormal fronto-striatal function that is not exclusive to the language system.

### 1.1. Fronto-striatal hyperactivation as compensation

Findings of regional hyperactivation in clinical samples are frequently interpreted in terms of neural “compensation.” This term suffers from imprecise usage in the RD literature, but a positive relationship between task performance and brain activation within

regions showing greater activation in patients relative to typical individuals is a defining characteristic of neural compensation (Cabeza et al., 2002; Hillary, 2008). In other words, neural compensation occurs when there is additional recruitment of neural resources (presumably observed as an increase in BOLD signal) to support task performance. This additional activation can be seen either in regions normally associated with a task, or observed as activation in additional regions not typically associated with the task in normal individuals. In the case of RD, fronto-striatal hyperactivation could reflect an increased reliance on these systems during reading to compensate for impairments in posterior brain regions (e.g., Shaywitz et al., 2002; Richlan et al., 2009; Hoefft et al., 2007). This interpretation is consistent with views of fronto-striatal regions as components of the articulatory system (Paulesu et al., 1993) recruited during compensatory subvocalization during reading. If hyperactivation in RD can be explained as articulatory compensation, we expect relatively specific co-localization between articulatory and hyperactive brain regions. In addition, consistent with compensation, levels of activation in these regions should show a positive relationship with performance.

Few studies of RD have directly examined the relationship between performance and hyperactivation in fronto-striatal regions and those that have do not clearly support a compensatory interpretation. Bach et al. (2010) examined the relationship between activation in the bilateral IFG during letter substitution/lexical decision and offline measures of reading and phonological skill. Although a positive correlation between reading performance and left IFG/insula activation was found when combining both RD and typical children, left IFG activity was reduced in RD relative to typical controls, suggesting activation in the left IFG during the task was related to performance, but not compensation, for the RD group. However, activation in the right IFG was correlated with phonological ability in the RD group only, suggesting that additional recruitment of the right IFG might serve a compensatory function. Bach et al. also found hyperactivation in the RD group in the left pre/post central gyrus, a region more consistently found to be overactive in RD. On the other hand, Ingvar et al. (2002) found that decreased reading skill across Swedish RD and control adults was associated with increased activation in the right IFG/insula and globus pallidus during silent reading, which the authors interpret as an impairment in right-lateralized prosodic processing.

These two studies provide conflicting evidence for a compensatory role of right frontal language regions in RD, which may be due to differing demands of the in-scanner tasks. During lexical decision, activity in the right IFG could reflect a compensatory increase in the inhibition processes required during lexical selection processes supported by this region as in Bach et al. (2010). This may be distinct from the role of the right IFG during the more naturalistic reading task that does not require inhibitory processes employed by Ingvar et al. (2002).

Right IFG involvement in phonological processing also appears to have a differential developmental trajectory in RD and typically developing readers. Shaywitz et al. (2002) found cross-sectional age-related activation increases in the bilateral IFG and putamen/thalamus in RD, but not typical, children. Activation in these

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