Reading in the Developing Brain
From Preliteracy to Fluent Reading

Dissertation

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Abstract

Reading acquisition changes our world. Not surprisingly, our brain undergoes significant structural and functional changes throughout reading development that result in a unique reading signature in the brain. These large-scale networks of skilled-adult reading generally encompasses three principal streams. The dorsal stream is predominantly linked to indirect phonological reading, i.e., grapheme-phoneme conversion. In contrast, the ventral stream is primarily associated with fast and automatized whole-word recognition. Both streams converge in the frontal stream devoted to a plethora of linguistic operations, for example sophisticated semantic analysis, and various domain-general functions. While the streams are well-researched in adults, their developmental trajectories during reading acquisition are not conclusively examined until today. In the present dissertation, I thus aimed to shed light on the development of the reading net-work from different angles. The overall aim of my dissertation is to advance our understanding of (A) the functioning of the three principal reading streams in literate but not yet adult-like reading children, and (B) the neural prerequisites of future reading acquisition before formal literacy instruction starts.

In Liebig et al. (2017), we systematically tested prelexical, orthographic, phonological, and lexico-semantic processing in eight to 13-year-old children to approach the child-reading system. Our results suggest a processing advantage of the ventral and the frontal stream, linked to all central component processes of single word recognition. In contrast, the dorsal stream showed a focal response confined to prelexical and phonological processing. In sum, we observed largely overlapping neural signatures favoring interactive activation in the child-reading network to accomplish written word recognition.

In the two further studies of the present dissertation, we examined the neural prerequisites of reading in preliterate kindergarten children. Longitudinally following the same cohort of children, literacy was assessed after two years of structured instruction. In Liebig et al. (2021),

we showed that neural response-selectivity to faces, auditory, and spoken words in language and reading streams is sensitive to detect interindividual differences in rapid automatized naming, a critical cognitive-linguistic precursor of literacy. Moreover, the neural response to faces predicted future reading fluency. Most importantly, the neural underpinnings of the observed brain-behavior relationships were detected in the future principle reading streams. The findings thus strongly emphasize that interindividual differences in the reading network manifest before reading instruction.

In the third empirical study of the present dissertation (Liebig et al., 2020), we used a multifactorial approach and could generalize these interindividual differences to environmental-demographic factors, genotypes, and neurophysiology. In sum, the findings of the present dissertation suggest that interindividual differences in the neural systems for language and reading affect cognitive-linguistic precursors of reading and future literacy acquisition and might thus serve as early biological markers of reading acquisition.

Taken together, the key findings of my dissertation foster our knowledge about the neural underpinnings of the central component processes of reading in children. In future research, these could inform computational and neurocognitive models of reading acquisition.

The results of the kindergarten children emphasize that interindividual differences in the neural systems strongly involved in reading occur early, i.e., before the onset of reading acquisition and are thus a cause rather than consequence of successful or impeded reading acquisition. Thus, the results of my thesis strongly suggest a much-needed rethinking of reading intervention. Based on the new insights of the empirical studies of my dissertation and previous literature, I propose a revised neurodevelopmental account of reading acquisition.

Glossary

General remark. Left-hemispheric brain regions are described unless expressly stated (right, bilateral).

ABR	auditory brainstem response
ACC	anterior cingulate cortex
AG	angular gyrus
AROM	associative read-out model
BA	Broca's area
BOLD	blood-oxygen level dependent
EEG	electroencephalography
ERP	event related potential
FFA	fusiform face area
FuG	fusiform gyrus
fMRI	functional magnetic resonance imaging
FWE	family-wise error
IAM	interactive activation model
IFG	inferior frontal gyrus
IOG	inferior occipital gyrus
ITG	inferior temporal gyrus
IPL	inferior parietal lobe
MFG	middle frontal gyrus
MOG	middle occipital gyrus
MROM	multiple read-out model
MTG	middle temporal gyrus
MVPA	multivoxel pattern analysis
OT	occipito-temporal
PPC	posterior parietal cortex
RAN	rapid automatized naming
ROI	region of interest
RSA	representational similarity analysis
SMG	supramarginal gyrus
SOG	superior occipital gyrus
SPL	superior parietal lobe
STG	superior temporal gyrus
STS	superior temporal sulcus
TP	temporo-parietal
vOT	ventral occipito-temporal
VWFA	visual word form area

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APPENDIX

I Theoretical Part

1 Introduction to Literacy

Multiple parts of the brain need to be synchronized and orchestrated to perform the highly complex and demanding task we call reading. For skilled readers, this happens automatically – or are you aware that print is detected by the retina every time you pick up a book or article? However, when children learn to read, they are confronted with a highly complex and challenging task as they have to map a novel visual symbol system, i.e., letters and letter combinations, onto partially pre-existing spoken language representations (Ziegler et al., 2020). Consequently, the visual and spoken language system and the neural pathways that link them undergo significant structural and functional changes (Dehaene et al., 2015). The learning process comprises many stages over the course of several years (Frith, 1986) and eventually ends up in a unique signature in the brain (Rueckl et al., 2015). My dissertation's primary goal is to shed further light on the neurodevelopmental trajectory and the prerequisites of this reading signature.

Language and Reading

Language and reading are highly intertwined. When children start learning to read, the pre-existing neural network for spoken language established during early childhood needs to be reorganized and fine-tuned to become responsive to print and print-speech convergences (Dehaene et al., 2015). I will only briefly outline one of the most influential neurocognitive models and significant neural correlates of language comprehension before introducing the principal theme, i.e., reading and how it is acquired.

Language Comprehension

When the sound waves of spoken words reach our ears, our brain, tuned to speech sounds already in infants (see Chládková & Paillereau, 2020, for a recent review), automatically listens. First, the auditory stimulus reaches the cochlear. From there, the electrical signal is sent along the cochlea nerve to arrive at the auditory brainstem (cf., *BOX 1* for the role of the speech-evoked auditory brainstem response in language and reading). The auditory brainstem then propagates preprocessed neural impulses from the periphery to the thalamus and primary auditory cortex, which roughly corresponds to the Heschl's gyrus and the underlying planum temporale of the STG.

BOX 1| Spoken Language and the Auditory Brainstem

The principal nucleus of the auditory brainstem, the inferior colliculus, receives binaural information. It is tonotopically organized and involved in integrating spectral and temporal information. The neural response represents the incoming sound with great fidelity and high temporal and spectral precision (Chandrasekaran et al., 2014; Skoe & Kraus, 2010). Some of its neurons are tuned to auditory stimuli' sustained, phase-locked features, others to fast-changing transitions. The auditory brainstem propagates the preprocessed information to higher-level cortical areas. It is also an important hub where major ascending and descending pathways of the auditory cortex, the thalamus, and the collicular system converge (Skoe & Kraus, 2010). Consequently, neurons within the brainstem are constantly shaped by top-down control to optimize the transmission of (behaviorally) relevant data (Skoe et al., 2013; White-Schwoch & Kraus, 2013). Whether and how the auditory brainstem response is modulated by attention is still a matter of debate (Forte et al., 2017; Lehmann & Schönwiesner, 2014). A growing body of literature shows that the quality of the speech-evoked auditory brainstem response is essential for language and literacy. More specifically, neural stability and precision are linked to phonological abilities (Bonacina et al., 2019; Lam et al., 2017; White-Schwoch & Kraus, 2013) and language (Tecoulesco et al., 2020). Similarly, children with poor reading skills or developmental dyslexia show unstable and indistinctive brainstem responses to speech sounds (Chandrasekaran et al., 2009; Hornickel et al., 2011; Hornickel & Kraus, 2013).

According to the influential boxological dual-route model of speech processing (e.g., Hickok & Poeppel, 2007, 2016; Poeppel et al., 2012), language processing is assumed to split into two directions. These routes are linked to the ventral and dorsal stream of the TP language system on the brain level. The ventral stream is thought to directly map the speech signal onto lexical and semantic representations, while the dorsal stream maps phonological information onto articulatory representations. The bilaterally organized ventral stream progresses signals for language comprehension from posterior parts of the ITG and MTG to its anterior counterparts. In the dorsal stream, auditory speech signals are processed in the posterior parietal and temporal lobes and articulatory networks of the frontal lobe. The model was supported by several neuroimaging studies directly testing the dual-stream approach (e.g., Fridriksson et al., 2016; see Hickok & Poeppel, 2016, for a summary). However, the assumed functional dichotomization of language processing needs at least partly to be attributed to the experimental manipulation aiming to isolate the respective subprocesses (e.g., Cloutman, 2013; Rauschecker, 2018). In natural language processing, both streams most certainly work hand in hand to achieve highly efficient online processing of speech signals. In general, one reason for the success of the dual-stream model might be that it is also applicable to sensory-motor processing and (of higher interest for my dissertation) reading. It might thus even be a domain-general principle of how the brain processes sensory information (Hickok & Poeppel, 2016). Not surprisingly, dual-route approaches will accompany us throughout the present thesis.

Based on neuroimaging studies, there is converging evidence that, in its essence, three key regions underlie language comprehension in adults, i.e., the STG, MTG, and IFG (Binder et al., 2009; Price, 2012; Rodd et al., 2015; Walenski et al., 2019). Semantic retrieval and binding are additionally associated with a widely distributed network encompassing the SMG and AG of the parietal lobe (Binder et al., 2009; Kaiser et al., 2021; Price, 2012). The IFG is a highly integrative hub, associated with consolidating multiple kinds of linguistic information and non-linguistic functions (Friedman & Robbins, 2021; Menon & D'Esposito, 2021; Rae et al., 2015). Among them are affective-semantic retrieval and cohesion (Jacobs et al., 2015, 2016; Kuhlmann et al., 2016). Likewise, the IFG is strongly involved in syntactic parsing, detection of rule violation, and speech production (Friederici, 2011). Many of these linguistic mechanisms are already broadly acquired by very young infants (e.g., van der Kant et al., 2020) or kindergarten children (Sylvester et al., 2016, 2021a, 2021b), favoring an early maturation of the neural systems for language comprehension.

Development of Language Comprehension

Indeed, two independent reviews have suggested that activity in the left-lateralized critical regions linked to language comprehension named above is already broadly established by the age of three. Only within the subregions of the IFG there is a shift from semantic to syntactic processing that matures later during development in parallel to increasing sensitivity to syntactic information (Weiss-Croft & Baldeweg, 2015). Recently, however, this view was partially questioned (Enge et al., 2020). In their meta-analysis pooling across multiple studies, they report both similarities and differences in the child compared to the adult language system. Firstly, they found that the left-lateralization of speech processing is not yet fully established by the age of nine. Secondly, children compared to adults more consistently activated the bilateral STG most certainly due to a more substantial reliance on semantic and (low-level) syntactic information associated with the TP language system. In sum, the language system is not fully mature in children but rather refines and fine-tunes during development with increasing language competence, possibly until young adulthood (Skeide & Friederici, 2016; Wang, Yamasaki, et al., 2021).

Systems of Skilled Reading

While the evolution of language is already highly astonishing (Corballis, 2017), humans additionally developed a complex system to retain and preserve the spoken language, which is fast and transient by nature. Not surprisingly, language and reading share many component skills, which, as a consequence, has partly led to similar cognitive, computational, and neural models of language and reading. To understand how reading is acquired, we first need to focus on the basis, which is skilled reading. Thus, I will outline some influential computational models and the principal cortical networks of proficient adult reading.

Computational Models of Skilled Reading

Reading had fascinated researcher way before neuroimaging became a standard scientific method. A massive branch of research developed computational models to simulate reading (e.g., Coltheart, 2006; Coltheart et al., 1993, 2001; Perry et al., 2010). In dual-route models, reading (aloud) is achieved in a sequence of interacting stages using two major routes, a direct orthographic route and an indirect phonological route (Coltheart et al., 1993, 2001; Elliott et al., 2012; Grainger & Jacobs, 1994; Perry et al., 2010). As already outlined before, this potentially general principle of neural mechanism is also resembled in (neuro-)cognitive models of language (Hickok & Poeppel, 2016), reading (Grainger & Ziegler, 2011), and reading development (Grainger et al., 2012; Pugh et al., 2000; Ziegler et al., 2008). In contrast, IAMs (McClelland & Rumelhart, 1981; Rumelhart & McClelland, 1982) represent neuronal plausible features, connectivity, and interactivity patterns. Usually, an IAM consists of three layers simulating visual word recognition. Reading starts at the level of simple visual features, which are then combined to letters in the second layer. The third layer resembles the orthographic lexicon. All three levels are highly intertwined, given bottom-up and top-down connections that are either excitatory or inhibitory.

The MROM (Grainger & Jacobs, 1996) is a prominent example of an IAM for reading. Its subsequent version, the AROM (Hofmann et al., 2011), is augmented by a fourth associative layer accounting for semantic associations and spreading activation in the network. The AROM simulates the semantic network based on simple co-occurrences of words by considering all associations between items. With its architecture, the AROM is not only able to account for several psycholinguistic phenomena (e.g., Briesemeister et al., 2009) but makes precise, testable predictions about their neural correlates (Hofmann & Jacobs, 2014). It thus, serves the gold standard of a reciprocal relationship between neuroimaging and cognitive computational modeling. Precisely, it is demanded that neuroimaging data should constrain and refine cognitive computational models and vice versa (Price, 2018; Protopapas et al., 2016; Taylor et al., 2013). The three activation layers are thought to simulate reading processes in the ventral stream, while the association layer predicts additional activation in the IFG. However, one must keep in mind that research moves from universal models towards reader-specific, individual simulations (Hofmann et al., 2020). These bear the possibility to also account for interindividual differences in neural response timing and strength (Gluth & Rieskamp, 2017).

Neuroimaging Skilled Reading

The first crucial step of reading, i.e., letter identification, has been associated with the occipital cortex (Boros et al., 2016; Dehaene et al., 2015). After this low-level but highly specialized analysis, the processing of print most certainly ramifies into different streams. The lower ventral stream is devoted to direct orthography-based whole-word reading, and the upper dorsal stream is linked to indirect phonologically mediated reading. Both converge in the frontal stream. However, these three large-scale networks are tightly intertwined and connected to various further bilateral cortical and subcortical areas supporting different aspects of the complex cascade of steps needed to make meaning out of symbols (Price, 2012; Skeide et al., 2017). In skilled adult reading, the component processes that makeup written word recognition, i.e., prelexical, orthographic, phonological, and lexico-semantic processing, have been linked to dissociable neural networks (Froehlich et al., 2018; Welcome & Joanisse, 2012).

The ventral stream is preferential to real, familiar, and frequent words over false fonts (Dehaene et al., 2010; Glezer et al., 2009). A further prominent observation is higher activation for unfamiliar but pronounceable letter strings or exception words than regular words (Coltheart, 2006; Taylor et al., 2013). In sum, these findings highlight its role as the direct orthographic lexical route of reading.

In skilled, fluent readers, the posterior parts of the ventral stream, i.e., the vOT, are the host of fast and automatized whole-word processing of familiar words (Grainger & Ziegler, 2011). Interestingly, also pseudohomophones elicit enhanced activation in the ventral stream (Braun et al., 2009; Kronbichler et al., 2007). In particular, the so-called VWFA (cf., *BOX 2* for additional details) located in the FuG has been extensively researched in the last decades (Cohen & Dehaene, 2004; Dehaene & Cohen, 2011; McCandliss et al., 2003). Its fascination might partly be attributed to its highly reproducible location regardless of the underlying language and writing system (Rueckl et al., 2015). Within the vOT, a posterior-anterior gradient of increasing print-specificity and abstraction has been postulated (Taylor et al., 2019; Vinckier et al., 2007; Zhao et al., 2017). Whether the vOT is specifically devoted to the prelexical recognition of print, whether it is the host of the orthographic lexicon, or whether it has more heterogeneous response capacities beyond visual word processing, is still a matter of debate (Cohen & Dehaene, 2004; Dehaene & Cohen, 2011; Glezer et al., 2009; Kronbichler et al., 2007; Price & Devlin, 2003, 2011). Recently, the latter idea was emphasized by the structural and functional connectivity of the VWFA with language and attentional networks (Chen et al., 2019). In any case, the posterior ventral stream is an efficient system for rapid recognition of visual word forms in skilled adult reading.

BOX 2| Neural Plasticity in the vOT

The vOT is systematically organized and encompasses selective subregions specifically tuned to discernable behaviorally relevant object categories. For example, it hosts the FFA fine-tuned to face recognition and the VWFA devoted to print (Dehaene & Cohen, 2011; McCandliss et al., 2003). The functional division seen in adults is already broadly established in infants. However, the adult-like category specificity is not yet mature and undergoes substantial changes during development (Deen et al., 2017). In general, neurons of the vOT have high plasticity, which manifests in the fine-tuning of neurons to behaviorally relevant stimuli even in adulthood. This functional and structural plasticity is especially true for face processing (Gomez et al., 2017). While the activation for some visual objects, such as houses, appears more stable along with childhood, it seems that the response to faces increases with age until late adolescence (Golarai et al., 2015). Response-selectivity to faces is of particular interest here due to its tight connection to reading and reading acquisition (Dehaene & Cohen, 2007; Dehaene-Lambertz et al., 2018; Monzalvo et al., 2012; Nordt et al., 2021). It has been hypothesized that the development of the VWFA might have its roots in the pre-existing spatial organization and its pre-existing connections to language areas (Saygin et al., 2016). Moreover, the sensitivity to line junctions (Szwed et al., 2009) might facilitate reading acquisition.

Also, the response properties of the anterior parts of the ventral stream might be more heterogeneous than previously thought, depending on the specific task and stimulus material used (Braun et al., 2019; Price & Devlin, 2003, 2011; Taylor et al., 2019; Zhao et al., 2017). More specifically, the MTG is assumed to be additionally involved in (whole-word) phonology and semantic processing during reading (Braun, Hutzler, et al., 2015; Taylor et al., 2019; Zhao et al., 2017).

In contrast, the dorsal stream tends to be used for low frequency and pseudowords in skilled adult reading (Coltheart, 2006; Taylor et al., 2013). It primarily relies on the TP language network and has classically been associated with indirect reading, i.e., grapheme-phoneme mapping (Boros et al., 2016; Braun, Hutzler, et al., 2015). Recently, the STG (Richlan, 2019) was identified as an essential convergence zone for letter-speech-sound integration. The PPC (subsuming the SMG and AG), being highly heterogeneous in structure, function, and connectivity (Scolari et al., 2015), might additionally be involved in phonological processing, semantic retrieval, and (abstract) concept coding (Binder et al., 2009; Kaiser et al., 2021).

The two posterior streams project onto the frontal stream, comprising the IFG, is implicated in the higher-level binding and integration of information (Binder et al., 2009; Kuhlmann et al., 2016; Walenski et al., 2019). As already briefly described (cf., *Language Comprehension)*, the IFG is associated with a plethora of cognitive functions, including motor control, working memory, decision-making (Friedman & Robbins, 2021; Menon & D'Esposito, 2021; Rae et al., 2015), empathy, and emotion (Aryani et al., 2018; Jacobs, 2015b; Kuhlmann et al., 2016). Reading-induced activation in the IFG is linked to covert articulation, phonological recoding and memory, syntactic parsing, semantic retrieval, and binding (Price, 2012).

Recently, research heads towards a more unified and interactive activation view of visual word recognition. Meaning that reading is instead based on a highly distributed pattern of component processes linked to different parts of the principal reading streams, right-hemispheric homologs, and subcortical structures (Braun et al., 2019; Huth et al., 2016; Price & Devlin, 2011).

Reading Acquisition

Early language development lays the foundation for future reading acquisition. This has been impressively shown by behavioral and neuroimaging studies able to draw a line between language processing in newborns, infants, or kindergarten children and future reading proficiency (Hämäläinen et al., 2013; Leppänen et al., 2012). During phonological development, children establish phonological representations and learn to distinguish between different phonemes. Stable and reliable phonological representations and processing skills are crucial prerequisites to establish specific grapheme-phoneme correspondences during the first steps of reading acquisition (Ziegler & Goswami, 2005). In this chapter, I will firstly explain how language- and phonology-based cognitive-linguistic skills form the prerequisite of later reading acquisition. Secondly, different facets of reading acquisition and the learning-induced neural changes are outlined.

Cognitive-Linguistic Preliterate Skills

Noisy, fuzzy, or otherwise degraded representations weaken phonological coding and finally hamper the establishment of stable and unambiguous connections between a spoken sound and the corresponding orthographic character (Ziegler & Goswami, 2005). This leads to underspecified storage of word spellings, impairing word recognition and reading fluency (Snowling et al., 2020; Torgesen et al., 1994; Ziegler et al., 2008, 2009). Not surprisingly, there has been a great effort to identify and characterize which language-related cognitive-linguistic preliterate skills facilitate or hamper future reading acquisition. Among these, phonological awareness, RAN, phonological skills, and verbal short-term memory have been identified as important behavioral predictors of successful reading development (Landerl et al., 2013; Torgesen et al., 1994). The specific impact of the decisive cognitive-linguistic precursors of reading, however, highly depends on the nature of the orthographic system (Ziegler et al., 2010). For the dissertation, I focus on phonological awareness and RAN as cardinal behavioral predictors of literacy. Their strong relationship has been reliably shown in multiple large-scale cross-linguistic studies at a concurrent (Landerl et al., 2013) as well as a longitudinal level (Caravolas et al., 2012; Landerl et al., 2019).

RAN tasks assess a child's speed and accuracy in naming familiar stimuli such as digits, letters, and colors. Rapidly naming objects and fluent reading share many subprocesses, such as saccadic eye movement, working memory, lexical access, and mapping of visual objects onto language representations (Norton & Wolf, 2012). Not surprisingly, RAN is a strong predictor of later reading fluency across orthographies (Caravolas et al., 2012; Landerl et al., 2019). Phonological awareness refers to the ability to represent, recognize, access, and manipulate any phonological unit within a word, which is essential to map orthography onto phonology and hence bootstrap reading acquisition (Ziegler et al., 2014, 2020). Most certainly, phonological awareness and reading stand in a reciprocal relationship: phonological awareness fosters reading, and reading facilitates phonological awareness (Perfetti et al., 1987). Children with good phonological awareness might naturally break words into smaller units and are thus more sensitive to analyze letter strings. Reversely, children who grasped the alphabetic principle will refine and deepen their sensitivity to different units of a word (Wang, Pines, et al., 2021). In general, phonological awareness appears to be a particularly strong predictor in early school years since the first reading steps are characterized by sequential letter to sound mapping (Boets et al., 2010). This effect decreases with increasing reading experience, i.e., when children switch to direct whole-word-based processing (Landerl et al., 2013, 2019).

A handful of studies assess the structural and functional underpinnings of the cognitive-linguistic preliterate skills. On the structural level, a positive relationship between RAN, and phonological awareness, among others, grey matter volume of the TP language system and the vOT (Beelen et al., 2019; Raschle et al., 2011) as well as the fiber tracts that interconnect them (Vanderauwera et al., 2015) is reported. On the subcortical level, the speech-evoked auditory brainstem response (cf., *BOX 1*) is sensitive to interindividual differences in phonological awareness and RAN (Bonacina et al., 2019; Lam et al., 2017; White-Schwoch et al., 2015; White-Schwoch & Kraus, 2013). Meaning that a stable and precise subcortical processing of language correlates with good preliterate skills. On the cortical level, Raschle et al. (2012) found a positive relationship between phoneme-sensitive response in the vOT (lingual gyrus) and the STG and pseudoword repetition skills in typically developing children. In line with this, the STG response linked to phoneme and rhyme processing in six-year-old emergent readers predicted future reading skills (Wang et al., 2020a). In a recent connectivity analysis, children with better phonological awareness and RAN skills had a better integration of the reading network, i.e., stronger connectivity within bilateral parts of the future reading streams, among others (Benischek et al., 2020). In its essence, these findings strongly suggest that there are interindividual differences in the structural and functional neural architecture already in preliterate kindergarten children, which are associated with the cognitive-linguistic skills that facilitate reading acquisition. Most importantly, these interindividual differences in neural structure and function are primarily located in the language and reading networks, in particular the ventral and dorsal stream.

How to Crack the Alphabetic Code

To achieve the ultimate goal of reading, i.e., to make sense out of abstract shapes and symbols, children need to master a complex trajectory starting at the level of pattern perception and recognition. In alphabetic writing systems, children need to learn how to split words into graphemes and map them onto the corresponding phonemes, i.e., crack the alphabetic code (Liberman et al., 1974). Usually, these correspondences are learned through explicit teaching at school. As soon as the grapheme-phoneme rules are established, children can use their knowledge to decode every possible written word and retrieve the pre-existing representation of the corresponding spoken word form from the phonological lexicon (Ziegler & Goswami, 2005). Increasing exposure to print propels the repeated pairing of orthographic codes with the respective phonological form, in turn, bootstrapping an orthographic lexicon. Thus, explicit instruction becomes increasingly superfluous as phonological decoding provides the opportunity to become a powerful self-teaching device (Share, 1995; Ziegler et al., 2014).

Computational Models of Reading Acquisition

Based on this learning loop, Ziegler et al. (2014) implemented a computational model that incorporates the core principles of phonological decoding and the so-called self-teaching hypothesis (hereafter denoted as self-teaching connectionist model, cf., *Figure 1*). The model is based on the connectionist dual-route model (Perry et al., 2007, 2010), which encompasses an indirect prelexical and a direct lexical route (cf., *Computational Models of Skilled Reading*) The connectionist dual-route model was adopted for reading development to specifically test whether basic phonological decoding is, in fact, sufficient to activate correct candidates in the phonological lexicon, whether self-teaching without any external signals allows stable learning as soon as the alphabetic principle is established, and whether this is sufficient to bootstrap an orthographic lexicon (Ziegler et al., 2014). Importantly, the self-teaching connectionist model differs from previous approaches like the historically influential parallel distributed model by Harm and Seidenberg (1999) that requires extensive explicit teaching, i.e., feedback on millions of learning trials.

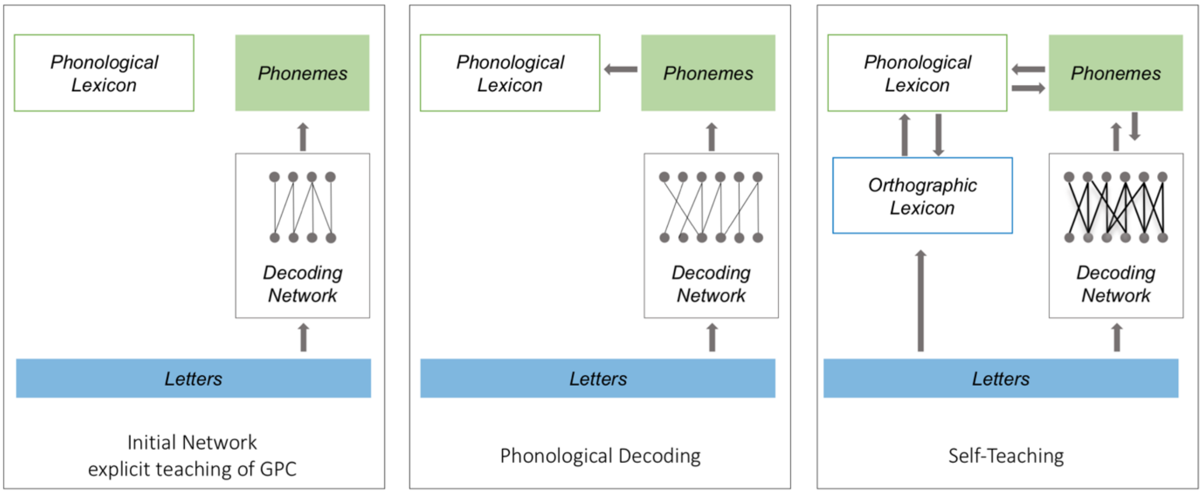


Figure 1. **Illustration of the Self-teaching Connectionist Model.** In a first step a small set of grapheme-phoneme correspondences is explicitly taught to the initial network. Based on these rules, the decoding network is able to decode words that have a pre-existing entry in the phonological network (phonological decoding). In the self-teaching phase, an orthographic lexicon is established. When a phonological entry is activated, an ortho-graphic entry is created. The phonology is also used to generate a teaching signal to refined and strengthen the GPC rules (bidirectional arrows). The figure was adapted from Ziegler et al. (2014, 2020).

In a first step, a small set of grapheme-phoneme correspondences is pre-trained to the pre-lexical network using supervised learning, i.e., mimicking the first steps of reading acquisition when basic spelling principles are explicitly taught. In the self-teaching phase, the model is presented with written words that match the scope of children's vocabulary. The decoding network generates potential (but at least in the beginning, possibly incorrect) phoneme sequences, which in turn activate possible candidates in the phonological lexicon. In their simulations, the correct candidate was automatically chosen as soon as a preset activation threshold was reached. With each retrieval, a direct connection is set up between the letter string and its phonological counterpart. Hence, the retrieved phonological word itself provides a teaching signal. Repeated activation then leads to the growth of an orthographic lexicon enabling direct orthographic reading (see Ziegler et al., 2020 for a summary of the model). In their simulations (Perry et al., 2019; Ziegler et al., 2020), the authors showed that this relatively simple developmental model is, in fact, able to rapidly learn more than 80 % of several thousand words when pre-training the associative network with a set of 65 grapheme-phoneme correspondences only. This can be seen as a proof of concept that phonological decoding and self-teaching are highly powerful developmental tools (Share, 1995). However, there are also 20 % of words that were not learned. These irregular words most certainly need to be learned using a different set of mechanisms like direct instruction of a small set of sight words, morphology, or the use of additional information like prior knowledge and context (Share, 1995). One of the various benefits of computationally modeling language and reading is that one can deliberately and specifically impair certain modules or associates and examine the consequences for the learning process. Within the framework of the self-teaching connectionist model, individual learning trajectories were recently simulated using large-scale personalized models (Perry et al., 2019; Ziegler et al., 2020).

Neurocognitive Models of Reading Acquisition

The reading-induced progression from auditory-based grapheme-phoneme conversion, to phonological coding and finally direct orthographic reading has also been captured by neuro-cognitive models. According to the grain size theory of reading, the initially slow and laborious decoding that marks early stages of reading acquisition, is gradually replaced by two types of location-invariant parallel encoding processes (Grainger et al., 2012, 2016; Grainger & Ziegler, 2011). The so-called coarse-grained coding allows the direct mapping of letters onto whole-word representations, whereas the fine-grained coding supports position-sensitive phonological decoding. At the neural level the dual-route approach is also reflected in the grain size theory. Precisely, rapid parallel coarse-grained orthographic coding is associated with the ventral stream (e.g., Boros et al., 2016; van der Mark et al., 2009), whereas fine-grained phonologically-based coding is linked to the dorsal stream (Dębska et al., 2019). According to the grain size theory increasing reading experience is accompanied by a dorsal-to-ventral shift. This hypothesis has been confirmed by neuroimaging studies: The adult-reading network is marked by greater functional connectivity of regions associated with orthographic processing, while children show greater functional connectivity of reading-related regions linked to phonological processing (Liu et al., 2018). How fast children switch the reading strategy, though, depends on the transparency of the orthographic system and the individual reading proficiency (Richlan, 2014; Richlan et al., 2009, 2010, 2011).

Similar to the grain size model, the classical neurodevelopmental model of reading acquisition as proposed by Pugh et al. (2000) postulates that during the first steps pf reading acquisition children strongly rely on the dorsal stream while the ventral stream only emerges later in development. According to the authors, the bilaterally distributed dorsal TP network functions in conjunction with the frontal stream, i.e., IFG, responsible for phonological memory, syntactic processing and semantic retrieval. When children start to learn to read, the relations among orthographic, phonological, morphological, and lexico-semantic features need to be discovered. To establish these, in particular the grapheme-phoneme rules, attentionally-driven learning mechanisms need to be applied, which are linked to the dorsal stream. The dorsal stream consequently becomes the expert for rule-based analysis and integration of phonological and orthographic information. According to the neurodevelopmental model of reading acquisition, the development of the dorsal system not only precedes but even shapes and guides the subsequent emergence of the ventral reading stream. In other words, it is assumed that the ventral stream matures relatively late during reading acquisition and critically depends on the integrity of the dorsal stream. The model is illustrated in *Figure 2*. More recently (Pugh et al., 2013), the neuro-developmental model was augmented by bilateral regions beyond the classical reading streams and also subcortical circuits supporting reading acquisition. However, the classical model is largely based on cross-sectional studies, or assumptions were even derived from evidence of skilled adult reading reported in studies of the beginning of the 21st century (Pugh et al., 2000; Sandak et al., 2004). Also, it has a strong focus on functional differences between typical and impaired reading development (cf*., BOX 3* for a brief overview of developmental dyslexia). Not surprisingly, the classical model has been questioned due to more recent contradicting evidence. For example, an early engagement of the ventral stream during the first steps of reading acquisition has reliably been shown (see Chyl et al., 2021, for a recent review). Besides, the model does not sufficiently explain or propose testable model-based predictions of the developmental trajectory of the dorsal-to-ventral shift, i.e., from grapheme-phoneme conversion to whole-word-based reading. Another aspect of the model that needs to be further specified is the assumption that the dorsal stream is strongly connected to the frontal stream (Pugh et al., 2000). A claim, for which the authors do not provide any empirical evidence or testable hypotheses of how the functional connectivity might look like. Likewise, it is largely neglected, how the frontal stream might be shaped during reading acquisition. Summarized, the assumptions of the model need to be updated based on recent pediatric neuroimaging of reading, and augmented by a developmental account for the frontal stream and the interrelation of all three reading streams.

The classical model has been evaluated in two meta-analyses (Richlan et al., 2009, 2011), in which the authors primarily focused on the assumptions about developmental dyslexia (cf., *BOX 3*). In the classical model, an early and thus primary dysfunction in the TP causing a secondary dysfunction in the vOT is proposed. In the meta-analysis (Richlan et al., 2011), this assumption was explicitly tested comparing children and young adults with developmental dyslexia. Based on the results the patterns predicted by the classical model had to be partly rejected or modified. Consequently, Richlan (2012, 2014) proposed a new model, in which the TP network of the dorsal stream is divided into a dorsal part, the IPL (subsuming the SMG), and a ventral part, i.e., the STG. While the IPL is assumed to be linked to general attentional mechanisms and thus rather resembles task-related demands during reading, the STG is thought to play a key role in multimodal letter-speech-sound integration (Richlan, 2019). In contrast, the vOT might be linked to both whole-word processing and grapheme-phoneme conversion (Schurz et al., 2010). Additionally, Richlan (2012, 2014) proposed to split the frontal stream into the IFG and PRG, the latter being devoted to prelexical articulatory processes. Please note, that the classical neurodevelopmental model was updated with a primary focus on dysfunctions in developmental dyslexia. In contrast, possible learning-induced maturation of the streams during reading acquisition are only strived.

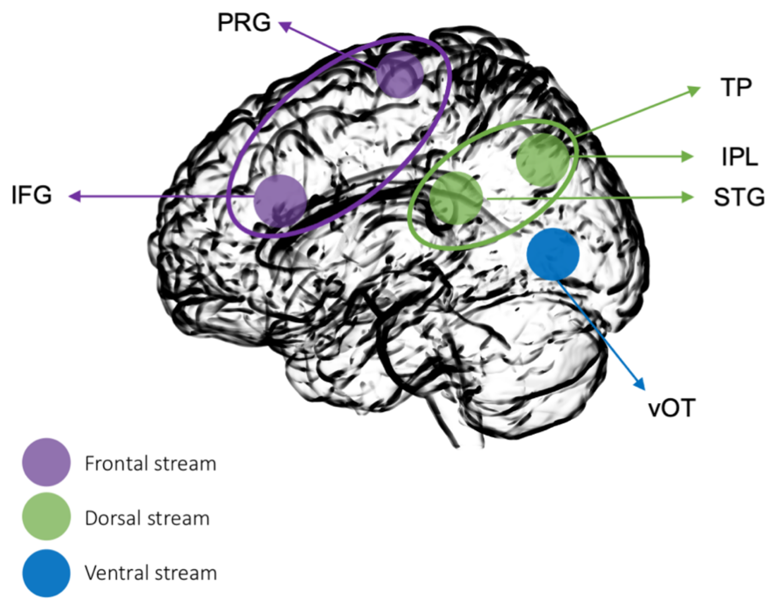


Figure 2. Neurodevelopmental Models of Reading. Schematic overview of the classical model (Pugh et al., 2000) and the new model (Richlan, 2012, 2014). According to the classical model the first steps of reading are linked to the temporo-parietal cortex (TP) and inferior frontal gyrus (IFG). The vOT critically depends on the TP and develops late in development. In the new model, the frontal stream is complemented by the precentral gyrus (PRG). The dorsal stream is split in superior temporal gyrus (STG) and inferior parietal lobe (IPL). The ventral stream is thought to support reading from early on.

While the classical neurodevelopmental model (Pugh et al., 2000) posits assumptions about all three principal reading streams, Price and Devlin (2011) specifically focus on the developing ventral stream during reading acquisition. Their hierarchical neurofunctional model of the emergence and response-selectivity of the vOT can be accounted to IAMs of reading (McClelland & Rumelhart, 1981; Rumelhart & McClelland, 1982). According to their interactive account (Price & Devlin, 2011), increased responsiveness to print is the product of an integrated interplay of bottom-up sensory-driven processes and top-down predictions from higher-level areas linked to phonological and semantic integration. As generally assumed in IAMs, the top-down predictions are refined during the approximation of bottom-up and top-down information until they are maximally consistent (Price & Devlin, 2011). The exact composition of the recurrent and reciprocal interactions depends on the stimulus and the task, possibly also explaining the observed differences in response properties of the vOT between studies (Glezer et al., 2009; Wang et al., 2019). According to the interactive account, the vOT response is weak in preliterate children as the written words do not trigger any phonological or lexico-semantic representation, and thus top-down predictions are mainly absent. During the early stages of reading acquisition, there is a steep rise in neural activity in the vOT as prediction errors are frequent due to imprecise top-down feedback and thus a prolonged process of rapprochement between top-down and bottom-up information. With increasing reading proficiency, the vOT activation declines as the predictions become specific and the error smaller. In sum, the developmental trajectory of neural activity in the vOT during reading acquisition can be described as an inverted U-shaped function according to the interactive account (Price & Devlin, 2011).

BOX 3| Developmental Dyslexia

Dyslexia is a developmental disorder that affects reading on different linguistic levels despite normal intelligence, adequate education, and lack of obvious sensory or neurological damage (Heine et al., 2012). Depending on definitional criteria, it has a prevalence from 3-7 % (Moll, Kunze, et al., 2014). Several theories of dyslexia exist that focus on different aspects and assume different underlying causes of the diverse endophenotypes. The causes of such a complex cognitive disorder like dyslexia are most certainly best captured by multifactorial and dimensional theories (Snowling et al., 2020). Compared to neurotypical readers, children and adults with developmental dyslexia show functional and structural differences in all three principle reading streams and also in subcortical structures like the thalamus, hippocampus, and the brainstem. On the neurofunctional level, children and adults with developmental dyslexia show underactivation in the principle reading streams that are accompanied by compensatory overactivation in and beyond the reading network (Chyl et al., 2021; Richlan, 2012, 2014; Richlan et al., 2009, 2011).

Neuroimaging Reading Acquisition

Two large-scale meta-analyses depict children's neural systems for reading (Houdé et al., 2010; Martin et al., 2015). The latter identified the core child-reading network that coarsely mirrors the classical three-fold system established in skilled adult reading (cf., *Neuroimaging Skilled Reading*), i.e., resembling the familiar posterior dual-stream architecture converging at the level of the frontal stream.

The Ventral Stream

The ventral visual stream needs to be fundamentally reorganized during reading acquisition to become responsive to linguistic input (Dehaene et al., 2010, 2015). Of particular importance for the present thesis is the rapid emergence of print-sensitivity in the FuG (Lochy et al., 2016; Van de Walle de Ghelcke et al., 2020) during reading acquisition (Church et al., 2008; Chyl et al., 2018; Dehaene-Lambertz et al., 2018; Gaillard et al., 2003; Monzalvo et al., 2012). The ventral response to print can already be detected before formal reading instruction at school starts (Centanni, Norton, et al., 2018) or after a short (artificial) grapheme-phoneme training (Brem et al., 2010; Pleisch et al., 2019). Interestingly, the vOT also becomes responsive to phonological information during reading development (Dębska et al., 2019; Wang et al., 2020a, 2020b). In line with the interactive account of the vOT development (Price & Devlin, 2011), neural response in the ventral stream depends on reading proficiency (Centanni, Norton, et al., 2018; Chyl et al., 2018; Dębska et al., 2019) and increases in the course of reading development (Dehaene et al., 2015; Dehaene-Lambertz et al., 2018). The postulated posterior-anterior gradient of increasing print-specificity and abstraction well-known in adults (Taylor et al., 2019; Vinckier et al., 2007; Zhao et al., 2017) is also present in fluently reading children (van der Mark et al., 2009).

The Dorsal Stream

As already briefly mentioned, the TP language network needs to be reorganized to become responsive to print during reading development (Dehaene et al., 2015). The STG, being devoted to letter-speech-sound integration, might be one of the decisive regions driving and guiding this process. In line with this assumption, STG activation positively correlates with reading skills in children. The association is true for phonological tasks, print-specific response, and print-speech coactivation (Chyl et al., 2018). The PPC, more specifically the SMG, might crucially support grapheme-phoneme mapping (Booth et al., 2007), as it is linked to covert articulation, monitoring of inner speech, and stores phonological representations (Koelsch et al., 2009; Raizada & Poldrack, 2007). A skill-related increase in SMG activation was recently shown across different phonological tasks (Dębska et al., 2019).

The last decades of research confirmed that the dorsal and ventral stream development cannot be separated into first and second (Pugh et al., 2000) but might instead go hand in hand. In fact, during reading acquisition, letter-speech-sound integration modulates the dorsal and ventral stream response as recently shown in an artificial letter-learning paradigm mimicking the first steps of reading acquisition in prereaders (Karipidis et al., 2017, 2018; Pleisch et al., 2019; Plewko et al., 2018). Nonetheless, the generally assumed dorsal-to-ventral shift during reading acquisition (Ziegler & Goswami, 2005) is supported by neuroimaging studies showing a developmental decrease in activation of the STG of the dorsal stream linked to sensory, auditory representations accompanied by an increase in phonological processing in PPC and IFG (Bitan, Burman, et al., 2007; Liu et al., 2018).

The Frontal Stream

The meta-analytic child-reading map identified by Martin et al. (2015) shows the highest convergence of recruitment across studies for the IFG (18 out of 20), which has been positively correlated with age and reading skill in children and adolescents (Bitan, Cheon, et al., 2007;

Bitan et al., 2006; Koyama et al., 2011; Liu et al., 2018; Turkeltaub et al., 2003). In general, the functional and structural heterogeneity and widely distributed connectivity of the IFG (Briggs et al., 2019), already briefly outlined in *Language Comprehension*, emphasizes its contribution to various aspects of reading acquisition. However, the frontal stream is also assumed to mature relatively late during development (Phan et al., 2021). Likewise, the role of the IFG might change in the course of reading development.

Interaction and Integration of Reading Streams

Reading acquisition involves changes in the activation patterns of multiple regions within and beyond the language and reading streams and affects the interaction and integration of these regions (Price, 2012; Turkeltaub et al., 2002). The theory of interactive specialization (Johnson, 2001, 2011) argues that cognitive development is based on changes in the connectivity between brain regions driving functional specialization. Recent studies on functional connectivity in emergent to intermediate readers strongly suggest that interactive processing of the central parts of the large-scale reading networks is an essential driver of reading acquisition (Smith et al., 2018) and critical for normal reading development (Cui et al., 2016; Morken et al., 2017). The neural networks also become more specialized over time. Meaning that adults show reading-task-specific functional connectivity patterns while the signature of functional connectivity is highly similar across component processes in children (Liu et al., 2018).

Despite the reviewed large body of neuroimaging studies examining individual aspects of reading, the division of work among the central component processes of single word recognition is still largely unknown (Backes et al., 2002; Shaywitz et al., 1998; with a focus on developpmental dyslexia). In particular, the neural correlates of prelexical, orthographic, phonological, and lexico-semantic processes during reading have only once been systematically tested in typically developing children (Pugh et al., 1996). Not surprisingly, the fMRI methods and results of this early landmark study are no longer conform to current standards.

From Preliteracy to Literacy

To gain a more profound knowledge of the trajectories of reading development and facilitate or understanding why some children fail to become efficient readers, there is an increasing effort to examine the neural predictors of future reading proficiency before the onset of literacy (Chyl et al., 2021). Here, different aspects of neural integrity are targeted: Structural studies examine morphological differences in grey matter (e.g., Houston et al., 2014; Linkersdörfer et al., 2014; Phan et al., 2021) and white matter tracts (e.g., Moulton et al., 2019; Vanderauwera et al., 2015) in relation to future literacy. However, the observed brain-behavior relationships are not confined to structural indices. On the neurophysiological level, there is a strong link between basic auditory processing and later reading development not only in kindergarten children (Hämäläinen et al., 2013) but already in newborn event-related potentials (Leppänen et al., 2012; Schaadt et al., 2015). It has also been shown that the auditory brainstem response to speech sounds is a potential biomarker of future reading (White-Schwoch et al., 2015; cf., also *BOX 1*). These findings strongly suggest, that interindividual differences occur early during development and on various levels of neural processing.

There has been a growing amount of longitudinal fMRI studies in the last decades (Bach et al., 2013; Ben-Shachar et al., 2011; Hoeft et al., 2007; Yamada et al., 2011, for early examples). Thus, the below summary is confined to the most recent ones. In its essence, all these longitudinal studies strongly emphasize functional differences in the future reading streams at kindergarten age that directly affect subsequent reading acquisition (Chyl et al., 2021). For example, preliterate print-sensitive response in the FuG (Centanni et al., 2019) and print-speech convergence in the FuG, PPC, and IFG (Karipidis et al., 2017, 2018; Preston et al.,

2016) predicted future reading skills, which means that interindividual differences in neural response in all three future reading streams exist at a preliterate age. Also, the integrity of the neural systems of spoken language processing in kindergarten children is strongly related to subsequent reading performance (Jasińska et al., 2021; Yu et al., 2018). Similarly, spoken language ability in emergent readers shapes print-speech convergence, e.g., in the bilateral IFG, STG, MTG, and parietal regions. In the same cohort of children, interindividual differences in print-speech coactivation in the MTG and the STG predicted reading proficiency one year later (Marks et al., 2019).

These longitudinal results impressively demonstrate that the sensitivity of critical regions of the future reading streams, primarily ventral and dorsal, systematically differ before the onset of literacy acquisition.

One of the characteristics of these previous studies is that they use rather effortful tasks, possibly confounding the processes related to task performance and the neural representations genuinely related to the neural predictors of literacy. Likewise, the choice of stimulus material is mainly confined to the linguistic domain. Dehaene-Lambertz et al. (2018) approached these shortcomings and used a simple target-detection task to examine the neural reorganization of vision and language throughout the first year of reading instruction. They found that reading fluency is associated with response selectivity to visual stimuli. More specifically, they report that reading fluency correlated with increased activation of words and numbers in the vOT and the right cerebellum. The same association was found for face-selective responses in the right FuG. Using a data-driven computational approach to examine the maturation of the vOT, Nordt et al. (2019) recently examined the development of several visual categories in children, adolescences, and adults. Yet, only the word-selective response was associated with general reading skills. However, the replication of these findings and application in longitudinal predictive settings is still to be made.

2 Research Questions and Hypotheses

The overall aim of this dissertation is to advance our understanding of (A) the functioning of the three principal reading streams in literate but not yet adult-like reading children, and (B) the neural prerequisites of future reading acquisition before formal literacy instruction starts.
I examined the first category of fluently reading children (A) in Liebig et al. 2017 (Study I), focusing on the following research questions:

1) *In fluently reading children, what are the neural underpinnings of prelexical, orthographic, phonological, and lexico-semantic processing?*
2) *How is the processing of the basic subcomponents of single word recognition distributed among the principal reading streams in children?*

Children that fell in the second category (B) were examined in Liebig et al. 2021 (Study II) and Liebig et al. 2020 (Study III). Using a longitudinal design examining neural processing in pre-literate children at the end of kindergarten and testing their reading proficiency at the end of second grade, I specifically addressed these questions:

3) *How are interindividual differences in cortical and subcortical processing mirrored in the cognitive-linguistic precursors of literacy?*
4) *Does the preliterate neural response predict future literacy?*

Below, I will elaborate on how I developed the main research questions and specify the overall hypotheses. More fine-grained sub-questions and detailed hypotheses, e.g., about specific brain regions, are outlined in the summaries of the three empirical studies (Summary of the Dissertation Studies).

Question 1. In fluently reading children, what are the neural underpinnings of prelexical, orthographic, phonological, and lexico-semantic processing?

Written word recognition is based on four central components: prelexical, orthographic, phonological, and lexico-semantic processing. In adults, these component processes have often been linked to separable neural networks (Froehlich et al., 2018; Taylor et al., 2013; Welcome & Joanisse, 2012). Here, phonological components are primarily associated with the dorsal stream, while prelexical and orthographic processing predominantly leads to enhanced activity in the ventral stream. Lexico-semantic processing is additionally associated with the frontal stream. In children, however, detailed yet comprehensive specification of the neural underpinnings of all basic component processes is mainly missing (see Pugh et al., 1996; for an exception). Previous research either focused on single aspects of word reading or approached reading from a clinical perspective examining different groups (e.g., Bach et al., 2010; Bitan, Burman, et al., 2007). In Study I (Liebig et al., 2017), we approached these shortcomings: Firstly, we examined all four central component processes in the same cohort of fluently reading children and adolescences (nine to 13 years old). Secondly, we examined a wide range of neurotypical readers instead of comparing different groups, which requires the use of arbitrary cut-offs to separate typical from atypical development or good from poor readers at the expense of power and variance (Button et al., 2013). To do so, we developed an fMRI paradigm to disentangle the four basic component processes that makeup word reading and specifically test their neural underpinnings.

In Study I, we mainly focused on the core regions of the child-reading network identified in the meta-analysis by Martin et al. (2015) using an ROI-based account. To answer the present first research question, I also examine the neural response on the whole-brain level to determine whether children primarily engage the three principal reading streams when solving the different reading tasks. It is generally acknowledged that the first steps of reading acquisition are based on auditory-based print-speech conversion that is associated with the dorsal stream

(Ziegler & Goswami, 2005). According to the classical neurodevelopmental model of reading acquisition, this is mirrored in the early establishment of the dorsal stream (Pugh et al., 2000). Recent studies, however, challenge this view by showing the early importance of the ventral stream (Brem et al., 2010; Dębska et al., 2019; Lochy et al., 2016; Van de Walle de Ghelcke et al., 2020). Since we examined fluently reading children after five to eight years of schooling, the developmental trajectory cannot be evaluated in the scope of Study I. It is, however, testable whether there is still a processing advantage of the dorsal stream or whether processing has already largely shifted to the ventral stream (Boros et al., 2016; Ziegler & Goswami, 2005). Following the principles of the theory of interactive specialization (Johnson, 2001, 2011), the neural signatures of the component processes might be less discernable in children than in skilled adult readers (Froehlich et al., 2018). Besides, pediatric studies indicate that children recruit further complementary right-hemispheric and subcortical regions for language and reading (Enge et al., 2020). Thus, a more distributed activation pattern encompassing regions beyond the principal reading streams is expected, possibly gradually increasing with task demands.

Question 2. How is the processing of the basic subcomponents of single word recognition distributed among the principal reading streams in children?

In Study I, we used the core regions of the child-reading network as identified by Martin et al. (2015) to neurofunctionally test the degree of modularization and specification of the three principal streams after some years of reading experience. More specifically, we examined whether the ventral, dorsal, and frontal reading streams work in concert to process the basic subcomponents of single-word reading or whether each stream has highly specialized response properties and only responds to selective component processes. Approaching these open questions about the child's reading system will not only shed light on the neural underpinnings of single-word reading but also allowed to test different theoretical models of reading (dual-route vs. interactive activation; Coltheart, 2006).

For prelexical processing, we hypothesized that it might primarily or even exclusively engage the posterior parts of the ventral stream, thought to be devoted to fast and automatized pre-lexical processing of print (Dehaene & Cohen, 2011). Orthographic processing might solely engage the ventral stream, while phonological information might be exclusively linked to the dorsal stream (strictly dual-route). In contrast, following the idea of IAM, the two streams might show joint activation to solve both orthographic and phonological tasks. However, similar response patterns also favor the interactive specialization hypothesis that argues for less discernable response patterns during development (Johnson, 2001, 2011). In this case, though, the response pattern of all reading tasks should yield similar neural signatures. We also approached whether the often assumed dorsal-to-ventral shift during reading acquisition is accomplished in fluently reading children. The degree of a ventral advantage might be associated with individual reading proficiency, i.e., degree of automatization. Precisely, children with better reading skills might more strongly rely on the ventral stream and vice versa. To test this hypothesis, we correlated the BOLD signal of the ROIs of the child-reading mask with (out-of-scanner) reading performance.

Based on previous research in children and adults (Martin et al., 2015), we hypothesized that both phonological processing but, in particular, lexico-semantic processing to be associated with the frontal reading stream. According to the classical neurodevelopmental model (Pugh et al., 2000), the IFG supports reading acquisition from early on (e.g., Church et al., 2008; Gaillard et al., 2003). In the same vein, Martin et al. (2015) identified a large cluster in the frontal stream showing consistent activation across studies. Nonetheless, the response properties of the frontal stream are also thought to mature and fine-tune during reading development. In particular, there is an age-related (Bitan, Cheon, et al., 2007; Turkeltaub et al., 2003) and reading-skill-related (Bitan, Cheon, et al., 2007; Koyama et al., 2011) increase in neural activation. Consequently, neural response in the frontal stream might generally be less pronounced compared to the posterior reading streams.

Question 3. How are interindividual differences in preliterate subcortical and cortical processing mirrored in the cognitive-linguistic precursors of literacy?

In Study II (Liebig, Froehlich, et al., 2021) and Study III (Liebig et al., 2020), we studied the neural prerequisites of future reading. More specifically, we examined cortical processing of vision and language (Study II) and subcortical language processing (Study III) in kindergarten children in relation to cognitive-linguistic prereading skills. Similar to Study I, we examined the brain-behavior relationships with a continuous approach to capture various developmental trajectories.

While the cognitive-linguistic precursors of future literacy are well-described (Caravolas et al., 2012; Landerl et al., 2013, 2019; Moll, Ramus, et al., 2014), their neural underpinnings are seldomly examined (Benischek et al., 2020; Raschle, Zuk, Ortiz-Mantilla, et al., 2012; Wang et al., 2020a; Wang, Pines, et al., 2021). To shed light on the neural underpinnings of the cognitive-linguistic precursors of literacy can also facilitate our understanding of the developmental trajectory of reading. Interindividual differences in these regions might also affect the first steps of reading acquisition. Thus, a primary aim of Study II was to advance our understanding of the neural correlates of the cognitive-linguistic precursors in preliterate children. To achieve this, we used a simple viewing and listening paradigm and tested whether the neural response is sensitive to interindividual differences in phonological awareness and RAN. Note that several aspects of our methodological approach differ from previous research: Instead of using a demanding auditory phonological judgment task (Raschle, Zuk, & Gaab, 2012; Wang et al., 2020a), we used a passive paradigm to avoid task-induced confounds in the neural response. To get a more comprehensive picture of the brain-behavior relationships, we did not confine our analysis to the auditory modality (Raschle, Zuk, & Gaab, 2012; Wang et al., 2020a) but examined auditory and visual processing. Based on the preliminary findings, which report a decisive role of the STG (Raschle, Zuk, & Gaab, 2012; Wang et al., 2020a), we hypothesized that this might also be replicated in the scope of Study II. More specifically, both the visual and the auditory response in the STG might be sensitive to capture interindividual differences in the cognitive-precursors of reading. Since visual stimuli were also included, we might also observe a brain-behavior relationship in the ventral stream (Raschle, Zuk, & Gaab, 2012).

In Study III, we went one step further and used a multifactorial approach to examine gene-brain-behavior relationships on the subcortical level. There is growing evidence showing that the auditory brainstem response to complex speech sounds is sensitive to differences in reading performance and language abilities in English-speaking children (Chandrasekaran et al., 2009; Hornickel et al., 2011; Hornickel & Kraus, 2013; Tecoulesco et al., 2020). More specifically, children with poor reading skills or developmental dyslexia show a less stable and imprecise brainstem responses to speech. The same pattern has been observed in preliterate children, revealing a physiologic link between early phonological awareness skills, RAN and the neural representation of speech (Bonacina et al., 2019; Lam et al., 2017; White-Schwoch et al., 2015; White-Schwoch & Kraus, 2013). Recently, we could replicate these association in a German-speaking group of preliterate and literate children (Neef, Müller, et al., 2017; Neef, Schaadt, et al., 2017). Thus, the subcortical response to speech might also be sensitive to the ample cognitive-linguistic preliterate skills, i.e., phonological awareness and RAN, in German-speaking children. In particular, a stable and faithful brainstem response to speech sounds might be associated with higher performance. I tested this hypothesis by running some additional analysis on the data of Study III.

Question 4. Does the preliterate neural response predict future literacy?

It is essential to clarify the causal role of preliterate neural functioning to gain a deeper insight into the first steps of reading acquisition. After all, shortly before formal reading instruction starts, the preliterate neural state forms the basis of the neurofunctional changes induced by reading acquisition. A more profound knowledge of the causal relationships might then help to precisely target learning difficulties occurring early in development. To examine these causal relationships, we longitudinally examined the brain-behavior relationships in Study II and Study III to test whether preliterate neural processing predicts literacy two years later.

More precisely, in Study II, we examined cortical visual and auditory processing. In contrast to most of the longitudinal neuroimaging studies reviewed in the introduction (Chyl et al., 2021), we employed a passive fMRI paradigm to test possible neurofunctional markers of future reading. Furthermore, we included linguistic and non-linguistic material to gain a more comprehensive picture (see Dehaene-Lambertz et al., 2018; Monzalvo et al., 2012; Nordt et al., 2019, for a similar approach). Accordingly, one of the major aims of Study II was to test whether different aspects of preliterate response capacities are sensitive to predict future reading: Will the relationship be confined to linguistic material, or do non-linguistic encoding of faces, also predict future literacy? We chose to examine visual face processing based on previous results indicating differences in face-selective response between typical readers and readers with dyslexia (Monzalvo et al., 2012). Likewise, face processing correlated with reading skills in emergent readers (Dehaene-Lambertz et al., 2018). Next, we aimed to find out whether there is a brain-behavior relationship in both modalities. After all, the first steps of reading acquisition rely heavily on auditory-based processes, and thus spoken language processing might be a stronger predictor of emergent reading. Lastly, we hypothesized that the reading-sensitive regions might be located in the future reading streams, particularly the ventral and dorsal streams. If we find a brain-behavior relationship in the longitudinal examination, this would strongly emphasize that differences in the reading streams already manifest in the prereading brain. The neural integrity would thus not be a result of but rather be a prerequisite for successful reading acquisition.

On the subcortical level (Study III), we approached similar questions and hypothesized that the preliterate brainstem response to complex speech sounds might predict future literacy not only in English-speaking preliterate children (White-Schwoch et al., 2015) but also in our German cohort. If the data could confirm this assumption, this would be strong evidence that interindividual differences in early subconscious language processing, i.e., at a level where the incoming sound waves need to be thoroughly extracted and mimicked, affects future reading acquisition. Consequently, poor reading abilities might have its roots in the auditory brainstem. Unquestionably, the preprocessed representation is handed over to the auditory cortex and higher-level cortical regions, which then have to deal with the incoming signal, whether it is variable and fuzzy or precise and stable.

Taken together, we tested whether subcortical speech processing and task-independent cortical processing of spoken and written language and faces are potential objective biological markers of future literacy.

II Empirical Part

3 General Methodology

To examine the cortical reading streams, the neural prerequisites of reading, and approach the research questions, different neuroimaging paradigms and methods were applied, briefly summarized in the next section. For details about the materials, data acquisition, pre-processing, and analysis of the empirical studies conducted in the scope of my dissertation, I refer the reader to the original publications (Liebig et al., 2017, 2020; 2021).

Neuroimaging Techniques and Paradigms

In Study I and Study II, two different fMRI paradigms were used to examine cortical responses to visual and auditory stimuli. In Study III, the speech-evoked auditory brainstem response was tested.

Study I: Component Processes of Reading

In Liebig et al. (2017), participants were given five different two-forced choice tasks, to examine the neural correlates of the component processes of single-word reading. Thus, the experimental design consisted of a 5 x 2 factorial design with the factors task and target/ non-target. The visual control baseline task consisted of slashes tilted towards the same direction or not. The four reading tasks comprised letter identification (prelexical processing), orthographic-lexical decision, phonological-lexical decision, and semantic categorization (cf., *Figure 3* for examples). Each task consisted of 80 items (*N*= 40 targets/ 40 non-targets), carefully matched for confounding linguistic features (e.g., bigram frequency, neighborhood density). Pseudowords and pseudohomophones were created by exchanging one letter of an existing German noun (see Froehlich et al., 2016, 2018, for a detailed description of the materials). The experiment was divided into four runs, each comprising the five tasks presented in blocks.

FMRI data was acquired at the Center for Cognitive Neuroscience Berlin (CCNB) of the Freie Universität Berlin. Each run comprised 233 whole-brain functional T2*-weighted images. The session was completed with a T1-weighted anatomical scan. Data was preprocessed and analyzed using the SPM12 software package run in a Matlab (Mathworks) environment. The reading tasks were analyzed both on the whole-brain level and using a mask encompassing the core reading network of children (established by Martin et al., 2015). The component processes of reading paradigm, the fMRI setup, and ROIs are summarized in *Figure 3*.

Component Processes of Single Word Reading Paradigm

A

Level	Visual control	Prelexical	Orthography	Phonology	Lexico-Sematics
Task	**Baseline**	**Letter identification**	**Lexical decision**	**Lexical decision**	**Semantic categorization**
Example	///// ///\/	bdmrk hfgst	Ecke (*edge*) Hauß (*house*)	Waal (*whale*) Buhn (*buun*)	Katze (*cat*) Tisch (*table*)
Target	**same**	**‘r’ in string**	**word**	**pseudohomophone**	**living**
Non-target	**different**	**no ‘r’ in string**	**pseudoword**	**pseudoword**	**non-living**

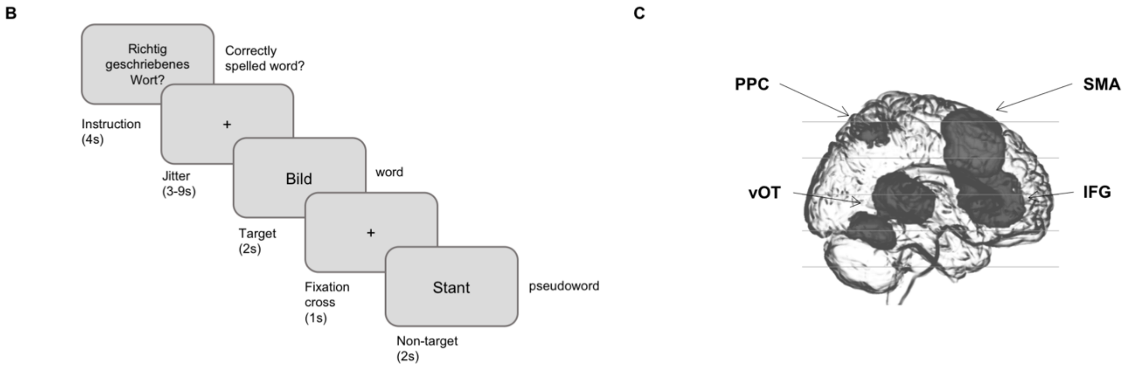


Figure 3. Experimental Setup Study I. (A) Table summarizes the five two-forced choice tasks to test the component processes of single word decoding. (B) The fMRI setup is depicted. (C) Regions of interest of the core child-reading network (Martin et al., 2015) rendered on the whole-brain. PPC = posterior parietal cortex, SMA = supplementary motor area, vOT = ventral occipito-temporal cortex, IFG = inferior frontal gyrus.

Study II: Preliterate Cortical Systems of Vision and Language

In Liebig et al. (2021), we used a passive fMRI paradigm to examine the neural systems of vision and language in preliterate children. Auditory language processing was tested with spoken words. Five visual stimulus categories were presented to test the ventral visual stream: checkerboards, houses, faces, and written words. In a rapid block design, stimuli (*N*= 15 checkerboards, *N*= 60 for all other categories) were presented in three consecutive runs (cf., *Figure 4* for examples). The visual angle and size were matched across conditions. The linguistic stimuli consisted of age-appropriate, highly frequent words carefully matched for important confounding features (e.g., bigram frequency, neighborhood density).

Before the actual fMRI experiment, children were carefully familiarized with the scanning procedure in a mock-scanner at the Max Planck Institute for Human Development Berlin. FMRI data was acquired at the CCNB of the Freie Universität Berlin. Each run comprised 68 whole-brain functional T2*-weighted images and was finished with a T1-weighted anatomical scan. Data was preprocessed and analyzed using the SPM12 software package run in a Matlab (Mathworks) environment.

Cortical Systems for Vision and Language Paradigm

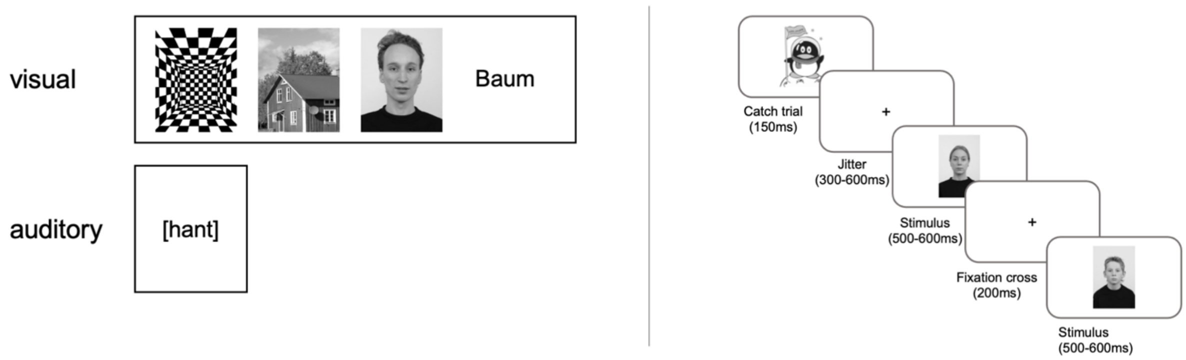


Figure 4. Experimental Setup Study II. Examples of the visual (checkerboards, houses, faces, written words) and auditory (spoken words) stimulus conditions (left), and the fMRI setup (right) are depicted.

Study III: Preliterate Subcortical Language Processing

In Liebig et al. (2020, and 2021 for an erratum due to missing collaborators in first publication), we tested the auditory system by recording brainstem responses to syllables. Before and after stimulation with the target syllables, 2000 clicks were presented to test the integrity of the auditory pathway and ensure stable recording throughout the session. Auditory language stimulation was started with the syllable train [da] and was followed by [ba]. The length of the Klatt-synthesized syllables was 170ms (engineered by the laboratory of Nina Kraus: Hornickel & Kraus, 2013; Skoe & Kraus, 2010). A total of 6000 epochs per syllable was presented to the right ear using insert earphones. During the whole procedure, children sat on a comfortable chair in an electrically shielded, soundproof booth. Since the auditory brainstem response is automatic and subconscious, children could simultaneously watch a movie of their choice. The tone of the movie was presented via loudspeakers.

The study was conducted at the Max Planck Institute for Human Cognitive and Brain Science Leipzig as part of the Legascreen project. To measure the auditory brainstem response, we used a vertical one-channel montage recording the response from the vertex (Cz) to the ipsilateral earlobe (reference), with the forehead as the ground using Ag/AgCl electrodes with an impedance < 5 kΩ. Three regions characterize the speech-evoked auditory brainstem response: the onset burst, i.e., an initial unvoiced portion of the stop consonant (voice-onset time), followed by the formant transition between consonant and vowel, and a final steady-state response to the vowel. Each speech sound has a unique spectrum of harmonics (Skoe & Kraus, 2010). The scalp-recorded auditory brainstem response reflects the aggregated output of neural populations of the brainstem and midbrain structures (Chandrasekaran & Kraus, 2010) pre-dominantly from the inferior colliculus, recently computationally modeled by Saiz-Alía and Reichenbach (2020). The auditory brainstem response faithfully mimics the incoming auditory signal (cf., *Figure 5*). Raw data was preprocessed using BrainVision Analyzer (BrainProducts), all further processing steps were computed with Matlab routines (The MathWorks).

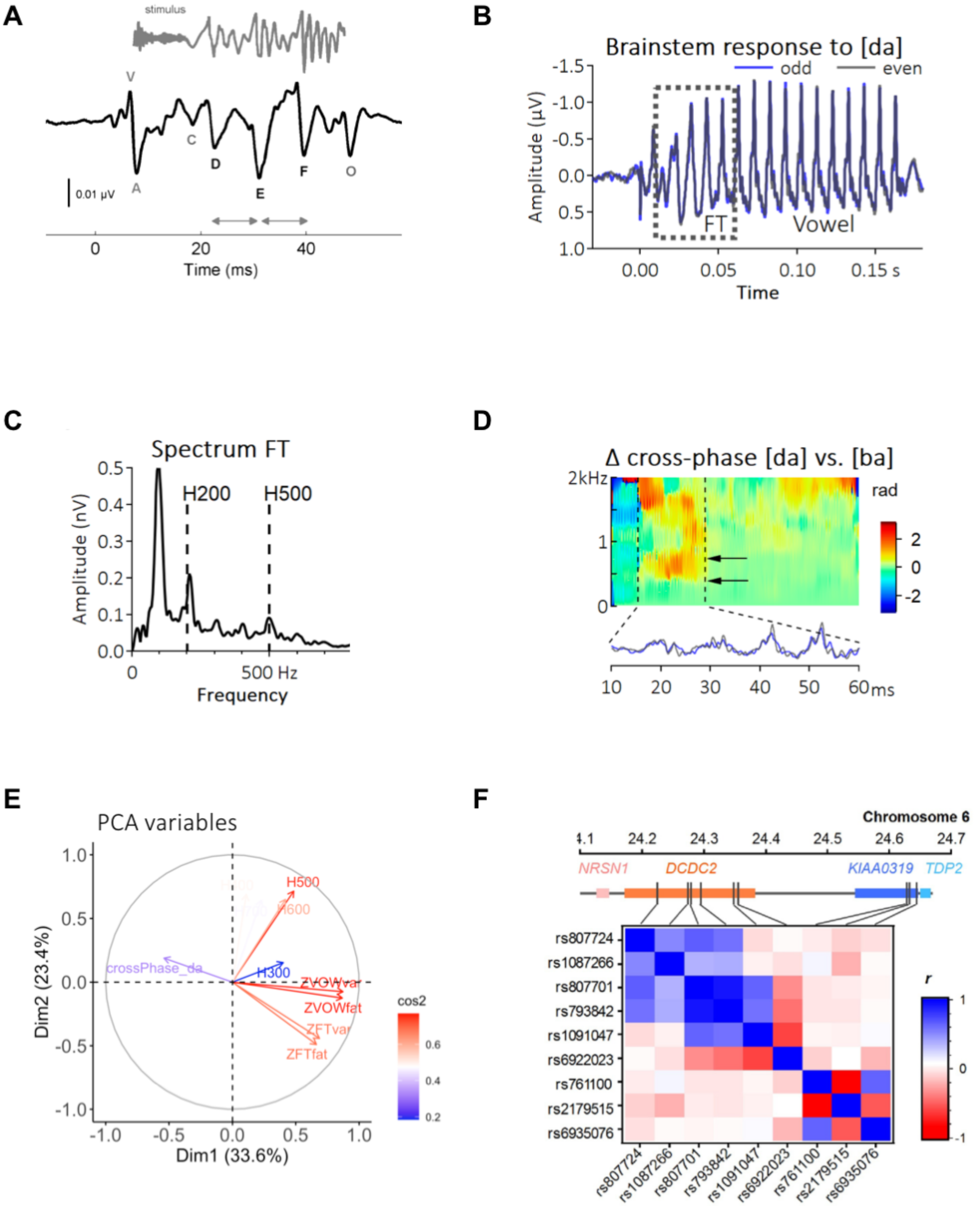


Figure 5. Neurophysiological and Genetic Data of Study III. (A) transient and sustained response features of the auditory brainstem response (ABR) to [da]. Stimulus evokes seven response peaks (indicated by capital letters) relating to major acoustic landmarks of the syllable with a time-lag of 7-8ms consistent with neural transmission between cochlea and brainstem. Extracted response metrics ABR: (B) Grand average response to the syllable [da]. The dotted square indicates formant transition (FT) period, blue and gray curve display the sub averages across even and odd responses. (C) Spectrum of the fast Fourier transformation applied to the grand averages of the ABR from 10-60ms. (D) Cross-phaseogramm indicates physiological differentiation between [da] and [ba] in the FT phase. (E) Loadings, communalities and uniqueness of the principal component analysis (PCA), first factor is extracted without rotation. (F) Gene and marker locations on the top of the correlation matrix are proportional to physical distances on chromosome 6. The correlation matrix demonstrates the linkage disequilibrium of neighbouring single nucleotide polymorphisms. H200– H700 = harmonics from 200-700 Hz; Ftvar = odd versus even trials during FT; FTfat = first-half versus second-half trials during FT; VOWvar = odd versus even trials during steady response to vowel; VOWfat = first-half versus second-half trials during vowel; crossP = delta cross-phase of [da] for odd versus even trials during FT; sound diff = delta cross-phase of [da] versus [ba] during FT; Dim1-2= first and second dimension of the PCA and explained variance in percent; cos2= squared coordinates..

Summary of the Dissertation Studies

Study I: Component Processes in Literate Children

Liebig, J., Froehlich, E., Morawetz, C., Braun, M., Jacobs, A. M., Heekeren, H. R., & Ziegler, J. C. (2017). Neurofunctionally dissecting the reading system in children. *Developmental Cognitive Neuroscience, 27*, 45-57.

Aims. In adults, the basic subcomponents of single-word reading have often been linked to separable networks (Hofmann & Jacobs, 2014; Taylor et al., 2013; Welcome & Joanisse, 2012). However, the knowledge about the specific contribution of each subcomponent to reading in children after some years of experience is still incomplete. Thus, the overall aim of Study I was to disentangle these basic subcomponents in fluently reading children covering the entire spectrum of (typical) reading development. We used comparable reading tasks, tapping into one specific component process (i.e., prelexical, phonological, orthographic, and lexico-semantic processing) to 'neurofunctionally dissect' the reading system in nine to 13-year-old children and young adolescences. More specifically, we aimed to examine two central questions: Firstly, how differentiated and specialized are the core parts of the reading system after some years of reading experience but not-yet adult-like reading. Secondly, we tested whether the response patterns favor a modular, dual-route view or an interactive activation approach.

Hypotheses. According to Martin et al. (2015) who meta-analyzed 20 neuroimaging studies examining reading in children, the core reading system of children consists of the vOT, PPC, IFG, and bilateral SMA. For the ROI-based analysis, we hypothesized that prelexical processing might primarily engage the posterior ventral stream (vOT). Orthographic processing might elicit stronger or more distributed activity in the vOT, possibly supported by a complementary response in the dorsal stream (PPC). The opposite pattern was expected for phonological processing. We expected that lexico-semantic processing and possibly phonological processing would elicit additional activity in the anterior parts of the ventral, the dorsal, and in particular, the frontal stream. Given the convergent involvement of the STG (part of the vOT ROI) and the bilateral SMA across studies (Martin et al., 2015), we hypothesized that these regions might be active during all component processes except prelexical processing.

Methods**.* To address these hypotheses, we used the component processes of reading paradigm (Figure 3***) in combination with fMRI in nine to 13-year-old children and early adolescences (*N*= 41, mean age $_{(SD)}$ = 11.9 $_{(1.03)}$, 18 female) with varying literacy abilities. On the behavioral level, decoding abilities and reading fluency were tested with word and pseudo-word reading (Salzburger Lese- und Rechtschreibtest, SLRT; Moll & Landerl, 2010); reading comprehension and speed was examined using a sentence judgment task (Salzbuger Lese-Screening, SLS; Mayringer & Wimmer, 2008). Non-verbal intelligence (Hamburg-Wechsler-Intelligenztest für Kinder; Petermann & Petermann, 2008) and scope of lexicon (Culture Fair Test; Weiß & Weiß, 2006) were examined to further characterize the sample. All children had a non-verbal intelligence within the normal range, and the sample covered a wide range of reading proficiency.

Whole-brain general linear models were generated for each subject and entered into a flexible factorial design for random effects on the group level to examine the neural correlates of the four component processes of visual word recognition (letter identification, orthographic and phonological decision, semantic categorization). Also, a literature-based ROI analysis was conducted to examine task differences. The child-reading network identified in the meta-analytic map of Martin et al. (2015) encompasses four ROIs: vOT, PPC, IFG, and (beyond the classical reading streams) bilateral SMA. Internally studentized residuals of the extracted mean beta values of the ROIs were computed to control for in-scanner task performance and used for further analysis. To examine activation patterns across regions and tasks, these were entered into a linear mixed model with *ROI* and *task* as within-subject factors and *age* as between-subject factor. *Subjects* were added as a random effect to account for the repeated-measures design.

Results. All results are illustrated in *Figure 6*. In the original publication, we mainly focused on the results of the ROI analysis. For the present dissertation, I also evaluated the whole-brain results. The analysis showed that children activated all parts of the classical reading streams across tasks relatively similarly. More specifically, letter identification was associated with two large clusters in the vOT, including the FuG and the bilateral IOG. Two smaller clusters were located in the other two reading streams (SPL, PRG).

The orthographic-lexical decision showed a large-scale activation network in the bilateral IOG and the ITG of the ventral stream. Here, peak activation was slightly more anterior compared to letter identification. A smaller cluster in the dorsal stream covering inferior and superior parts of the parietal lobe was also linked to orthographic decisions. Finally, we observed significant activation in different parts of the frontal stream (PRG, IFG). The activation in the principle reading streams was accompanied by significant bilateral activation in right-hemispheric homologs of the reading streams and beyond. In particular, enhanced activity in the IFG, ACC, bilateral SMA, right insula, and cerebellum.

Phonological-lexical decisions showed a similar response pattern covering large parts of all three principal reading streams: the SOG, ITG, FuG, and the bilateral IOG (ventral); the superior and the IPL (dorsal), and the PRG extending to the IFG (frontal). Again, we also observed significant activity beyond the reading network, in the right insular, right IFG, and the right MFG, the bilateral ACC, cerebellum, thalamus, and the hippocampus.

Semantic categorization was associated with significant activity in the ventral stream (MOG, FuG, MTG, bilateral IOG), and a small cluster in the IPL of the dorsal stream. Semantic categorization also elicited activation in the PRG and the IFG of the frontal stream. Further activation was found in the SMA, right insula, right IFG, and bilateral cerebellum.

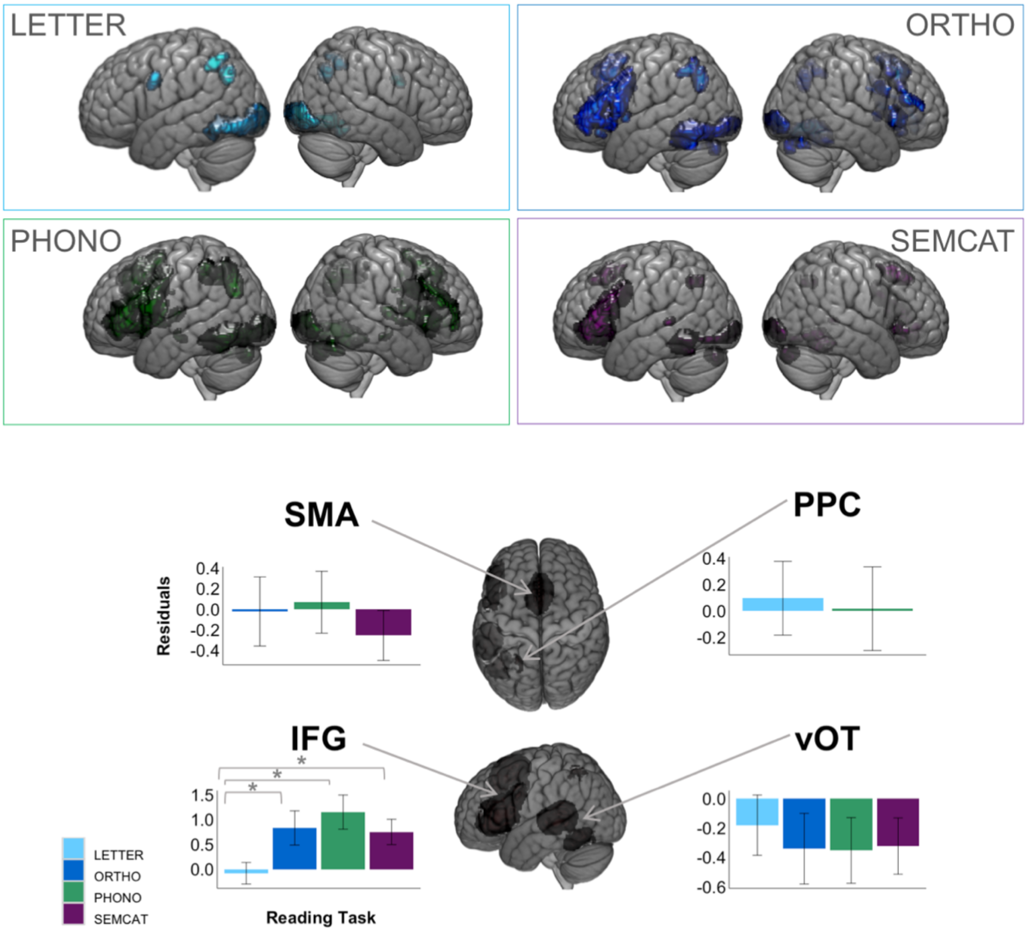


Figure 6. Results of Study I. (A) Whole-brain results of the component processes. Task-specific activation (reading task > visual baseline) was thresholded at $p < .001$ uncorrected and $p_{FWE} < .05$ corrected on peak level with $k > 15$ voxel. (B) Region of interest analysis. Bar plots show task comparison in the core regions of child-reading system (x-axis) and mean BOLD response (studentized residuals of beta values in arbitrary units, y-axis) thresholded at $p < .001$ uncorrected and $p_{FWE} < .05$ with $k > 15$ voxel. PPC = posterior parietal cortex, vOT = ventral occipito-temporal cortex, SMA = bilateral supplementary motor area, IFG = inferior frontal gyrus.

The ROI-based analysis essentially confirmed the whole-brain results. Letter identification was not confined to the posterior vOT but elicited additional activation in more anterior parts of the vOT (ITG, FuG). Furthermore, a small cluster in the SPL of the dorsal ROI and the PRG as part of the frontal ROI showed significant activity. Consistent with our hypotheses, orthographic-lexical decisions were associated with neural activity in the vOT. Similar to letter identification, vOT activation reached the ITG and FuG. However, the peak activation of the orthographic decisions was located anterior to the peak of letter identification. Orthographic decisions were also associated with significant activity in the IFG and bilateral SMA. We did not observe any significant activity in the PPC during orthographic-lexical decisions. Note, however, that the ROI of the dorsal stream (*k*= 128) was significantly smaller compared to the other ROIs (*k*= 2,809 – 3,433). The phonological-lexical decision was the only component task that elicited activity in all core regions of the child-reading system, i.e., vOT, PPC, IFG, and bilateral SMA. Interestingly, the vOT activity reached the MTG. Semantic categorization elicited activation in the vOT (including the MTG), the IFG, and the bilateral SMA, not the PPC (similar to orthographic-lexical processing). Comparing the component tasks across ROIs, we found that all tasks led to similar activity in the ventral stream (vOT). In the dorsal stream (PPC), significant activity was confined to prelexical and phonological processing with similar response strength. In the frontal stream (IFG), neural response during prelexical processing was significantly smaller compared to all other component processes. Phonological, orthographic, and lexico-semantic processing elicited comparable activity in the bilateral SMA. Against our hypothesis, we did not observe any significant brain-behavior relationships, i.e., no interindividual differences in neural response patterns with general reading development. This null result indicates that the neural processing of the component processes of single-word reading might already be highly automatized and stable in nine to 13-year-old children irrespective of the individual level of proficiency.

Conclusions. The cohort of literate children covering a wide range of reading skills showed a reading network that resembled the classical adult division into the dorsal, ventral, and frontal stream. ‘Neurofunctionally dissecting’ the component processes of single-word reading revealed both similarities and differences across component tasks. The most striking finding is that the posterior ventral stream was not only in charge of low-level prelexical processing but appeared to be involved in all four component processes. The dorsal stream showed the most selective response properties, being confined mainly to prelexical and phonological analysis. The frontal stream was primarily engaged by phonological and lexico-semantic processing. However, also orthographic yielded a significant response in the IFG, and prelexical letter processing was associated with the PRG.

Study II: Preliterate Visual and Auditory Processing

Liebig, J., Froehlich, E., Sylvester, T., Braun, M., Heekeren, H. R., Ziegler, J. C, & Jacobs, A. M., (2021). Neural processing of vision and language in kindergarten is associated with prereading skills and predicts future literacy. *Human Brain Mapping,* 2021, 1-17.

Aims. The main objective of the longitudinal study was to assess the neural underpinnings of cognitive-linguistic prereading skills and, most importantly, the neural predictors of future reading acquisition in preliterate kindergarten children. For this purpose, we used the passive fMRI paradigm (cf.*, Figure 4*), stimulating the ventral visual stream (checkerboards, houses, faces, written words) and the auditory language stream (spoken words). Firstly, we examined the concurrent relationships of the neural response-selectivity and two of the cardinal cognitive-linguistic predictors of literacy, i.e., phonological awareness and RAN. Secondly, we tested the potential of task-independent preliterate visual and auditory neural processing to predict reading fluency in the same group of children after two years of formal reading instruction at school. In sum, we aimed to shed light on interindividual differences in the neural 'reading readiness' shortly before reading instruction in elementary school starts.

Hypotheses. Based on recent (longitudinal) studies examining the neural underpinnings of the first steps of reading acquisition (Centanni et al., 2019; Chyl et al., 2018; Karipidis et al., 2017, 2018), we expected response-selectivity to faces and possibly written words in the ventral stream to correlate with the cognitive-linguistic preliterate skills. In particular, we expected a brain-behavior relationship associated with the vOT, bilateral FuG, and the MTG; and possibly also the SPL as part of the dorsal stream. Of particular interest was the relationship between face processing and cognitive-linguistic skills. The neural response to faces in the ventral stream differs between children with and without dyslexia (Monzalvo et al., 2012) and correlates with reading fluency (Dehaene-Lambertz et al., 2018). Thus, we hypothesized that this relationship is already established at an earlier time point during development. We expected that the cognitive-linguistic precursors of reading correlate with face-sensitive responses in the ventral stream. Since our cohort of children was genuinely preliterate and had minimal letter knowledge, hypotheses for written words were less specific. For auditory language processing, we additionally expected interindividual differences in response-selectivity in the dorsal stream, e.g., SPL and planum temporale, sensitive to phonological awareness skills and RAN performance. The bilateral STG has previously been identified as a critical key region for letter-speech-sound integration in emergent readers (Karipidis et al., 2017, 2018). Consequently, we hypothesized that response-selectivity in the bilateral STG to both visual and auditory stimuli might be sensitive to interindividual differences in cognitive-linguistic prereading skills.

The most crucial goal of Study II was to test the predictive power of preliterate neural task-independent processing. Based on previous findings (Dębska et al., 2016; Monzalvo & Dehaene-Lambertz, 2013), we hypothesized that preliterate auditory language processing in the dorsal stream might predict future literacy. Due to the observed strong relationship between face encoding and literacy skills (Dehaene-Lambertz et al., 2018; Monzalvo et al., 2012), we hypothesized that face-selective response in the ventral stream might predict future reading fluency. Keeping in mind that our cohort of children was truly preliterate, we considered the possibility that the processing of written words might not show any longitudinal brain-behavior relation. However, if the sensitivity to written words in reading-related regions like the vOT could nevertheless predict future reading fluency, this would be robust evidence for the idea of the ‘reading readiness’ of these regions to print before literacy (Dehaene & Cohen, 2007; Dehaene-Lambertz et al., 2018).

Methods. We longitudinally followed a large sample of 90 children from the end of kindergarten to the end of the second year of elementary school (emergent readers). Fifty-four of these children (5-6-years-old, $M_{(SD)}$ = 5.6 $_{(.47)}$, 28 female) successfully participated in the fMRI session, and their data were analyzed in the scope of Study II. Besides the passive fMRI paradigm, children completed a screening to test several cognitive-linguistic precursors of literacy (Bielefelder Screening zur Früherkennung von Lese-Rechtschreibschwierigkeiten, BISC; Jansen, 2002) at kindergarten age. At the end of the second year of elementary school, 48 of these children returned for the assessment of their literacy skills (7-8-years-old, $M_{(SD)}$ = 7.6 $_{(.48)}$, 27 female). Non-verbal intelligence within the normal range was verified using the Wechsler intelligence scale for children (WISC; Petermann & Petermann, 2014). The children completed several tests to characterize their literacy skills: pseudoword decoding and word reading (SLRT; Moll & Landerl, 2010), sentence judgments (SLS; Mayringer & Wimmer, 2008), reading comprehension (Ein Leseverständnistest für Erst- bis Sechstklässler, ELFE; Lenhard & Schneider, 2006), and spelling (Deutscher Rechtschreibtest, DERET; Stock & Schneider, 2008).

Neural systems for vision and language were examined on the whole-brain level. Experimental conditions were entered into a general linear model, and basic contrast maps were generated for each stimulus condition. The single-subject maps were then entered into second-level flexible factorial design, and baseline contrasts of each stimulus category against the global null were examined. Cognitive-linguistic precursors of literacy (phonological awareness, RAN) and reading fluency (combined score of word and pseudoword reading) were entered into second-level simple regression analyses to test the brain-behavior relationships. Here, baseline contrasts for the conditions of interest (faces, written words, spoken words) and differential contrasts of the visual stimuli isolating the category-specific activation (*faces* > *[houses, written words]; written words* > *[houses, faces]*) were used. The contrast of *written words* > *[houses, faces]* did not yield any significant activity on the whole-brain level and was thus re-tested with a more focal literature-based ROI analysis. Besides FWE-correction for voxelwise analysis, regressions results were also controlled for multiple testing (cf., *Figure 7* for the respective thresholds).

Results. The concurrent brain-behavior analysis showed that face-selective response in the IOG and the bilateral FuG located in the ventral stream was positively associated with performance in RAN. Neural response to written words in the dorsal stream, i.e., the STG and SMG, was negatively correlated with RAN.

Similarly, higher neural responses to spoken language in the dorsal stream (bilateral precuneus, SPL) and the frontal stream (PRG) were associated with lower RAN. Note that the developmental trajectories of the non-linguistic and linguistic stimuli went in opposite directions. While the stronger response to faces was associated with better RAN, a stronger response to written and spoken words was associated with poor performance.

Against our hypotheses, phonological awareness did not show any brain-behavior association. This null result indicates that the passive viewing and listening task was not sensitive to detect interindividual differences in phonological awareness. Besides, it might strengthen the importance of RAN.

In the longitudinal predictive analysis, visual processing of faces in the IOG, ITG, and MTG predicted future reading fluency. The stronger neural activation in the ventral stream in response to faces in kindergarten, the better the reading performance two years later. None of the other contrasts tested predicted reading fluency.

Conclusions. Our key findings can be summarized as follows: Brain activity elicited by the passive viewing and listening tasks was sensitive to interindividual differences in preliterate RAN skills and predicted future reading fluency. Importantly, we found interindividual differences in the neural sensitivity to RAN, one of the most critical behavioral predictors of literacy, solely in those regions that will become key components of the ventral, dorsal, and frontal reading stream. Most importantly, the neural response to faces in the ventral stream clearly predicted reading fluency two years later and might thus have the potential to become an objective marker of reading acquisition.

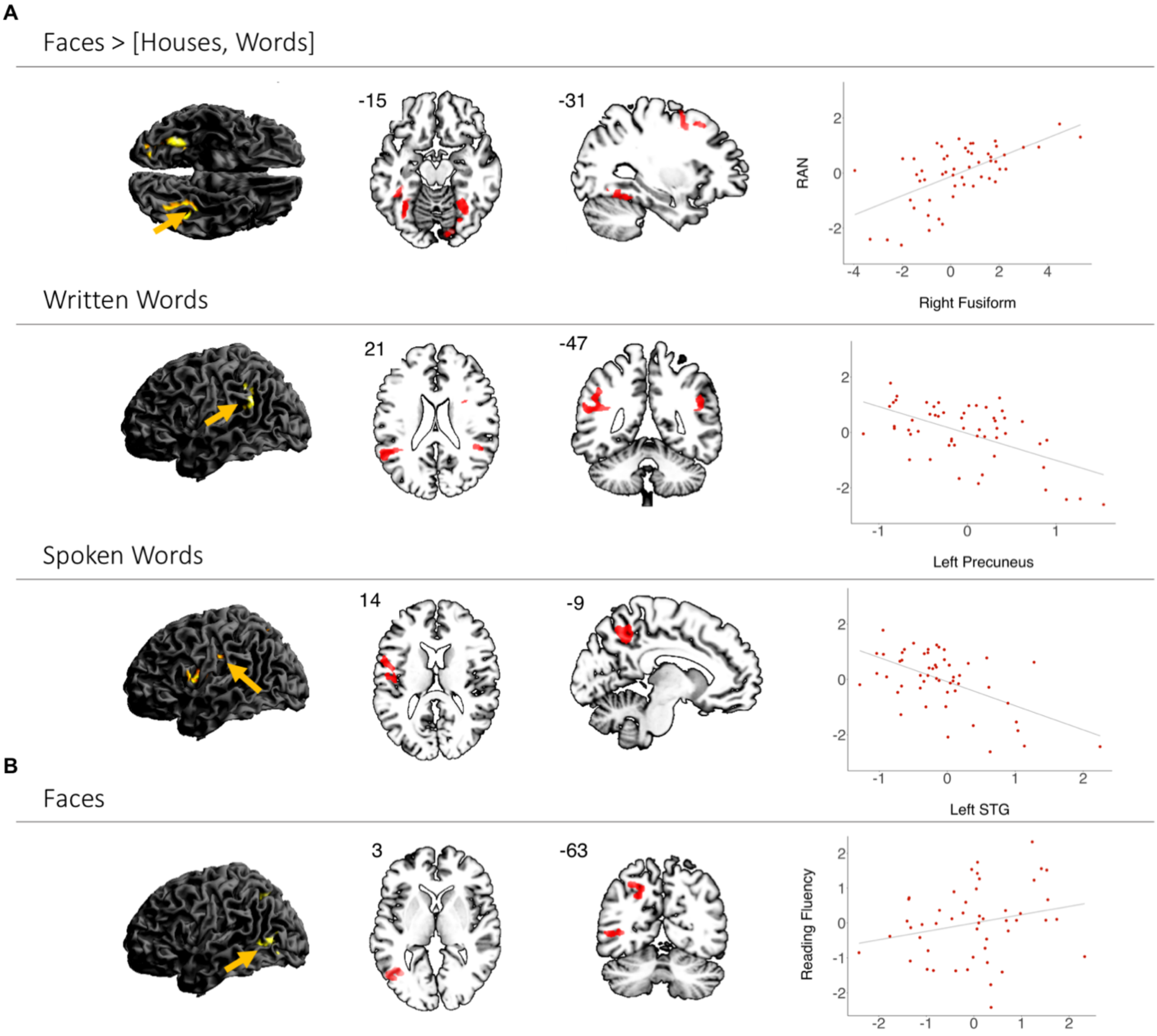


Figure 7. Results of Study II. (A) Concurrent brain-behavior analysis. Positive correlation between differential contrast of faces and rapid automatized naming (RAN), negative correlation between baseline contrasts of written and spoken words and RAN. (B) Longitudinal prediction of literacy. Baseline contrast of faces predicts reading fluency two years later. Left: Whole-brain rendering of regression with (A) RAN and (B) reading fluency as covariate of interest. Yellow arrows indicate plotted region in scatter plot. Middle column: Selected slices, numbers indicate location in MNI space. Right: Scatter plots of brain-behavior relationship. X-axis: Mean BOLD signal of regions of interest in arbitrary units; y-axis: studentized residuals of (A) RAN and (B) reading fluency (composite score of word and pseudoword reading). Whole-brain results thresholded at $p < .001$ (uncorrected), $p_{FWE} < .05$, additionally controlled for number of regression models at (A) $p_{corr} < .006$ and (B) $p_{corr} < .0125$.

Follow Up analyses. For the present dissertation, I ran some additional analyses to interlink the results of the dissertational studies. More specifically, I tested whether the reading-sensitive preliterate regions identified in Study II can predict the component processes of reading in an independent sample, i.e., the literate children examined in Study I. Besides, I computed further regression models to test whether preliterate cortical processing predicts future reading comprehension and spelling skills as these were targeted in Study III. A more detailed description of the follow up analysis is provided in the *Supplementary*.

Preliteracy ROIs. I extracted the regions of the dorsal, ventral and frontal stream sensitive to RAN and reading fluency to test these in an ROI-based analysis in Study I. These encompassed: the IOG, bilateral FuG, bilateral precuneus (including the SPL), STG (including the SMG), and the PRG.

Contribution to subcomponents of reading. The add-on analysis aimed to examine what these 'reading sensitive' regions become experts for in fluently reading children. For that purpose, I conducted the same analysis as reported in Study II. Meaning that activation across ROIs and tasks was examined (6 regions x 4 reading tasks in a linear-mixed model with *ROI* and *task* as within-subject factors). In sum, I examined the brain-behavior relationships to test if those regions identified in the preliterate brain (Study II) can also predict reading skills in an independent sample (Study I).

Hypotheses. Based on my findings in Study I, examining the core reading system in fluently reading children, I hypothesized that the IOG and the bilateral FuG might be primarily (but not exclusively) associated with prelexical processing. In contrast, all four component processes might be associated with the posterior parts of the ventral stream. Orthographic and, in particular, phonological processing showed a widely distributed response pattern in large parts of the widespread reading and language network. Thus, I hypothesized that all preliterate reading-sensitive ROIs located in the ventral and frontal stream might become devoted to orthographic and phonological lexical processing. Phonological processing might additionally be linked to the dorsal ROIs. Lexico-semantic processing might primarily show significant response in the FuG, PRG, and possibly the STG. Besides, the preliterate reading-sensitive ROIs might show differences in their response pattern depending on the reading skills.

Results. In general, only four ROIs that showed preliterate sensitivity to RAN or reading fluency were associated with the subcomponents of single-word reading: the IOG, left and right FuG, and the PRG. Although I also hypothesized that the STG might be associated with orthographic, phonological, and lexico-semantic processing, the results align with Study I. We could not identify any contribution of the STG to the component processes of reading. Similarly, the missing association of the bilateral precuneus is in line with the observed subordinate role of the dorsal stream in the subcomponents of reading in fluently reading children.

Within the ROIs, I found differential activation patterns. Activation was confined to phonological processing in the IOG. The FuG was associated with orthographic, phonological, and semantic processing. All four component processes were associated with activation in the right FuG. In both hemispheres, orthographic and phonological processing showed a significantly stronger response compared to lexico-semantic processing. In the PRG, activation was confined to orthographic and phonological processing showing similar response strength. The neural response was not modulated by general reading skills.

Longitudinal prediction of literacy. I extended the examination of the longitudinal prediction of reading conducted in the scope of Study II and also tested whether the preliterate neural response to vision and language predicts reading comprehension (ELFE; Lenhard & Schneider, 2006) and spelling (DERET; Stock & Schneider, 2008) as tested in Study III.

Hypotheses. The hypotheses of the principal analysis of Study II also apply to the follow-up analyses.

Results. There was no further systematic relationship between preliterate cortical visual and auditory processing and future literacy beyond reading fluency. This null-effect emphasizes that the component processes necessary for successful pseudoword decoding and single word might be most suitable to examine potential preliterate neural markers.

Study III: Preliterate Subcortical Language Processing

Liebig, J., Friederici, A., Neef, N., & LEGASCREEN Consortium, (2020). Auditory brainstem measures and genotyping boost the prediction of literacy: A longitudinal study on early markers of dyslexia. *Developmental Cognitive Neuroscience*, 46, 100869.

Aims. In Neef et al. (2017), we examined the largely unknown impact of dyslexia risk genes on early auditory processing in preliterate and literate children and the genetic influence on literacy in fluently reading children. For that, we chose genes that have previously been associated with reading and dyslexia, i.e., *KIAA0319* and *DCDC2*. In animal models, both genes are linked to neural spike time precision (Centanni et al., 2014; Truong et al., 2014) and precision of auditory processing (Centanni et al., 2016). Recently, the physiological consequence of altered functions in *KIAA0319* and *DCDC2* was also associated with neural variability in children (Centanni, Pantazis, et al., 2018). The results of Neef et al. (2017) indicate that a higher amount of risk alleles of *KIAA0319* is associated with less stable auditory brainstem response to speech sounds. In the second analysis conducted in the scope of Neef et al. (2017), we examined the influence of the genetic risk variants on literacy in eleven to 13-year-old children. *KIAA0319* showed a significant association with writing and spelling performance in fluently reading children, while *DCDC2* explained significant reading speed and comprehension variance. In Study III, we went one step further and examined the triad of genes, brain, and behavior. For that purpose, we tested the predictive value of multiple influencing factors on future literacy acquisition in a large cohort of German-speaking children. The longitudinal design allowed us to track literacy development from preliteracy to emergent reading. Specifically, we tested the impact of (1) environmental-demographic factors, (2) two ample genetic risk genes, (3) the preliterate auditory brainstem response to speech, and (4) cognitive-linguistic preliterate skills on future reading and spelling.

Hypotheses. In Neef et al. (2017), we showed that the genetic risk variant of *KIAA0319* negatively affects response consistency in the auditory brainstem to speech and thus might hamper phoneme encoding at a very early stage in the auditory pathway. *DCDC2*, however, only showed a trending effect. Here, a higher genetic risk was associated with more stable responses to speech sounds in the auditory brainstem. Based on these preliminary findings, we hypothesized that these genotypes could also improve future literacy prediction. Next, we aimed to improve the prediction models by adding metrics capturing the integrity of the auditory brainstem response. Although it is desirable to define objective markers of future literacy, we also added behavioral precursors of literacy as these reliably predict future reading (Caravolas et al., 2012; Landerl et al., 2013, 2019; Moll, Ramus, et al., 2014).

Methods. A final sample of 93 children at the end of kindergarten was analyzed (4-7-years old, $M_{(SD)}$= 5.8 $_{(.90)}$, 46 female). Before literacy acquisition, we also assessed non-verbal intelligence (WISC; Petermann & Petermann, 2014), general language development, and demographic-environmental information. A subsample of 75 children also completed a screening testing several cognitive-linguistic precursors of literacy (BISC; Jansen, 2002). Eighty-one children of the larger sample were re-tested at different stages of early literate age (elementary school grade 1-3: 6-9-years-old, $M_{(SD)}$= 8.5 $_{(.9)}$). Reading comprehension (ELFE; Lenhard & Schneider, 2006), and spelling (DERET; Stock & Schneider, 2008) were assessed. A subsample of 54 children also complemented a pseudoword decoding and word reading test (SLRT; Moll & Landerl, 2010). The median of all time points was computed whenever possible to ensure accurate reading and spelling performance measurement.

On the neural level, we tested the auditory brainstem response to the speech syllables [ba] and [da] at preliterate age. Three indices representing different features of the speech-evoked auditory brainstem response were extracted. The indices considered the neurophysiological response to the formant transition and steady-state period of the syllable. Neural stability (Pearson's correlation coefficient across subaverages) was quantified utilizing neural fatigue and trial-by-trial variability. For that, we correlated the first and the second half of a train for the former and between odd and even pairs for the latter. Frequency-specific time delay within syllables was captured by computing the delta cross-phase between subaverages. Physiological discrimination between different speech sounds was measured by extracting the delta cross-phase between syllables. Finally, the harmonics of the first formant were extracted using a fast Fourier transformation on the individual average across all trials. The magnitude of responses to the first formant contributes to phonemic identification and is thus, a spectral feature of response specificity. To identify the latent variable structure of these features, summarized in *Figure 5*, we conducted a principal component analysis. The first factor was used for further statistical analysis.

To examine the gene-brain-behavior relationships, multifactorial regression analyses were conducted. In particular, we considered demographic-environmental information (age, sex, non-verbal intelligence, parental education, family history of dyslexia), genotypes (*KIAA0319, DCDC2*), and auditory brainstem encoding (principal component scores). For the subsample of 75 children, cognitive-linguistic precursors of literacy (combined score of BISC subscales) were added to the analysis. Independent regression models were set up to predict future reading comprehension and spelling skills.

Results. The regression analyses predicted children's literacy skills to differing degrees. As commonly acknowledged (e.g., Dilnot et al., 2017; Ozernov-Palchik et al., 2019), our results validate that demographic-environmental factors consistently predict future literacy (25 % of variance in reading comprehension, 14 % in spelling).
On the genetic level, *DCDC2* (31 %) had a stronger influence on spelling than *KIAA0319* (23 %). Reading comprehension was generally less associated with gene expression.
Similarly, on the neural level, the auditory brainstem response had a significant impact on spelling (31 % in combination with *DCDC2*, 23 % in combination with *KIAA0319*) but not on reading comprehension.

Adding the preliterate cognitive-linguistic skills boosted prediction of all models (reading comprehension: 41 % *DCDC2*/ ABR/ preliterate, 33 % *KIAA0319*/ ABR/ preliterate; spelling: 44 % *DCDC2*/ABR/preliterate, 40 % *KIAA0319*/ ABR/ preliterate).

***Conclusions**.* Genotypes and neurophysiological metrics particularly boosted the prediction of writing and spelling. Most certainly, auditory-based grapheme-phoneme conversion is still required to accomplish oral dictation, even if children have already established an orthographic lexicon and are capable of direct reading strategies. After all, German has a very transparent orthography, and children quickly shift to whole-word reading (Grainger et al., 2012; Grainger & Ziegler, 2011). Thus, it is not surprising that genotypes and the auditory brainstem response resembling auditory-based reading strategies could not capture reading comprehension sufficiently. For successful reading comprehension, whole-word-based reading is strongly required instead. We also included the well-established cognitive-linguistic precursors of literacy in our models, which improved the prediction of both reading and writing. These results imply that adding (subjective) cognitive-linguistic precursors to (more objective) markers like demographic-environmental factors, genotypes, and neurophysiology complements the prediction of future literacy. In sum, our results suggest that gene-brain-behavior profiling has the potential to predict the success of future literacy acquisition. At the same time, however, the results imply the need for more sophisticated assessments to fully account for the complex cognitive profiles and learning trajectories constituting the basis of reading. In general, the small number of participants in terms of genetics makes it necessary to consider the observations as preliminary with a need for replication.

Follow Up analyses. For the present dissertation project, I ran some additional analyses to compare the results of Study II and Study III. See *Supplementary* for the detailed description of the analysis and results of all complementary analyses.

Concurrent gene-brain-behavior relationships. I explored the concurrent relationships between the two cognitive-linguistic precursors also examined in Study II. In parallel to the primary analysis of Study III, I set up multilevel models testing the impact of demographic-environmental factors, genotypes, and auditory brainstem metrics on phonological awareness and RAN.

Hypotheses. I expected an association with the genetic risk variants since both cognitive-linguistic skills strongly rely on auditory-based phonological processing, and the examined genes are associated with neural precision of auditory processing (Centanni et al., 2016; Centanni, Pantazis, et al., 2018). Like White-Schwoch et al. (2015) who reported stronger cross-sectional association than long-itudinal relationships of the auditory brainstem response and reading-related skills, I hypothesized that the auditory brainstem response is stronger associated with interindividual differences in the cognitive-linguistic preliterate skills (Bonacina et al., 2019; Lam et al., 2017; White-Schwoch et al., 2015) than observed for the longitudinal prediction.

Results. On the demographic-environmental level, a different pattern compared to the longitudinal assessment emerged. Instead of parental education, nonverbal intelligence drove the effect of the demographic-environmental model explaining 15 % variance in RAN and phonological awareness. Interestingly, family history of dyslexia had no significant impact neither in the main analysis of Study III nor in any additional analyses. This null-effect contradicts previous findings (e.g., Lyytinen et al., 2015) and thus, might seem surprising at first sight as developmental dyslexia is known to be heritable. However, phenotypes of dyslexia are very heterogeneous concerning the underlying causes and severity of symptoms. Thus, a binary classification into risk and no-risk might not be sufficient to reliably and specifically predict future literacy acquisition. This null-effect strengthens my dissertation's general approach to examine the children's developmental trajectories as a whole rather than dichotomously splitting them into groups.

Unexpectedly, neither *DCDC2* nor *KIAA0319* significantly improved the regression models. This null-effect contradicts the hypothesis. However, the sample size of 75 children is relatively small in terms of genetic analysis, and thus, the results need to be interpreted with caution. The mixed findings strengthen the need for replication in larger samples.

In contrast, the auditory brainstem response was associated with RAN (25 % *DCDC2*/ABR, 25 % *KIAA0319*/ABR) and phonological awareness (27 % *DCDC2*/ABR, 24 % *KIAA0319*/ABR [trending effect]). The results show a stronger brain-behavior relationship in the concurrent compared to the longitudinal analysis.

Prediction of reading fluency. In the second series of analyses, I tested the power of the multilevel regression models to predict reading fluency (combined score of word and pseudoword reading; data was only available for a subsample of 54 children).

Hypotheses. Firstly, I expected a strong relationship between the demographic-environmental factors and reading fluency, similar to the results obtained for spelling and reading comprehension. Secondly, *DCDC2* might have a more substantial impact than *KIAA0319.* Thirdly, the auditory brainstem response might additionally improve the prediction models since at least pseudoword reading requires grapheme-phoneme conversion.

Results. Similar to spelling, parental education significantly affected reading fluency (environmental-demographic model: 27 %). Adding *DCDC2* to the model improved the prediction of reading fluency to 46 %. In contrast, *KIAA0319* did not improve the regression. However, the auditory brainstem response did not improve the prediction of reading fluency (46 % *DCDC2*/ABR, 36 % *KIAA0319*/ABR).

To sum up, the preliterate auditory brainstem response to language might be better suited in concurrent correlational rather than longitudinal settings. Similar results were obtained by White-Schwoch et al. (2015), who report stronger cross-sectional compared to longitudinal relationships.

III Discussion

4 Discussion of the Research Questions

Question 1. In fluently reading children, what are the neural underpinnings of prelexical, orthographic, phonological, and lexico-semantic processing?

In Study I, we tempted to disentangle the neural underpinnings of the central component processes of single word recognition in fluently reading children. While we focused on the ROI analysis in the scope of Study I, I examined the whole-brain results to answer research question 1. The attempts to neurofunctionally dissect the reading system into its component processes revealed a network that resembled the classical division into the dorsal, ventral and frontal stream. However, the whole-brain findings were not confined to the principal streams. Children also recruited right-hemispheric homologs of the ventral and frontal stream and further subcortical structures with increasing task demands. Below, I will firstly discuss the findings within and secondly beyond the classical reading streams.

Activation within the Principal Reading Streams

The most important findings within the three principal reading streams can be summarized as follows. Apart from prelexical processing, the component tasks evoked highly overlapping but also partly discernable response patterns in the three principal large-scale language and reading streams favoring a highly interactive reading system. The vOT was not only in charge of low-level orthographic processing but appeared to be involved in all four components emphasizing a greater variety of response capacities than initially assumed (Braun et al., 2009; Cohen & Dehaene, 2004; Dehaene et al., 2005; Kronbichler et al., 2007; Schurz et al., 2010). Additionally, significant activity of the MTG during the phonological decision and the semantic categorization emphasizes its role in semantic processing and whole-word phonology (e.g., Braun et al., 2015; Schurz et al., 2010, in adults) and generalizes this approach to fluently reading children. As recently proposed, I support the idea that the PRG should be added to the frontal stream (Richlan, 2012, 2014). According to the results of

Study I, the PRG might not only be involved in prelexical phonological decoding or articulatory processes (Richlan, 2014) but might play a pivotal role in all component processes, at least in fluently reading children.

In general, in the cohort of children having some years of reading experience, the component processes of single word recognition have shifted mainly to the ventral and frontal stream. In contrast, the dorsal stream plays a subordinate, possibly supporting, role and is only strongly activated when the task explicitly asks for phonological analysis. The perfect left-lateralization observed further supports the assumed more focal function of the dorsal stream in fluently reading children.

Beyond the Classical Reading Streams

Recently, an increasing number of studies are looking beyond the classical language and reading streams when examining reading and reading acquisition (Alvarez & Fiez, 2018; Braun et al., 2019; Skeide et al., 2017). In particular, the three more complex component tasks, i.e., orthographic decision, phonological decision, and semantic categorization, elicited significant neural responses beyond the classical reading streams. It is not surprising that additional cortical and subcortical structures are involved in integrating linguistic, visual, and attentional functions required to accomplish reading.

The fluently reading children of Study I activated the bilateral SMA for orthographic, phonological, and lexico-semantic processing. Interestingly, the cluster size gradually enlarged with increasing task demands. The SMA is involved in articulatory recoding and speech motor control (Hertrich et al., 2016; Price, 2012) but is also part of the attentional control network (Bonini et al., 2014). Here, we cannot disentangle whether children recruited the bilateral SMA for articulatory recoding to facilitate lexical decisions. Instead, it is also possible that we tapped into the attentional control network, reflecting enhanced action monitoring and error processing in the two-forced choice tasks. To better understand the interplay of the SMA with those regions classically associated with reading, a graph-based effective connectivity analysis could shed line on the time-course of SMA contribution (bottom-up or top-down) and how the connectivity pattern might be shaped by reading development and task-demands. In their meta-analysis, Martin et al. (2015) also identified a convergent bilateral SMA cluster in the studies examining reading in adults. Consequently, it might be worth integrating the SMA into (developmental) reading accounts (Pugh et al., 2000, 2013).

We observed significant and widespread activation in the right-hemispheric homologs of the reading streams. As already stated, this was confined to the ventral and frontal stream as activation in the dorsal stream was perfectly left-lateralized. In the last decades, more and more attention has been dedicated to the right hemisphere and its connectivity patterns when examining reading (Broce et al., 2019; Horowitz-Kraus et al., 2014, 2015) and language (Chen et al., 2021, for a recent computational modelling approach). The results of Study I support the assumption that reading (acquisition) is supported by right-hemispheric activation. The supplementary recruitment of right-hemispheric homologs might also depend on the specific task since we observed an increase in right-hemispheric activation with increasing task demands.

The insula is reliably associated with language and reading. More specifically, it is linked to silent articulation and phonology (Price, 2012). In line with these previous findings, the right insula was associated with orthographic, phonological, and lexico-semantic processing in Study I. Previous studies report that the neural response in the insula is negatively correlated with processing speed (Yeatman et al., 2010) and reading skill (Monzalvo & Dehaene-Lambertz, 2013). Since we did not observe any interindividual differences in neural activity (depending on age or general reading skill), we cannot answer the question, whether there is an age- or skill-related decrease in the recruitment of the insula (Monzalvo & Dehaene-Lambertz, 2013; Yeatman et al., 2010).

Like the insula, the ACC is linked to various tasks and functions (Vassena et al., 2020). We identified enhanced neural responses in the bilateral ACC for orthographic and phonological processing. Already in 2013, Pugh et al. expanded their neurodevelopmental account of reading by right-hemispheric and subcortical regions associated with visual processing and attention (e.g., bilateral ACC, right vOT, and right IPL). In Study I, ACC contribution was confined to orthographic and phonological decisions, which could be attributed to the generally increased demands on the attention network and cognitive control (Shenhav et al., 2013) required to solve these component tasks. On the other hand, the anterior zone of the ACC is also associated with response suppression, especially with increasing difficulty in lexico-semantic retrieval, for example in conflicting situations (Price, 2012; Schauenburg et al., 2021). Thus, the observed neural response in the bilateral ACC could also indicate that children had to suppress the production of the stimuli or had difficulties deciding.

Phonological processing was additionally associated with significant activation in the thalamus and hippocampus. Both the thalamus and the hippocampus have ample connections with cortical regions (Pessoa, 2018), are generally involved in learning from feedback, have been associated with the performance of sequential procedural tasks (Pavlidou & Bogaerts, 2019), and recently also familiarity (Braun et al., 2019). The phonological component task might have directly tapped into these functions: To decide whether a written word sounded like a word, children had to sequentially decode the written stimuli to identify their sound pattern and had to decide based on familiarity.

Finally, we observed that orthographic, phonological, and lexico-semantic processing elicited a response in the cerebellum in fluently reading children. Cerebellar contribution to reading, particularly in the right hemisphere, has been reported for adults (Ang et al., 2020; D’Mello et al., 2020). Likewise, functional connectivity of the cerebellum with the ventral and frontal reading streams (Alvarez & Fiez, 2018) and the fronto-parietal attention network (Li et al.,

2021) emphasize its contribution to successful reading. In their meta-analysis, Martin et al. (2015) report convergent cerebellar activation in adults but not children. These findings contrast to the results of Study I, where orthographic and phonological processing elicited a significant response in the cerebellum. Thus, the general question arises, whether the cerebellum was not found in previous studies examining reading in children or was simply not reported due to a strong focus on cortical regions.

However, the role of the cerebellum during reading development remains vague. Recently, it was shown that microstructural properties of the cerebellum, together with the bilateral superior longitudinal fasciculus, predict future reading. Adding the structural indices to the model improved prediction beyond demographic information and cognitive-linguistic preliterate skills (Borchers et al., 2019; Bruckert et al., 2019). The authors argue that the cerebellum could mediate implicit learning and feedback processes, which are necessary to fine-tune timing and automatization of reading. Likewise, lately, the functional role of the cerebellum was examined during the first stages of reading acquisition using a longitudinal design (Li et al., 2021). They report a developmental shift of the cerebellar reading network from the bilateral to the right hemisphere. The findings of Study I support the assumption that children rely on sensorimotor circuits during reading development, possibly to maintain the sound representations. To achieve this, the cerebellum is co-activated with auditory-based phonological processing in the dorsal stream.

In sum, the knowledge of the exact contribution of subcortical structures to language and reading development is still very limited. In my opinion, the recent approach to examine reading acquisition more openly and hence looking at this complex learning process from different angles is highly promising. With the use of multimethodological and integrative approaches, we might eventually capture the multifaceted reading phenomenon. After all, reading is not confined to high-level abstract linguistic processing and representation. Instead, the higher-level association cortices depend on lower-level input that might aid the fast and time-sensitive online processes required for fluent automatized reading.

Question 2. How is the processing of the basic subcomponents of single word recognition distributed among the principal reading streams in children?

In the core analysis of Study I, we tested the functioning of the three classical reading streams using the mask of the child-reading network (Martin et al., 2015). We examined whether the component processes of single word recognition elicit discernable response patterns in the core regions of reading.

The Posterior Reading Streams

Firstly, the observed joint activation of the ventral stream for all component processes is in line with Richlan (2012, 2014) who proposed that the vOT might play a key role in both serial grapheme-phoneme conversion and direct lexical reading. According to our hypothesis, and as already has been seen in adults, the anterior part of the ventral stream, i.e., the MTG, was additionally involved in phonological whole-word representation and semantic processing (Braun, Hutzler, et al., 2015; Braun, Jacobs, et al., 2015). With Study I, we can generalize this finding to fluently reading children. In sum, we observed joined responsiveness during pre-lexical, orthographic, phonological, and lexico-semantic processing in the posterior parts of the ventral stream that progressed along a posterior-to-anterior axis (Olulade et al., 2015; van der Mark et al., 2009).

Secondly, the results of Study I emphasize a diminished role of the indirect dorsal route after some years of reading experience, and this is true for all component processes of single word recognition. Meaning, the dorsal stream was exclusively linked to prelexical and phonological processing, and thus in situations in which careful serial letter-by-letter analysis is required. To sum up, children primarily rely on the ventral and frontal stream with more focal and functionally fine-tuned recruitment of the dorsal stream. Thus, our results are in line with the generic dual-route architecture for reading development (Grainger et al., 2012; Grainger & Ziegler, 2011) and also the grain size model (Ziegler & Goswami, 2005) according to which the initial predominance of phonological recoding in the dorsal stream is replaced by an increasing role of direct orthographic processing in the ventral stream. The developmental trajectory should be examined in future studies starting with the onset of reading acquisition marked by auditory-based reading strategies and then follow the same cohort of children during the formation of an orthographic lexicon. Such a longitudinal study could depict the exact time-course of the shift from the dorsal to the ventral stream.

Against our hypothesis, we did not see a strong involvement of the posterior STG as reported by Martin et al. (2015). Neither on the whole-brain level nor in the ROI analysis. Although null results need to be cautiously evaluated, this might still support the idea of the STG as an essential convergence zone (Karipidis et al., 2017, 2018; Richlan, 2019). Our paradigm was explicitly designed to disentangle and separate the component processes of visual word recognition. Consequently, they might have skipped the central role of the STG, i.e., multi-modal integration. However, this hypothesis needs further examination in order to disentangle task-related from developmental effects. More specifically, the same component processes of reading paradigm designed for Study I could be applied to younger, less-advanced readers. If the STG were linked to specific component processes in emergent readers, this would favor a more decisive role of the STG during the first steps of reading.

The Frontal Reading Stream

Against our hypothesis, the frontal stream was not exclusively activated by phonological (Braun, Hutzler, et al., 2015) and lexico-semantic processing (Binder et al., 2009). In contrast, all component processes elicited significant activation in the frontal stream, and this was true even though the within-scanner performance was considered to partial out differences in task demands. Cluster size and peak locations, however, differed among tasks. Prelexical processing was only linked to the PRG. Instead, the more complex component processes elicited activity in the PRG and different parts of the IFG. The IFG is thought to be involved in reading from early on (Church et al., 2008; Gaillard et al., 2003; Martin et al., 2015).

In favor of an early importance of the IFG, Johnson (2001, 2011) argues for an anterior-posterior gradient reflecting automatization during development. The framework predicts that posterior lower-level brain regions are sufficient to support automatized skills while more anterior higher-level regions are needed during development. On the other hand, neural response strength and selectivity in the IFG and PRG increases with age and reading skill (Bitan, Cheon, et al., 2007; Bitan et al., 2006; Koyama et al., 2011; Skeide & Friederici, 2016; Turkeltaub et al., 2003; Wang, Yamasaki, et al., 2021), which is in line with structural plasticity in the IFG observed in advanced reading stages of literate children (Phan et al., 2021). The same pattern has been observed for semantic analysis (Weiss-Croft & Baldeweg, 2015) and syntactic parsing (Enge et al., 2020). Together, these findings indicate an ongoing (linguistic) specialization in the IFG in children and young adolescences. Consequently, future reading development research should clarify the exact role and maturation of the different aspects of the frontal stream to disentangle its various contributions. For that, a finer parcellation of the frontal stream (Huth et al., 2016) might be helpful to separate domain-general learning guidance (Johnson, 2001, 2011) from core-linguistic processing (Binder et al., 2009; Price, 2012).

In line with the whole-brain results, orthographic, phonological, and lexico-semantic processing elicited activation in the bilateral SMA. Thus, we could further confirm the converging evidence that the bilateral SMA might be a pivotal part of reading acquisition (Houdé et al., 2010; Martin et al., 2015).

In general, we did not see any interindividual differences in the response patterns modulated by general reading proficiency. Thus, the neural underpinnings of the component processes of single word recognition might generally be established in nine to 13-year-old literate children. Reviewing the critical findings of Study I, I argue for an early interaction of the reading streams and integration of all sources of information to accomplish written word recognition. Already prelexical processing tended to activate several parts of the reading streams, and the response patterns of phonological, orthographic, and lexico-semantic processing were quite similar. These findings support the idea of an interactive network account of visual word recognition, as implemented in computational models such as the AROM (Hofmann et al., 2011). However, future research needs to disentangle possible developmental effects, for example, not-yet matured task-dependent response-selectivity (Johnson, 2001, 2011), from a critical processing principle (Hofmann & Jacobs, 2014).

Question 3. How are interindividual differences in preliterate subcortical and cortical processing mirrored in the cognitive-linguistic precursors of literacy?

To answer this research question, the findings of Study II and Study III need to be evaluated. In Study II, cortical processing was examined using the passive fMRI paradigm, testing vision and language systems. Subcortical language processing was measured by recording the speech-evoked auditory brainstem response in Study III. In both studies, the sensitivity of the preliterate neural response to interindividual differences in two of the cardinal cognitive-linguistic precursors of literacy was assessed.

Cortical Sensitivity

In Study II, we examined if (A) a passive listening and viewing task is sensitive to capture interindividual differences in the cognitive-linguistic preliterate skills and (B) whether these are located in the future reading streams. Against our hypothesis, we did not observe any systematic relationship between phonological awareness and neural response patterns. In contrast, RAN was associated with task-independent visual and auditory processing in brain regions that will later become experts for reading. Accordingly, we can generalize the brain-behavior association observed in the rare ample studies examining the neural underpinnings of the cognitive-linguistic preliterate skills (Benischek et al., 2020; Wang et al., 2020a; Wang, Pines, et al., 2021) to task-independent processing.

As hypothesized, we also observed interindividual differences in the ventral stream. RAN performance positively correlated with face encoding in the bilateral FuG. The results emphasize the peculiar connection between face processing and reading (Dehaene-Lambertz et al., 2018; Monzalvo et al., 2012). Here, we can extend this relationship to preliterate processing. I will come back to the still highly debated relationship between face encoding and reading when answering research question 4.

Interestingly, the developmental trajectories of linguistic and non-linguistic development went in opposite directions. Face processing in the ventral stream was positively associated with RAN. At the same time, a stronger neural response to visual and auditory stimuli correlated with poor behavioral outcomes. The neural response to written words in the STG and SMG captured these interindividual differences in RAN. The STG has previously been identified as an essential convergence zone (Richlan, 2019) that rapidly becomes sensitive to audio-visual integration during reading acquisition (Karipidis et al., 2017, 2018). The SMG is generally associated with phonological processing (Binder et al., 2009; Price, 2012). Thus, the observed print sensitivity of the STG and SMG to performance differences in RAN might mark a child's ability to set up a network that maps visual information onto phonology. However, all children were truly preliterate, having minimal letter knowledge, and were thus not able to decode the briefly presented written words. Whether the observed relationship means that children yet tried to activate grapheme-phoneme correspondences during visual word processing and that RAN taps into this processing circuit needs to be further examined in future studies. A possibility to disentangle the unique contribution of the regions to RAN (print-speech conversion versus phonological processing) might be to contrast a simple letter identification against a phonological task. The neural activity in the STG and SMG could then be used to train a model that subsequently predicts RAN performance in an independent sample. Here, higher feature importance of the SMG would favor a decisive role of phonological processing. Higher importance of the STG would emphasize that successful audio-visual integration facilitates RAN.

There are at least two possible explanations for the observed negative brain-behavior relationship for the linguistic stimuli. For auditory language processing, we found that neural processing in the dorsal stream (precuneus, SPL) and also the PRG is sensitive to inter-individual differences in RAN. As recently reported, the bilateral precuneus shows developmental decreases during phonological processing in prereaders compared to emergent readers (Yu et al., 2018). Thus, less effortful but instead automatized and stable spoken language processing facilitates phonology-based cognitive-linguistic preliterate skills (Chyl et al., 2018). Another possibility is that our passive viewing and listening task tapped into the TP attention network (Cabeza et al., 2012; Sestieri et al., 2017). Thus, children who had attentional difficulties keeping track of the rapidly presented auditory stimuli might also exhibit attentional and executive problems when asked to name serially presented objects. Since both guiding one's attention and phonological processing are pivotal parts of reading acquisition, either interpretation agrees with our hypothesis that preliterate response-selectivity in the dorsal stream forms a neural underpinning of successful RAN performance, which, in turn, is a powerful predictor of reading.

Also, the PRG has been identified as an essential convergence zone for visual and articulatory representations and prelexical recoding (Monzalvo et al., 2012; Price, 2012), again emphasizing that RAN might tap into one of the critical factors of reading acquisition: print-speech conversion. Interestingly, we also found a strong involvement of the PRG in the cohort of older, fluently reading children of Study I. Indeed, the PRG was involved in all four component processes of single word recognition. Thus, I believe that the role of the PRG should be further examined in future research as it might not simply be involved in prelexical processing (Price, 2012; Richlan, 2012, 2014) but might rather play a key role in reading development. More specifically, a network analysis could examine whether the PRG serves as a hub connecting the posterior streams with the frontal reading stream or whether the PRG might even serve as a seed region from which the frontal reading stream is established.

To sum up the results of Study II, we found the neural underpinnings of interindividual differences in RAN in the future reading streams – all three of them and exclusively there. These brain-behavior relationships were true for both visual and auditory, linguistic and non-linguistic processing. The impact is two-fold: Firstly, the association of RAN with critical print-speech convergence zones in the future dorsal and frontal streams sheds light on the underlying neurocognitive functioning of this strong predictor of reading. Secondly, these findings emphasize that the brain's 'reading readiness' in all three future reading streams differs before reading onset. These early differences in neural functioning possibly hamper successful reading acquisition in children at the lower end of the spectrum.

Subcortical Sensitivity

Next, I wanted to shed light on the question whether these interindividual differences already manifest at the level of the auditory brainstem. The results clearly emphasize that subcortical speech processing is sensitive to cognitive-linguistic precursors, in particular RAN. Consequently, if language processing is hampered at the earliest stages of auditory processing this results in poor preliterate skills. Thus, the results of my dissertation complement previous results from English-speaking children (Bonacina et al., 2019; Lam et al., 2017; White-Schwoch et al., 2015; White-Schwoch & Kraus, 2013) and generalize the brain-behavior relationship to German-speaking children. The brainstem response to complex speech sounds forms the basis of any further higher-level processing. Meaning that if fed with unstable and imprecise input, the TP language system has to operate on these degraded, fuzzy representations to accomplish phonological analysis and lexical access, which possibly impedes the development of auditory-based phonological abilities decisive for the cognitive-linguistic precursors of reading.

I believe that combining auditory brainstem recording and fMRI in a multimethodological approach using the same set of stimuli would be highly promising. The combination would allow us to examine the entire processing pipeline. A stable and precise subcortical response might be associated with less effortful processing in the TP language system. In contrast, hyperactivation in the language system possibly complemented by compensatory processing in auxiliary regions might result from unstable and imprecise subcortical input. Shedding light on the exact relationship might further facilitate our knowledge of phonological deficits in reading acquisition and extend treatment options.

To sum up, preliterate neural processing was reliably associated with the cognitive-linguistic precursors of reading, especially RAN. This brain-behavior correlation was true for different brain levels, linguistic and non-linguistic stimuli, visual and auditory domains and was observed in two independent cohorts of children. These findings impressively emphasize that the neural 'reading readiness' varies substantially between children, meaning that interindividual differences in the neural underpinnings of the precursors of reading manifest early. Which in turn, clearly sets children at different starting points when reading acquisition starts.

Question 4. Does the preliterate neural response predict future literacy?

With the longitudinal approach of Study II and Study III, we aimed to identify neural markers that might help to identify children at risk to encounter reading difficulties later on.

Cortical Predictors

The preliterate neural response to faces in the ventral stream predicted reading fluency two years later. In contrast, and against our hypothesis, neural sensitivity to written words did not predict future reading fluency, possibly indicating that sensitivity to written words has no special status due to the missing behavioral relevance in preliterate children (Golarai et al., 2015). Accordingly, we have to conclude that passive print processing in kindergarten children is insufficient to predict the future reading outcome based on the results of Study II. However, we observed a relationship between written words and RAN in the dorsal stream on the concurrent scale. Likewise, weak activation in response to print in the ventral stream and its right-hemispheric homologs in preliterate children has recently been reported (Chyl et al., 2018). However, as Chyl et al. (2018) did not explicitly test for the predictive power of the observed print-sensitive activation, the question as to whether the preliterate print-specific response in the ventral stream can serve as a neural marker of future reading development remains open to be tackled.

In contrast to previous studies (e.g., Yu et al., 2018) and against our hypothesis, auditory language processing was not systematically associated with future reading fluency. In Yu et al. (2018), however, children had to solve a first-sound matching task, and functional connectivity was examined. Also, we examined a cohort of German-speaking children while Yu et al.'s (2018) study was conducted with English-speaking children. Thus, the results cannot directly be compared. Nonetheless, the passive listening task might not have been challenging enough to trigger the critical interindividual differences.

Similarly, the rapid block design might have prevented in-depth phonological analysis due to the rapid shift from stimulus to stimulus. Nonetheless, we observed a brain-behavior relationship in the concurrent correlational analysis. Thus, the missing brain-behavior association might also be due to the non-linear and dynamic changes in neural response properties and fine-tuning during reading acquisition (Dehaene et al., 2010; Jacobs, 2018).

To the best of my knowledge, Study II is the first attempt to identify neural markers of future reading using a passive viewing and listening task. Thus, whether passive auditory and visual word processing might be a better marker for the cognitive-linguistic precursors of literacy rather than future reading outcome should be re-tested in an independent larger sample, comparing active and passive tasks. Likewise, the German transparent orthography allows children to move from grapheme-phoneme conversion to whole-word-based reading strategies quickly. Thus, replicating the study in less transparent orthographies could yield different results (Landerl et al., 2019; Richlan, 2014).

We did observe a reading-sensitive response to faces in the IOG reaching to the MTG that could clearly be seen as a preliterate neural marker for future reading acquisition. This finding extends previous evidence observed in older literate children with developmental dyslexia, who showed a reduced response to faces in the right FuG that correlated with general reading skills (Monzalvo et al., 2012). The theory that face and print recognition share the exact same cortical circuits (Dehaene & Cohen, 2007) has recently been questioned. Instead, reading might encroach on formerly weakly specialized neurons lateral to the FFA (Dehaene-Lambertz et al., 2018) or limb-selective neurons are recycled (Nordt et al., 2021). Although the exact mechanisms of the functional specialization during reading acquisition are still debated all of them generally favor some sort of neural recycling (Dehaene & Cohen, 2007).

However, the question remains why the neural response to faces in the ventral visual stream might be a reliable predictor of successful reading acquisition. Firstly, the vOT is strongly connected to the left-hemispheric spoken language system (Gomez et al., 2017; Saygin et al., 2016). Secondly, neurons of the vOT have high plasticity and fine-tune their response properties to behaviorally relevant stimuli (Golarai et al., 2015). These two factors are in favor of the observed brain-behavior relationship of preliterate face encoding and future literacy.

A decisive prerequisite to successfully crack the alphabetic code (Liberman et al., 1974) is to gain insights into the phonological structure of spoken words (Ziegler & Goswami, 2005). Consequently, facial speech movements might be of particular interest shortly before and during reading acquisition to discover phonemes (see Sekiyama & Burnham, 2008, for an increased McGurk effect in emergent readers). Face encoding is already well-established and highly reproducible by the age of five (Dehaene-Lambertz et al., 2018). The observed positive correlation between face processing in the FuG and RAN accompanied by the association between face-sensitive response in the vOT and future reading fluency might therefore reflect increased attention to articulation, which supports reading acquisition.

Either way, preliterate neural response to faces in the ventral stream might be a promising objective non-linguistic biological marker of future reading.

Subcortical Predictors

The auditory brainstem response to spoken language explained only limited variance in future literacy. Compared to the longitudinal prediction, the precision of the auditory brainstem showed a more robust relationship on the concurrent scale (see research question 3). In general, this pattern is not surprising the onset of reading marks a turning point in a child's development. Reading acquisition leads to substantial reorganization of large parts of the cognitive system in a highly dynamic and non-linear manner (Dehaene et al., 2010; Jacobs, 2018). Besides, the missing predictive power might also be because the auditory brainstem response is continuously shaped by top-down modulation. Thus, the response capacities possibly change too quickly, depending on the individual experience (Chandrasekaran et al., 2014; Skoe et al., 2013), to longitudinally capture developmental differences. In the only other longitudinal study (White-Schwoch et al., 2015), studying English-speaking children, the authors evaluated both concurrent and longitudinal relationships between various cognitive-linguistic measures, reading, and the neural encoding of speech. In general, their results show the same tendency as described above, i.e., a stronger association in the concurrent compared to the longitudinal analysis.

The results, however, need to be cautiously compared with Study III. White-Schwoch et al. (2015) presented the syllable train in noise. This experimental setup might better trigger nuanced interindividual differences in the subcortical response to complex speech sounds. Furthermore, the English and German orthographic systems differ substantially.

Among the three literacy skills examined, which were spelling, reading fluency, and comprehension, the subcortical neural response only had a significant impact on future spelling. This might be because spelling faithfully captures the initial stages of reading acquisition. In contrast, reading fluency and, in particular, the complex measure of reading comprehension beyond the single word level might instead capture later stages. In general, the strength of association between the subcortical response to speech and literacy might also depend on the underlying orthographic system and the resulting reading strategy. Grapheme-phoneme conversion being predominant during literacy acquisition in the opaque English orthography might be better captured by the subcortical response.

In contrast, it might be less directly connected to direct orthographic processing, rapidly acquired in transparent orthographies (Grainger et al., 2012; Grainger & Ziegler, 2011). This reasoning is also supported when looking at the stronger predictive power of the auditory brainstem response and spelling. The oral dictation might have forced children to apply a serial letter-by-letter strategy. Together with the concurrent brain-behavior analysis (research question 3), the overall result of my thesis emphasizes that the speech-evoked brainstem response is particularly suited to predict auditory- and phonologically-based processes and serial grapheme-phoneme conversion. Simultaneously, it questions the suitability of the auditory brainstem response to speech sounds as a potential objective marker of future reading acquisition. In contrast, various concurrent studies have shown that the auditory brainstem response is less reliable in poor compared to typical reading children (Chandrasekaran et al., 2009; Hornickel & Kraus, 2013) and is correlated with reading performance (Hornickel et al., 2011; Neef, Schaadt, et al., 2017). Thus, assessing subcortical speech processing might be more suitable for concurrent examinations. More specifically, it could be added as an objective and easy-to-achieve objective tool to literacy assessment.

5 General Summary

The Component Processes of Written Word Recognition – How Children Read

One aim of my dissertation was to disentangle the component processes of reading in children. The results support computational and neural IAMs (Grainger & Ziegler, 2011; Hofmann et al., 2011; Hofmann & Jacobs, 2014). The assumed interactive activation is particularly true for the ventral and frontal stream showing joint responsiveness in all component processes. The additional analysis of the whole-brain results in the scope of the present dissertation revealed that in fluently reading children, single word recognition is strongly supported by right-hemispheric and subcortical processing, emphasizing the importance of looking beyond the principal reading streams in order to understand reading acquisition thoroughly. Whether the observed pattern truly depicts the nature of reading or might partly be attributed to less specialized and thus less discernable brain functioning in development (Johnson, 2001, 2011) needs to be tackled in future, longitudinal studies.

More specifically, I would apply an adopted paradigm of the component processes of single word recognition to younger, emergent readers to depict the developmental trajectory of the observed diminished role of the dorsal stream. After all, it might even be on the cards that the assumed prominent role of the dorsal stream is partly an experimental artifact since many studies used rhyming judgments to examine reading in children (Martin et al., 2015). Hence a task that precisely targets auditory-bases phonological analysis. Also, the majority of evidence of older, more advanced reading children stems from the beginning of the century (Houdé et al., 2010; Martin et al., 2015). Since then, though, the standards in (pediatric) neuroimaging have considerably changed. Thus, replicating these previous results by applying today's standards might help separate false from true effects. Besides, the fundamental conceptual approach of the present dissertation is to account for universal tendencies in reading development. Although it is essential to get a general idea of how reading changes the neurofunctional architecture, future model building should also consider individual developmental trajectories. As recently shown, using subject-specific corpora enhances reading simulation in adults (Hofmann et al., 2020). Such an approach also bears the chance to improve our knowledge of reading acquisition in children, which is most certainly shaped by the individual experience depending, for example, on the environmental-demographic background.

Neurofunctional Prediction of Future Literacy – A Promising Approach?

Although there is an increasing effort to examine the neural perquisites of literacy, they are still poorly understood (Chyl et al., 2021). The results of Study II and Study III might thus serve as landmark but also preliminary findings that future research can build on. Crucially, face-sensitive response in the ventral stream from IOG to MTG predicted reading outcome two years later. In a nutshell, this finding argues for two things. Firstly, the results emphasize the importance of the vOT during the first steps of reading acquisition, and this sensitivity might emerge even earlier, namely at the end of kindergarten. Hence, at a time when children deepen their meta-linguistic knowledge and prepare their neural system to learn to read (Ziegler et al., 2010). Secondly, the non-linguistic, task-independent encoding of faces might be a promising objective marker. The results of Study II indicate that face-sensitive response might be more suitable than passive language processing (visual and auditory) to predict future reading. However, since longitudinal studies of reading acquisition are still scarce, this needs to be replicated to verify this tendency across different orthographies.

The predictive analysis in Study III yielded mixed results. It has been repeatedly shown that the subcortical response to spoken language is sensitive to detect differences in cognitive-linguistic preliterate skills and also differs depending on reading skill (Bonacina et al., 2019; Hornickel et al., 2011; Lam et al., 2017). In line with the one other longitudinal auditory brainstem study (White-Schwoch et al., 2015), the cumulative results of the present thesis thus favor to use the auditory brainstem response to complex speech sounds in a concurrent rather than longitudinal design. The observed stronger relationship with spelling than reading fluency and reading comprehension emphasizes that the integrity of the auditory brainstem response is best suited to examine interindividual differences in auditory-based grapheme-phoneme strategies.

Combining Neuroimaging and Computational Models

Although it is often demanded to test how neuroimaging can advance computational cognitive models of reading acquisition and vice versa (Hofmann & Jacobs, 2014; Price, 2018; Taylor et al., 2013), it is seldomly applied until today. The self-teaching connectionist model (Ziegler et al., 2014, 2020) reliably simulates reading profiles of children based on the individual cognitive-linguistic skills mapped onto different components of the model (Perry et al., 2019). However, to the best of my knowledge, the model was not yet tested using objective neural markers. This could, however, provide additional information about the neurobiological plausibility of the computational model and thus help to evaluate and maybe fine-tune individual model parameters (Hofmann & Jacobs, 2014).

Thus, I will use the following section to develop some ideas on how to combine the results of the present dissertation and computational modeling of reading acquisition (see *Figure 1* and *8* for a boxological overview of the model). More specifically, I present some hypotheses on how preliterate visual and auditory neural functioning could be used to simulate individual learning trajectories in the self-teaching connectionist framework.

The *Phoneme* module of the self-teaching connectionist model (Ziegler et al., 2014, 2020) stores the phonological representations of speech sounds. The auditory brainstem has the task of mimicking the incoming speech signal faithfully. In Study III, the neural precision of the brainstem response to complex speech sounds was captured by neural variability and fatigue, among others. Thus, these indices could be entered as a grading factor to the *Phoneme* module. Higher neural precision would indicate more specific phoneme presentations, while less stable neural response might result in fuzzy phoneme representations. In turn, these imprecise representations might cause less stable grapheme-phoneme mapping during learning resulting in a higher probability of phoneme switching.

Similarly, the BOLD signal in response to print in preliterate or emergent reading children could be used to manipulate processing efficiency and specificity grapheme-phoneme mapping. In Study II, we observed a negative relationship between the neural response to written words in the dorsal stream, which might not directly map onto the visual decoding of letters. Instead, the neural response in the ventral visual stream might be better suited to be incorporated in the self-teaching connectionist model. In Study II, the face-sensitive response in the ventral stream reliably predicted future reading fluency. Thus, it would be highly interesting to test if the neural response to faces also improves the computational simulation of reading acquisition. If the hypothesis is confirmed, this would further prove the idea of a particular relationship between face encoding and reading. For that, the BOLD signal could modulate the *Letter* module of the self-teaching connectionist model. More specifically, a stronger face-sensitive neural response would result in stable letter identification.

However, an active fMRI paradigm more precisely tapping into letter identification would be better suited to improve the computational simulation. For example, the neural specificity in the vOT for similar letters (e.g., /b/ versus /d/) captured using an RSA could be mapped onto the *Letter* module. Here, greater response-specificity and thus differentiation between letters would indicate more stable letter identification. In contrast, poor neural differentiation could result in a higher probability of switching similar letters during learning.

The functioning of the *Phonological Lexicon* could be graded using the BOLD signal to spoken words in the dorsal stream, as identified in Study II. However, a decreased BOLD signal representing automatized and stable passive language processing might not directly map onto the integrity of the *Phonological Lexicon*. Instead, measuring interindividual differences in neural response patterns in a lexical decision task using words, pseudowords, and pseudo-homophones might more specifically capture the status of the lexicon. In general, it would be conceivable that active paradigms are better suited to trigger interindividual differences and thus further improve computational modeling of reading. Using a demanding task would be, on the other side, at the expense of having an objective, task-independent feature entered into the model.

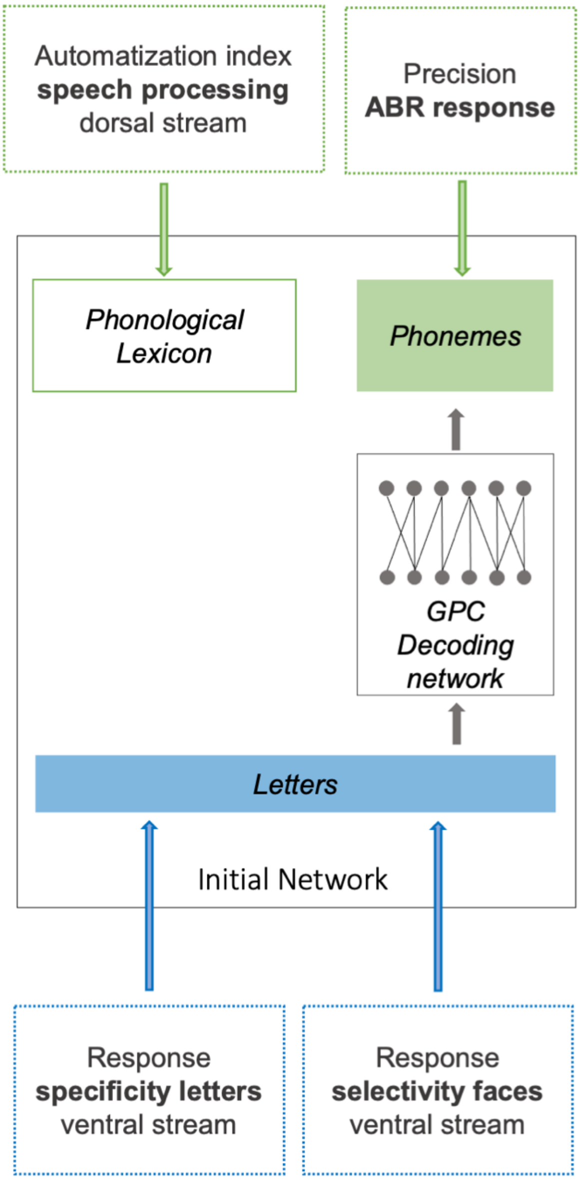


Figure 8. Preliterate Brain Responses added to the Connectionist Self-teaching Model.
The initial network of the model is depicted. During the first steps of reading acquisition, a small set of grapheme-phoneme correspondences (GPC) is explicitly taught. Dotted boxes above and below the module show hypotheses on how the neural integrity could be mapped as parameters onto the modules to create personalized models.

Automatization of speech processing could be taken as a measure of the size of the phonological lexicon. The stability of the auditory brainstem response (ABR) could determine the specificity of phoneme representations.
The neural response in the ventral stream could be mapped on the letter module. The preliterate neural delineation of similar letters or the strength of the face-selective response could be used to determine the probability of letter switching during learning. The individual brain responses would then be used to manipulate the initial network. To simulate an individual developmental trajectory, a full learning circle for each individual model is performed. In a longitudinal setting, the outcome of the simulation could then directly be compared with the child's reading skill (e.g., at the end of the 2nd grade of school).

6 Revised Neurodevelopmental Model of Reading Acquisition

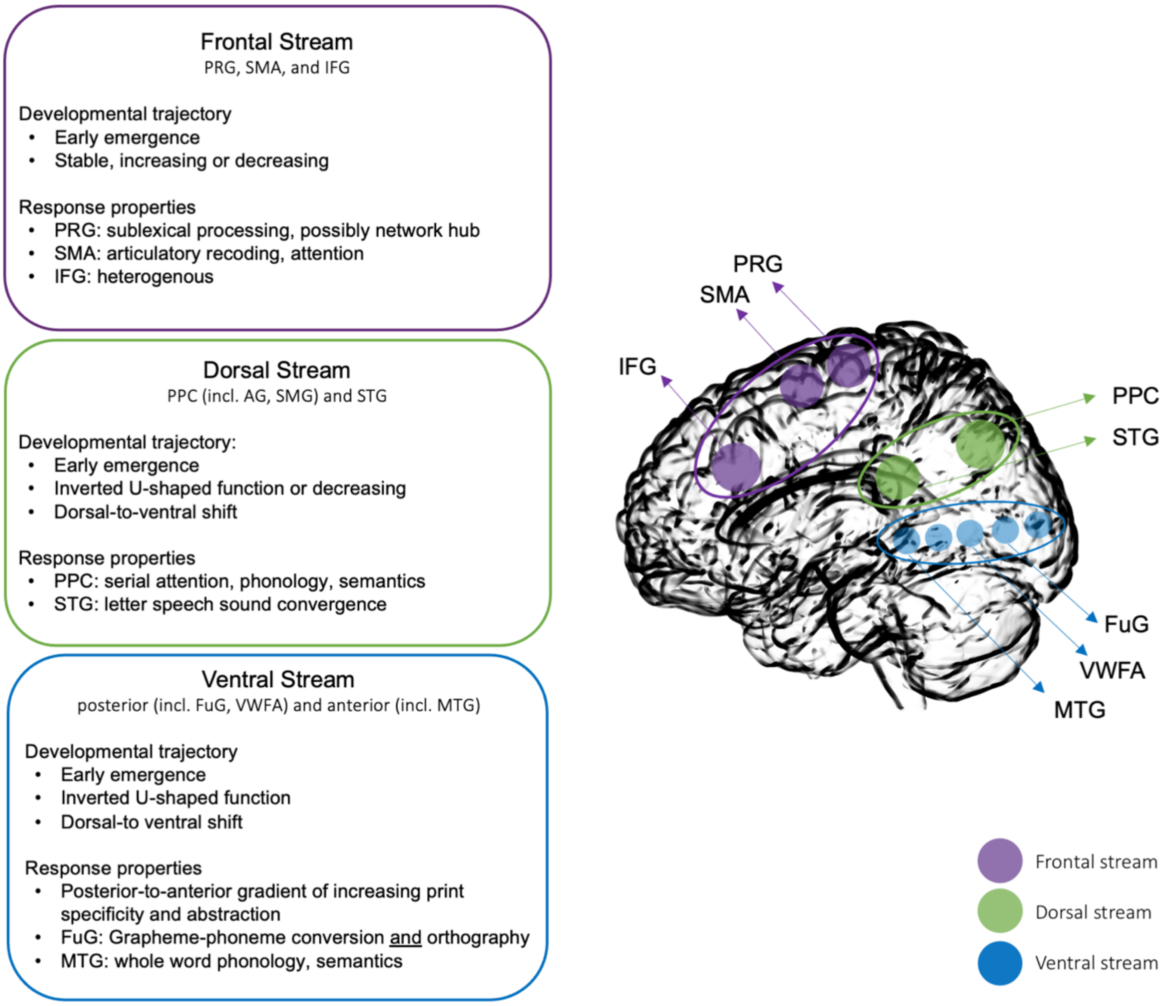
As far as I know, there are no recent attempts to update the developmental aspects of the classical neurodevelopmental model (Pugh et al., 2000) based on more recent findings. Even though some of its proposals have been challenged due to contradicting findings (Richlan, 2012; Richlan et al., 2011) derived from the cumulating evidence of (longitudinal) pediatric neuroimaging examining preliterate kindergarten, emergent or fluently reading children (Chyl et al., 2021). Likewise, the results of the empirical part of my dissertation contradict some of the key aspects of the classical model. Thus, I will use this chapter of my thesis to approach this open issue and propose a revised neurodevelopmental model of reading acquisition. The central brain regions and hypotheses about their maturation and functioning in reading children are summarized in *Figure 9.*

The Ventral Stream

The rapid emergence of the ventral stream, especially the VWFA, was recently confirmed by a longitudinal study in which the same children were scanned several times across the first year of school (Dehaene-Lambertz et al., 2018) - further complementing evidence that the ventral stream quickly becomes sensitive to print. Furthermore, this might even be true before the onset of reading acquisition (Brem et al., 2010; Karipidis et al., 2017, 2018; Lochy et al., 2016; Van de Walle de Ghelcke et al., 2020). The results of Study II queue up to this overall postulation: We observed that the face-sensitive response in the bilateral FuG is associated with interindividual differences in cognitive-linguistic preliterate skills. Even more critical, the neural function of the vOT at the end of kindergarten predicts future literacy. Thus, the first proposal of the revised neurodevelopmental model is the early importance of the ventral stream in reading acquisition. In line with the classical neurodevelopmental approach, the neural response in vOT is assumed to be shaped by reading skill, but this might already be true in six-year-olds (Ben-Shachar et al., 2011; Van de Walle de Ghelcke et al., 2020) or even in preliterate children (Study II). Finally, the interactive account of the vOT development (Price & Devlin, 2011) is incorporated in the revised model. Accordingly, an inverted U-shaped function of neural fine-tuning is assumed.

Based on several neuroimaging studies, I propose that the ventral stream might not exclusively be devoted to (prelexical) orthographic processing of letter strings but is also linked to grapheme-phoneme conversion (Cohen & Dehaene, 2004; Dehaene & Cohen, 2011; Price & Devlin, 2003; Richlan, 2019). The results of Study I support this hypothesis. In the cohort of fluently reading children, the ventral stream showed joined response to all component processes. Irrespective of whether the task required serial decoding, careful grapheme-phoneme conversion, or whole-word reading. Additionally, when tested in the cohort of fluently reading children of Study I, the preliterate reading-sensitive FuG ROI identified in Study II was associated with orthographic, phonological, and lexico-semantic processing. The additional analysis is described in the summary of Study II and the supplementary *(Study II: Preliterate Visual and Auditory Processing* and *Supplementary Material*).

Furthermore, the preliminary results of my thesis emphasize the assumed posterior-to-anterior gradient along the ventral stream. This gradient of increasing print-specificity and orthographic abstraction along the vOT has been repeatedly demonstrated in skilled adult readers (Taylor et al., 2019; Vinckier et al., 2007; Zhao et al., 2017). In contrast, only a few landmark studies in children indicate the same gradient of increasing print-specificity in fluently reading children (Olulade et al., 2015; van der Mark et al., 2009). In line with these pieces of evidence, we could rediscover a response pattern from lower-level orthographic analysis in the posterior vOT up to higher-level abstract linguistic information in the anterior vOT in the cohort of fluently reading children. While all component processes were implicated in the posterior parts of the vOT, phonological and lexico-semantic processing yielded additional peaks in the anterior vOT. Thus, the second thesis of the revised model is: In literate children, information is processed along a posterior-to-anterior axis in the vOT.



Frontal Stream

PRG, SMA, and IFG

Developmental trajectory
- Early emergence
- Stable, increasing or decreasing

Response properties
- PRG: sublexical processing, possibly network hub
- SMA: articulatory recoding, attention
- IFG: heterogenous

Dorsal Stream

PPC (incl. AG, SMG) and STG

Developmental trajectory:
- Early emergence
- Inverted U-shaped function or decreasing
- Dorsal-to-ventral shift

Response properties
- PPC: serial attention, phonology, semantics
- STG: letter speech sound convergence

Ventral Stream

posterior (incl. FuG, VWFA) and anterior (incl. MTG)

Developmental trajectory
- Early emergence
- Inverted U-shaped function
- Dorsal-to ventral shift

Response properties
- Posterior-to-anterior gradient of increasing print specificity and abstraction
- FuG: Grapheme-phoneme conversion <u>and</u> orthography
- MTG: whole word phonology, semantics

Figure 9. Revised Neurodevelopmental Model of Reading Acquisition. Hypotheses for the anatomical location, developmental trajectory, and response properties of the three principal reading streams are shown on the left. Right panel: schematic overview rendered on the whole-brain. Color coding: frontal stream = purple, dorsal stream = green, ventral stream = blue. PRG = precentral gyrus, SMA = supplementary motor area, IFG = inferior frontal gyrus, PPC = posterior parietal cortex, AG = angular gyrus, SMG = supramarginal gyrus, STG = superior temporal gyrus, FuG = fusiform gyrus, VWFA = visual word form area, MTG = middle temporal gyrus.

For adults, it has been shown that the gradient might end up at the level of the MTG devoted to whole-word phonology and semantic control (Braun, Hutzler, et al., 2015; Taylor et al., 2019; Zhao et al., 2017). The results of Study I indicate that this is also true for fluently reading children. However, the component tasks of single word recognition were not explicitly designed to test the neural specialization along the ventral stream. Likewise, the findings of Study I only depict the neural correlates of single-word reading at a relatively late stage of reading acquisition, i.e., after five to eight years of experience. The proposed hypotheses for a revised neurodevelopmental model thus need to be complemented by developmental accounts of the maturation of the discrete and specific response capacitates along the ventral stream. To examine the entire posterior-to-anterior axis up to the MTG, the experimental design established by Taylor et al. (2019) could be adapted. They simulated reading acquisition in young adults who learned artificial grapheme-phoneme correspondences to decode written words belonging to different artificial semantic categories. Using an RSA, they could delineate how the visual input is analyzed and transformed into abstract meaningful linguistic information in the vOT. Targeting the same paradigm in emergent and intermediate reading children would allow depicting the fine-tuning of response capacities along the entire vOT during reading acquisition.

The Dorsal Stream

In general, the PPC (subsuming the SMG and AG) is highly heterogeneous in function, cyto-architectonic structure, and connectivity (Scolari et al., 2015). Depending on the field of research, the PPC has either been associated with phonological and semantic operations in language and reading (Binder et al., 2009; Booth et al., 2002, 2007; Taylor et al., 2013) or attentional control mechanisms (Cabeza et al., 2012; Sestieri et al., 2017). Undoubtedly, reading and especially reading acquisition requires both – linguistic operations accompanied by domain-general attentional control mechanisms. Therefore, the exact contribution of the

PPC to reading might be highly task-dependent. However, for the revised neurodevelopmental model, I focus on those non-linguistic functions closely linked to reading acquisition, i.e., visual attention to control serial letter-by-letter encoding (Cabeza et al., 2012; Sestieri et al., 2017). The findings of Study I confirm the hypothesis that the PPC serves linguistic and non-linguistic aspects of reading: In the cohort of fluently reading children, the neural response in the IPL was linked to orthographic and phonological decisions, and semantic categorization, i.e., those tasks that required greater serial attention but also more sophisticated linguistic evaluation. In the more focal ROI analysis, dorsal activity was even confined to phonological processing. To make a correct decision in the phonological task, children had to ignore irrelevant spelling and focus on the phonological structure. In line with this, previous research has identified the PPC as sensitive to the conflict between phonological and orthographic information (Bitan, Burman, et al., 2007; Booth et al., 2002). On the other hand, the component task placed high demands on visuospatial processing as children had to serially shift their attention from letter to letter and retrieve the corresponding phoneme from memory (Cabeza et al., 2012; Sestieri et al., 2017).

As recently summarized by Chyl et al. (2021), the number of longitudinal studies examining the maturation of the dorsal stream during reading acquisition is still scarce. The few ample studies found activation in different portions of the PPC linked to reading and phonology (Łuniewska et al., 2019; Yu et al., 2018) but also report a growing involvement of the attention network with reading experience (Chen et al., 2019). Thus, they support the hypothesized two-fold role of the PPC for reading acquisition.

The same studies also indicate an inverted U-shaped development of the dorsal stream. Contrary to this assumption, we observed a negative correlation between the neural response in the dorsal stream and cognitive-linguistic preliterate skills in kindergarten children in Study II (see Chyl et al., 2018; Yu et al., 2018, for similar results). Future research needs to resolve this ambiguity by longitudinally examining reading acquisition trying to (A) neurofunctionally disentangle the multi-faceted functions of the dorsal stream and (B) depict the developmental trajectory of response strength (inverted U-shaped vs. decreasing).

To sum up: Derived from the preliminary evidence of the present dissertation and neuroimaging studies examining preliterate children and emergent readers, I propose that the function of the parietal part of the dorsal stream, defined as PPC (subsuming IPL, AG, SMG, and SPL), can cautiously be bisected. The core tasks during reading might be linguistic processes, particularly phonology and semantics, and non-linguistic serial attention.

My thesis yielded mixed results concerning the STG. In Study II, the STG response to written words showed a brain-behavior relationship with RAN. These results align with several longitudinal pediatric neuroimaging studies emphasizing the primary importance of the STG for reading development (Chen et al., 2019; Karipidis et al., 2017, 2018; Morken et al., 2017). Indeed, the STG is thought to be a critical audio-visual convergence zone, fostering automated letter-speech-sound integration. This integration is thought to be one of the key factors in the transition from slow serial to fast parallel reading strategies (Ziegler et al., 2014). In line, Martin et al. (2015) identified a convergent STG cluster for children but not for adults.

Contrary to the results of the meta-analysis, in Study I, none of the component processes was linked to enhanced activity in STG – neither when applying the child-reading mask (Martin et al., 2015) nor when testing what the preliterate reading-sensitive ROI identified in Study II possibly become an expert for in literate children. However, Martin et al. (2015) partly attribute the developmental differences to the biased experimental designs of the pediatric studies. While neural results for young adults were primarily derived from lexical decision tasks, reading in children was often tested using visual rhyming judgments. The results of Study I support this interpretation of a task-dependent engagement of the STG. As in fact, the component tasks of reading comprised lexical decisions rather than rhyming. Another possibility is that the STG is more important during the earliest steps of reading acquisition (Sandak et al., 2004; Turkeltaub et al., 2002) with a diminishing role as soon as automated letter-speech-sound integration is achieved. The latter interpretation, though, contradicts previous findings in adults (Richlan, 2019) that suggest an essential role of the STG in reading also later on. In skilled readers the STG is thought to automatically bind prelexical orthographic and phonological information (Richlan, 2019). However, those studies yielding significant STG contributions to reading in adults used highly peculiar paradigms. More specifically, congruency effects in letter-speech-sound integration comparing uni- and bimodal stimulation were examined (e.g., Van Atteveldt et al., 2010), which might be somewhat distant to natural reading circumstances.

In sum, the STG contribution to reading seems to be highly task-dependent, and the role of the STG might change throughout reading development. However, there is no doubt about its decisive role in the first steps of reading acquisition. The STG possibly forms the neural underpinning for automated letter-speech-sound integration and thus the emergence of a neurofunctional system of skilled reading. Consequently, the STG is incorporated in the revised neurodevelopmental model of reading.

In general, we observed a diminished role of the dorsal stream compared to the ventral and frontal stream when dissecting the component processes of single-word reading in fluently reading children (Study I). Thus, the often-assumed dorsal-to-ventral shift during reading development (Grainger et al., 2012; Grainger & Ziegler, 2011) is also incorporated in the revised neurodevelopmental account of reading.

The Frontal Stream

In line with the model proposed by Richlan (2012, 2014), the frontal stream is divided into the PRG and IFG in the revised developmental model proposed in the present dissertation. Martin et al. (2015) showed that the IFG is associated with reading in children in every single study examining various aspects of reading, such as single letter decoding, rhyming, semantic judgments, and sentence comprehension. Thus, the meta-analysis supports (A) the reliable finding of an early IFG engagement in reading (Church et al., 2008; Gaillard et al., 2003), and (B) that the IFG is involved in various components of reading as described in numerous reviews and meta-analyses (Binder et al., 2009; Price, 2012; Turkeltaub et al., 2002; Walenski et al., 2019).

Furthermore, the IFG is linked to cognitive control, behavioral monitoring, and top-down modulation from semantic to orthographic layers during reading (Hofmann & Jacobs, 2014). However, the maturation of the response capacities of the IFG has not been ultimately defined yet (Enge et al., 2020). In Study I, the IFG was strongly associated with orthographic, phonological, and lexico-semantic processing supporting the heterogenous role of the IFG. We could also replicate the previously reported increase in IFG activity with task demands (Bitan, Burman, et al., 2007; Bitan, Cheon, et al., 2007). In contrast, the BOLD signal did not yield any interindividual skill- or age-related modulation, indicating a stabilized role of the IFG in fluently reading children.

The results of Study I support the approach to separate the frontal stream into IFG and PRG (Richlan, 2012, 2014) and extend this approach to reading development. Contrary to Richlan (2014), the role of the PRG might not be confined to prelexical phonological analysis and articulatory recoding, but the PRG might be a pivotal part of each of the central component processes – and hence word reading in fluently reading children in general. In line with this assumption, the PRG has been associated with semantic and phonological language processing in children (Weiss-Croft & Baldeweg, 2015) and semantic retrieval and word selection in adults (Price, 2012). In favor of the early importance of the PRG in reading, the preliterate PRG response to spoken language was negatively correlated with RAN in Study II. The pre- and postcentral gyri have previously been identified as essential convergence zones for visual and articulatory representations (Monzalvo et al., 2012; Price, 2012). In line with this argumentation, the preliterate reading-sensitive PRG ROI (Study II) was associated with orthographic and phonological processing when testing its future specialization in an independent sample, i.e., the fluently reading children of Study I. The PRG might thus additionally serve as a critical network hub possibly mediating between posterior and frontal reading streams during reading acquisition.

In Study I, we observed joint activation in the bilateral SMA for all component processes except prelexical decoding. Likewise, the bilateral SMA has been convergently identified in the two large-scale meta-analyses of reading in children (Houdé et al., 2010; Martin et al., 2015) and adults (Martin et al., 2015; Price, 2012; Turkeltaub et al., 2002). Thus, I argue that the bilateral SMA should be incorporated in neurodevelopmental accounts of reading. Whether reading-related activation in the bilateral SMA is linked to articulatory recoding, planning, or inhibition (Hertrich et al., 2016; Price, 2012) or whether it mirrors attentional processes of the control network (Bonini et al., 2014) is still an open question.

In sum, I outlined several hypotheses about possible key regions of the principal reading streams, their functioning, and maturation during reading acquisition. Some of them could directly be derived from previous pediatric neuroimaging and the overall findings of my thesis; others are only based on preliminary pieces of evidence. For the latter, I proposed some ideas on how to test, refine, or completely discard these tentative hypotheses of the revised neurodevelopmental account of reading.

7 Limitations and Future Directions

Throughout the discussion, I already outlined some limitations of the results of the three empirical studies and the proposed revision of neurodevelopmental models of reading. Likewise, I suggested how future research could shed further light on the questions that remains open. Below, I additionally summarize the most important methodological limitations. In the last parts, I finalize my thesis with implications for education and therapy and outline central goals, I believe, future pediatric neuroimaging of reading should pursue.

Methodological Limitations

One of the major limitations of Study I is the block design that made it impossible to separate correct from incorrect trials and examine response differences depending on lexical status. Although we only included children with a sufficient number of correct trials (see Liebig et al., 2017, *2.1. Participants*), response patterns might have differed when only correct responses had been included. More importantly, an event-related (instead of a block) design would have allowed to specifically compare the BOLD signal to words, pseudowords, and pseudohomophones. These differential contrasts bear the chance to get a deeper insight into the functional specificity of the regions of the large-scale reading network and, thus, more detailed knowledge of fine-grained aspects on functional delineation within reading regions.

Likewise, there are methodological limitations in Study II that need to be tackled in future research. In the original design of the fMRI study, checkerboards were included as a visual baseline condition. Unfortunately, the fast-changing checkerboards were most certainly perceived as moving patterns as they elicited large-scale activation even beyond the ventral stream and thus had to be excluded from analysis (see Dehaene-Lambertz et al., 2018, for the same problem). Thus, visual stimuli were contrasted against the global null rather than a visual control task for the baseline contrasts. To keep the fMRI experiment as short as possible and thus feasible for the very young children, we did not include an auditory baseline task, but again the BOLD signal to spoken words was contrasted against the global null. From a theoretical perspective, we focused on the simple brain-behavior relationships to establish the groundwork. Thus, in the next step, I would like to test if face-encoding could improve prediction models of reading beyond environmental-demographic and cognitive-linguistic precursors.

One crucial limitation of Study III is that we measured a simple train of speech syllables in isolation. Future research should instead use speech-in-noise (White-Schwoch et al., 2015) or speech-weighted carrier noise (De Vos et al., 2020), which might elicit more significant inter-individual differences due to increased processing demands and simultaneously more closely resembles natural language processing. Furthermore, they report an increase in subcortical synchronization from the preliterate to the literate stage in children with developmental dyslexia. This finding suggests a comparatively late maturation of the subcortical response in children who will develop dyslexia. Thus, interindividual differences in the auditory brainstem response might be more prominent and thus diagnostically conclusive in children who encounter reading difficulties later on. Thus, it might be worth replicating Study III with a group-based approach.

Generally, future studies should examine all possible combinations, as developmental trajectories can differ between children with good and poor literacy skills and children with or without a family history of developmental dyslexia (Chyl et al., 2021; Ozernov-Palchik & Gaab, 2016). Thus, it is desirable to examine larger samples carefully balanced for different reading levels and proficiencies. This would allow to conduct both a continuous analysis and a group comparison.

Implications for Education and Therapy

In school, teaching methods quickly shift from learning to read to learning through reading. Thus, children who stick to slow and laborious reading strategies and possibly do not even access the meaning of what they have read are quickly left behind (Heine et al., 2012). These reading difficulties can result in a lack of motivation to further read and, thus, may lead to massive differences in reading experience between good and poor readers. Little practice, in turn, increases the gap in reading proficiency that is likely to persist until adulthood (Heine et al., 2012; Lüdtke et al., 2019; Schulte-Körne et al., 2003). Consequently, reading difficulties can have substantial consequences for the child's development, not only affecting academic achievements (Bruck, 1987; but see Schulte-Körne et al., 2003, for contrary results) but also the social-emotional development (Carroll & Iles, 2006; Klassen et al., 2013). In 2000 the first Programme for International Student Assessment (PISA; OECD, 2006) documented for Germany that almost 25 % of the 15-year-old pupils have insufficient reading competence, meaning that they only acquired the most basic reading skills. Even in the latest PISA test, the reading competence of children attending school in Germany ranks minimally above the mean of the members of the Organization for Economic Co-operation and Development (OECD, 2021). Likewise, approximately 12 % or 6.2 million adults who attended school in Germany are considered functionally illiterate, meaning their social participation is reduced or limited (Grotlüschen et al., 2020; Rüsseler et al., 2019). Most importantly, these numbers do not specifically consider developmental dyslexia, which has a prevalence of approximately 4-5 % within the German population (Moll, Kunze, et al., 2014).

Thus, early diagnosis of impending reading difficulties and early targeted intervention preventing or lessening the impact of reading difficulties is urgently required. Currently, developmental dyslexia is typically diagnosed at the end of grade two, and thus intervention only starts after years of reading failure (Heine et al., 2012; Ozernov-Palchik & Gaab, 2016). The late onset of treatment is despite today's knowledge that cognitive-linguistic precursors

(Caravolas et al., 2012; Landerl et al., 2013, 2019; Moll, Ramus, et al., 2014), neural structure, and function differ between children at preliterate age (Chyl et al., 2021) and that early intervention maximizes the therapeutic outcome (Wanzek et al., 2018). The claim for an early onset of reading therapy was recently endorsed by a structural neuroimaging study showing a grey matter volume increase in decisive regions of the ventral and dorsal reading network during the earliest phases of reading acquisition, i.e., within the first two years of primary school. This phase of high plasticity is followed by a stabilization of grey matter volume in more advanced readers (end of second to fifth grade; Phan et al., 2021). The observed plasticity in the posterior reading streams thus provides a biological explanation, why preventive or early interventions are more effective (Wanzek et al., 2018).

In line with this, the findings of the present thesis clearly favor an earlier onset of preventive support and treatment. Firstly, I found clear evidence that children show substantial differences in their preliterate subcortical and cortical responses related to decisive cognitive-linguistic precursors of reading. Secondly, differences in the integrity of the neural response predicted future literacy. On the cortical level, these functional differences occurred in exactly those regions identified by Phan et al. (2021) in their structural analysis, i.e., in the future dorsal and ventral reading stream.

However, the role of neuroimaging should not stop as soon as early preventive intervention is established. In contrast, it should also be used to test the effectiveness of the intervention. Examining the neural correlates of treatment would help understand whether the reading intervention directly affects the core regions of the future reading network or rather strengthens complementary domain-general mechanisms, which then indirectly support reading and thus lead to a better outcome. For example, one could test whether a RAN or letter identification training targets decisive reading-related regions like the STG or FuG (Brem et al., 2010; Karipidis et al., 2017, 2018) or rather affects the TP attention network (Cabeza et al., 2012; Sestieri et al., 2017).

For the subcortical level, it has already been suggested that music training facilitates speech perception in noise (e.g., Kraus et al., 2014) and also the neural representation of speech syllables in the auditory brainstem in children at risk to develop dyslexia (Kraus et al., 2014; Kraus & Chandrasekaran, 2010). There is also a growing body of studies examining intervention-induced changes in cortical structure (e.g., Krafnick et al., 2011; Partanen et al., 2021) and function (see Barquero et al., 2014, for a meta-analysis) in reading children.

To the best of my knowledge, a similar approach is absent for intervention programs developed to improve cognitive-linguistic preliterate skills (e.g., Kelly et al., 2019; Vander Stappen & Reybroeck, 2018; examples of behavioral trainings). The missing systematic evaluation contradicts our knowledge of (A) the relevance and predictive power of the cognitive-linguistic precursors has repeatedly and reliably been shown (Landerl et al., 2013, 2019), and that (B) learning-induced changes in the neural response occur quickly. For example, learning-induced changes in the neural response pattern already manifest after a short grapheme-phoneme or artificial letter training (Brem et al., 2010; Karipidis et al., 2017, 2018). The latter shows that behavioral changes are also mirrored in neural plasticity, which is true on a relatively short time scale.

In sum, within my dissertational work, I argue for two changes in the remediation of reading difficulties: Firstly, intervention needs to start before the onset of formal reading instruction to gain the maximal outcome. Secondly, it should become mandatory to not only systematically evaluate reading intervention programs regarding their behavioral outcome (Richardson & Lyytinen, 2014; Wißmann et al., 2013, as examples of empirically tested intervention programs) but also to keep records of the intervention-induced changes in neural structure and function.

Naturalistic Neuroimaging or '*Welcome to the Real World*'
(Hutzler et al., 2007, p.124)

This dissertation contributes to the growing field of pediatric neuroimaging of reading acquisition. The highest reading level examined in my thesis, and most of the developmental studies cited, though, is single word reading. Although single word decoding and recognition undoubtedly form the basis, reading rather starts than stops there. Whether we are reading for pleasure, education, or professional reasons, words are seldomly read in isolation. Skilled adult readers commonly read 250 words per minute (Dimigen et al., 2011) relying on a fast and dynamic orchestration of a plethora of distributed component processes. Natural reading requires the brain to update the incoming perceptual information and simultaneously integrate it into a mental model of comprehension (Kintsch & Van Dijk, 1978). For the single word level, we have a rough idea, which processes and regions are involved (Price, 2012). However, when it comes to natural reading, the neural network has not yet been adequately defined (Jacobs & Willems, 2018). Instead, neurocognitive research traditionally applies artificial, laboratory-contrived paradigms to study reading. While these short and straightforward paradigms are most certainly easier to control and test, the results do not generalize to the plethora of daily applications of reading (Jacobs, 2015a, 2015b; Kandylaki & Bornkessel-Schlesewsky, 2019) which range from fact-checking to modern literature and poetics (Schrott & Jacobs, 2011).

In the last decades, there have been repeated calls to move towards more ecologically valid designs (Jacobs, 2015a, 2015b) that reflect reading conditions more realistically to get a more accurate and complete picture of reading in the brain (Jacobs, 2015a, 2015b; Jacobs & Willems, 2018; Kandylaki & Bornkessel-Schlesewsky, 2019). Still, modifying the experimental setup to make it technically possible to study natural reading does not substitute valid research questions and hypotheses. By contrast, examining reading in less controllable, rich contexts requires specific hypotheses that link the various linguistic levels involved with the underlying neural activity. These hypotheses should be derived from modern statistical and computational approaches against which the neural correlates of naturalistic stimuli can be tested (Alday, 2019). To achieve this, there is an increasing need to integrate experts from different fields, such as neuroscientists, linguists, and possibly even literary theorists aided by computational engineering, mathematics, and physics. This will enable the development of sophisticated concepts on a number of theoretical and methodological issues (Kandylaki & Bornkessel-Schlesewsky, 2019; Kuiken & Jacobs, 2021).

Various lines of research have started to follow this approach and moved from single word to sentence or even text-level (Alday, 2019). Ecologically valid paradigms, however, are largely missing in the field of functional neuroimaging, with rare examples examining the neuro-functional correlates when reading sentences (Citron et al., 2019) or book passages (Hsu et al., 2019; Hsu, Jacobs, Altmann, et al., 2015; Hsu, Jacobs, & Conrad, 2015). This can partly be attributed to methodological caveats. For example, it is difficult to perfectly align the time-sensitive and quickly-evolving reading process with the sluggish BOLD signal. Recently, this issue was overcome by combining fMRI with eye movements (Schuster et al., 2020, 2021).
In general, eye movement studies are particularly suited to examine how reading evolves in natural settings (Fechino et al., 2020; Hawelka et al., 2015; Jacobs et al., 2019; Usée et al., 2020), since they specifically examine the interplay of top-down and bottom-up processes. The advantage is especially true when applied in multimethodological environments, such as with sophisticated machine learning tools (Xue et al., 2019, 2020) or neurophysiology (Dimigen et al., 2011; Weiss et al., 2016). With the latest development of child-friendly eye movement recording systems, examining the development of reading has also come in the focus of eye movement studies (Eilers et al., 2019; Tiffin-Richards & Schroeder, 2020).

With these recent methodological improvements in mind, I believe that pediatric neuroimaging should likewise move forward to natural reading paradigms. Indeed, when reading is taught at school, children progress from decoding single words to reading short sentences and paragraphs within the first year of elementary school, which means that children quickly shift from slow, laborious grapheme-phoneme conversion to whole-word-based reading strategies. Especially in transparent orthographies, this usually is the crucial moment in which children with and without reading difficulties diverge (Heine et al., 2012). In my opinion, this transition from single words to sentences and entire texts needs to be closely monitored by neuroimaging to fully characterize the neural underpinnings. This would shed more and much-needed light on the interindividual trajectories leading to successful or impeded automatization of reading. To achieve this, I propose to combine fMRI and eye movements (see Himmelstoss et al., 2020, for a guideline) in longitudinal designs using ecologically valid stimuli. Such an approach would allow us to simultaneously study multiple perceptual and linguistic phenomena: How do visuomotor and linguistic processes interact on the neural level? How is this interplay shaped throughout reading development? Which neural signature characterizes the shift from phonological recoding to orthographic reading? What can go wrong during this process, possibly leading to dysfluency? Approaching these questions would deepen our understanding of the automatization of reading during acquisition and bridge the gap between developmental and educational applications.

8 Bibliography

Alday, P. M. (2019). M/EEG analysis of naturalistic stories: A review from speech to language processing. *Language, Cognition and Neuroscience*, *34*(4), 457–473. https://doi.org/10.1080/23273798.2018.1546882

Alvarez, T. A., & Fiez, J. A. (2018). Current perspectives on the cerebellum and reading development. *Neuroscience & Biobehavioral Reviews*, *92*, 55–66. https://doi.org/10.1016/j.neubiorev.2018.05.006

Ang, C., Zhang, J., Chu, M., Li, H., Tian, M., Feng, X., Zhang, M., Liu, L., Meng, X., & Ding, G. (2020). Intrinsic cerebro-cerebellar functional connectivity reveals the function of cerebellum VI in reading-related skills. *Frontiers in Psychology*, *11*, 420. https://doi.org/10.3389/fpsyg.2020.00420

Aryani, A., Hsu, C.-T., & Jacobs, A. M. (2018). The Sound of Words Evokes Affective Brain Responses. *Brain Sciences*, *8*(6), 94. https://doi.org/10.3390/brainsci8060094

Bach, S., Brandeis, D., Hofstetter, C., Martin, E., Richardson, U., & Brem, S. (2010). Early emergence of deviant frontal fMRI activity for phonological processes in poor beginning readers. *NeuroImage*, *53*(2), 682–693. https://doi.org/10.1016/j.neuroimage.2010.06.039

Bach, S., Richardson, U., Brandeis, D., Martin, E., & Brem, S. (2013). Print-specific multimodal brain activation in kindergarten improves prediction of reading skills in second grade. *Neuroimage*, *82*, 605–615. http://dx.doi.org/10.1016/j.neuroimage.2013.05.062

Backes, W., Vuurman, E., Wennekes, R., Spronk, P., Wuisman, M., van Engelshoven, J., & Jolles, J. (2002). Atypical Brain Activation of Reading Processes in Children With Developmental Dyslexia. *Journal of Child Neurology*, *17*(12), 867–871. https://doi.org/10.1177/08830738020170121601

Barquero, L. A., Davis, N., & Cutting, L. E. (2014). Neuroimaging of Reading Intervention: A Systematic Review and Activation Likelihood Estimate Meta-Analysis. *PLOS ONE*, *9*(1), e83668. https://doi.org/10.1371/journal.pone.0083668

Beelen, C., Vanderauwera, J., Wouters, J., Vandermosten, M., & Ghesquière, P. (2019). Atypical gray matter in children with dyslexia before the onset of reading instruction. *Cortex*, *121*, 399–413. https://doi.org/10.1016/j.cortex.2019.09.010

Benischek, A., Long, X., Rohr, C. S., Bray, S., Dewey, D., & Lebel, C. (2020). Pre-reading language abilities and the brain’s functional reading network in young children. *NeuroImage*, *217*, 116903. https://doi.org/10.1016/j.neuroimage.2020.116903

Ben-Shachar, M., Dougherty, R. F., Deutsch, G. K., & Wandell, B. A. (2011). The Development of Cortical Sensitivity to Visual Word Forms. *Journal of Cognitive Neuroscience*, *23*(9), 2387–2399. https://doi.org/10.1162/jocn.2011.21615

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. *Cerebral Cortex*, *19*(12), 2767–2796. https://doi.org/10.1093/cercor/bhp055

Bitan, T., Burman, D. D., Chou, T.-L., Lu, D., Cone, N. E., Cao, F., Bigio, J. D., & Booth, J. R. (2007). The interaction between orthographic and phonological information in children: An fMRI study. *Human Brain Mapping*, *28*(9), 880–891. https://doi.org/10.1002/hbm.20313

Bitan, T., Burman, D. D., Lu, D., Cone, N. E., Gitelman, D. R., Mesulam, M.-M., & Booth, J. R. (2006). Weaker top-down modulation from the left inferior frontal gyrus in children. *NeuroImage*, *33*(3), 991–998. https://doi.org/10.1016/j.neuroimage.2006.07.007

Bitan, T., Cheon, J., Lu, D., Burman, D. D., Gitelman, D. R., Mesulam, M.-M., & Booth, J. R. (2007). Developmental changes in activation and effective connectivity in phonological processing. *NeuroImage*, *38*(3), 564–575. https://doi.org/10.1016/j.neuroimage.2007.07.048

Boets, B., De Smedt, B., Cleuren, L., Vandewalle, E., Wouters, J., & Ghesquière, P. (2010). Towards a further characterization of phonological and literacy problems in Dutch-speaking children with dyslexia. *British Journal of Developmental Psychology*, *28*(1), 5–31. https://doi.org/10.1348/026151010X485223

Bonacina, S., Otto-Meyer, S., Krizman, J., White-Schwoch, T., Nicol, T., & Kraus, N. (2019). Stable auditory processing underlies phonological awareness in typically developing preschoolers. *Brain and Language*, *197*, 104664. https://doi.org/10.1016/j.bandl.2019.104664

Bonini, F., Burle, B., Liegeois-Chauvel, C., Regis, J., Chauvel, P., & Vidal, F. (2014). Action Monitoring and Medial Frontal Cortex: Leading Role of Supplementary Motor Area. *Science*, *343*(6173), 888–891. https://doi.org/10.1126/science.1247412

Booth, J. R., Burman, D. D., Meyer, J. R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2002). Functional Anatomy of Intra- and Cross-Modal Lexical Tasks. *NeuroImage*, *16*(1), 7–22. https://doi.org/10.1006/nimg.2002.1081

Booth, J. R., Cho, S., Burman, D. D., & Bitan, T. (2007). Neural correlates of mapping from phonology to orthography in children performing an auditory spelling task. *Developmental Science*, *10*(4), 441–451. https://doi.org/10.1111/j.1467-7687.2007.00598.x

Borchers, L. R., Bruckert, L., Dodson, C. K., Travis, K. E., Marchman, V. A., Ben-Shachar, M., & Feldman, H. M. (2019). Microstructural properties of white matter pathways in relation to subsequent reading abilities in children: A longitudinal analysis. *Brain Structure and Function*, *224*(2), 891–905. https://doi.org/10.1007/s00429-018-1813-z

Boros, M., Anton, J.-L., Pech-Georgel, C., Grainger, J., Szwed, M., & Ziegler, J. C. (2016). Orthographic processing deficits in developmental dyslexia: Beyond the ventral visual stream. *NeuroImage*, *128*, 316–327. https://doi.org/10.1016/j.neuroimage.2016.01.014

Braun, M., Hutzler, F., Münte, T. F., Rotte, M., Dambacher, M., Richlan, F., & Jacobs, A. M. (2015). The neural bases of the pseudohomophone effect: Phonological constraints on lexico-semantic access in reading. *Neuroscience*, *295*, 151–163. https://doi.org/10.1016/j.neuroscience.2015.03.035

Braun, M., Hutzler, F., Ziegler, J. C., Dambacher, M., & Jacobs, A. M. (2009). Pseudohomophone effects provide evidence of early lexico-phonological processing in visual word recognition. *Human Brain Mapping*, *30*(7), 1977–1989. https://doi.org/10.1002/hbm.20643

Braun, M., Jacobs, A. M., Richlan, F., Hawelka, S., Hutzler, F., & Kronbichler, M. (2015). Many neighbors are not silent. FMRI evidence for global lexical activity in visual word recognition. *Frontiers in Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00423

Braun, M., Kronbichler, M., Richlan, F., Hawelka, S., Hutzler, F., & Jacobs, A. M. (2019). A model-guided dissociation between subcortical and cortical contributions to word recognition. *Scientific Reports*, *9*(1), 1–12. https://doi.org/10.1038/s41598-019-41011-9

Brem, S., Bach, S., Kucian, K., Kujala, J. V., Guttorm, T. K., Martin, E., Lyytinen, H., Brandeis, D., & Richardson, U. (2010). Brain sensitivity to print emerges when children learn letter–speech sound correspondences. *Proceedings of the National Academy of Sciences*, *107*(17), 7939–7944. https://doi.org/10.1073/pnas.0904402107

Brem, S., Maurer, U., Kronbichler, M., Schurz, M., Richlan, F., Blau, V., Reithler, J., van der Mark, S., Schulz, E., & Bucher, K. (2020). Visual word form processing deficits driven by severity of reading impairments in children with developmental dyslexia. *Scientific Reports*, *10*(1), 1–14. https://doi.org/10.1038/s41598-020-75111-8

Briesemeister, B. B., Hofmann, M. J., Tamm, S., Kuchinke, L., Braun, M., & Jacobs, A. M. (2009). The pseudohomophone effect: Evidence for an orthography–phonology-conflict. *Neuroscience Letters*, *455*(2), 124–128. https://doi.org/10.1016/j.neulet.2009.03.010

Briggs, R. G., Chakraborty, A. R., Anderson, C. D., Abraham, C. J., Palejwala, A. H., Conner, A. K., Pelargos, P. E., O'Donoghue, D. L., Glenn, C. A., & Sughrue, M. E. (2019). Anatomy and white matter connections of the inferior frontal gyrus. *Clinical Anatomy*, *32*(4), 546–556. https://doi.org/10.1002/ca.23349

Broce, I. J., Bernal, B., Altman, N., Bradley, C., Baez, N., Cabrera, L., Hernandez, G., De Feria, A., & Dick, A. S. (2019). Fiber pathways supporting early literacy development in 5–8-year-old children. *Brain and Cognition*, *134*, 80–89. https://doi.org/10.1016/j.bandc.2018.12.004

Bruck, M. (1987). The adult outcomes of children with learning disabilities. *Annals of Dyslexia*, *37*(1), 252–263. https://doi.org/10.1007/BF02648071

Bruckert, L., Borchers, L. R., Dodson, C. K., Marchman, V. A., Travis, K. E., Ben-Shachar, M., & Feldman, H. M. (2019). White Matter Plasticity in Reading-Related Pathways Differs in Children Born Preterm and at Term: A Longitudinal Analysis. *Frontiers in Human Neuroscience*, *0*. https://doi.org/10.3389/fnhum.2019.00139

Button, K. S., Ioannidis, J. P., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S., & Munafò, M. R. (2013). Power failure: Why small sample size undermines the reliability of neuroscience. *Nature Reviews Neuroscience*, *14*(5), 365–376.

Cabeza, R., Ciaramelli, E., & Moscovitch, M. (2012). Cognitive contributions of the ventral parietal cortex: An integrative theoretical account. *Trends in Cognitive Sciences*, *16*(6), 338–352. https://doi.org/10.1016/j.tics.2012.04.008

Caravolas, M., Lerv\aag, A., Mousikou, P., Efrim, C., Litavskỳ, M., Onochie-Quintanilla, E., Salas, N., Schöffelová, M., Defior, S., & Mikulajová, M. (2012). Common patterns of prediction of literacy development in different alphabetic orthographies. *Psychological Science*, *23*(6), 678–686. https://doi.org/10.1177%2F0956797611434536

Carroll, J. M., & Iles, J. E. (2006). An assessment of anxiety levels in dyslexic students in higher education. *British Journal of Educational Psychology*, *76*(3), 651–662. https://doi.org/10.1348/000709905X66233

Centanni, T. M., Booker, A. B., Chen, F., Sloan, A. M., Carraway, R. S., Rennaker, R. L., LoTurco, J. J., & Kilgard, M. P. (2016). Knockdown of dyslexia-gene Dcdc2 interferes with speech sound discrimination in continuous streams. *Journal of Neuroscience*, *36*(17), 4895–4906. https://doi.org/10.1523/JNEUROSCI.4202-15.2016

Centanni, T. M., Booker, A. B., Sloan, A. M., Chen, F., Maher, B. J., Carraway, R. S., Khodaparast, N., Rennaker, R., LoTurco, J. J., & Kilgard, M. P. (2014). Knockdown of the Dyslexia-Associated Gene Kiaa0319 Impairs Temporal Responses to Speech Stimuli in Rat Primary Auditory Cortex. *Cerebral Cortex*, *24*(7), 1753–1766. https://doi.org/10.1093/cercor/bht028

Centanni, T. M., Norton, E. S., Ozernov-Palchik, O., Park, A., Beach, S. D., Halverson, K., Gaab, N., & Gabrieli, J. D. (2019). Disrupted left fusiform response to print in beginning kindergartners is associated with subsequent reading. *NeuroImage: Clinical*, *22*, 101715. https://doi.org/10.1016/j.nicl.2019.101715

Centanni, T. M., Norton, E. S., Park, A., Beach, S. D., Halverson, K., Ozernov-Palchik, O., Gaab, N., & Gabrieli, J. D. (2018). Early development of letter specialization in left fusiform is associated with better word reading and smaller fusiform face area. *Developmental Science*, *21*(5), e12658. https://doi.org/10.1111/desc.12658

Centanni, T. M., Pantazis, D., Truong, D. T., Gruen, J. R., Gabrieli, J. D., & Hogan, T. P. (2018). Increased variability of stimulus-driven cortical responses is associated with genetic variability in children with and without dyslexia. *Developmental Cognitive Neuroscience*, *34*, 7–17. https://doi.org/10.1016/j.dcn.2018.05.008

Chandrasekaran, B., Hornickel, J., Skoe, E., Nicol, T., & Kraus, N. (2009). Context-dependent encoding in the human auditory brainstem relates to hearing speech in noise: Implications for developmental dyslexia. *Neuron*, *64*(3), 311–319. https://doi.org/10.1016/j.neuron.2009.10.006

Chandrasekaran, B., & Kraus, N. (2010). The scalp-recorded brainstem response to speech: Neural origins and plasticity. *Psychophysiology*, *47*(2), 236–246. https://doi.org/10.1111/j.1469-8986.2009.00928.x

Chandrasekaran, B., Skoe, E., & Kraus, N. (2014). An integrative model of subcortical auditory plasticity. *Brain Topography*, *27*(4), 539–552. https://doi.org/10.1007/s10548-013-0323-9

Chen, L., Wassermann, D., Abrams, D. A., Kochalka, J., Gallardo-Diez, G., & Menon, V. (2019). The visual word form area (VWFA) is part of both language and attention circuitry. *Nature Communications*, *10*(1), 1–12. https://doi.org/10.1038/s41467-019-13634-z

Chen, L., Wu, J., Hartwigsen, G., Li, Z., Wang, P., & Feng, L. (2021). The role of a critical left fronto-temporal network with its right-hemispheric homologue in syntactic learning based on word category information. *Journal of Neurolinguistics*, *58*, 100977. https://doi.org/10.1016/j.jneuroling.2020.100977

Chládková, K., & Paillereau, N. (2020). The What and When of Universal Perception: A Review of Early Speech Sound Acquisition. *Language Learning*, *70*(4), 1136–1182. https://doi.org/10.1111/lang.12422

Church, J. A., Coalson, R. S., Lugar, H. M., Petersen, S. E., & Schlaggar, B. L. (2008). A developmental fMRI study of reading and repetition reveals changes in phonological and visual mechanisms over age. *Cerebral Cortex*, *18*(9), 2054–2065. https://doi.org/10.1093/cercor/bhm228

Chyl, K., Fraga-González, G., Brem, S., & Jednoróg, K. (2021). Brain dynamics of (a)typical reading development—A review of longitudinal studies. *Npj Science of Learning*, *6*(1), 1–9. https://doi.org/10.1038/s41539-020-00081-5

Chyl, K., Kossowski, B., Dębska, A., \Luniewska, M., Banaszkiewicz, A., Żelechowska, A., Frost, S. J., Mencl, W. E., Wypych, M., & Marchewka, A. (2018). Prereader to beginning reader: Changes induced by reading acquisition in print and speech brain networks. *Journal of Child Psychology and Psychiatry*, *59*(1), 76–87. https://doi.org/10.1111/jcpp.12774

Citron, F. M., Cacciari, C., Funcke, J. M., Hsu, C.-T., & Jacobs, A. M. (2019). Idiomatic expressions evoke stronger emotional responses in the brain than literal sentences. *Neuropsychologia*, *131*, 233–248. https://doi.org/10.1016/j.neuropsychologia.2019.05.020

Cloutman, L. L. (2013). Interaction between dorsal and ventral processing streams: Where, when and how? *Brain and Language*, *127*(2), 251–263. https://doi.org/10.1016/j.bandl.2012.08.003

Cohen, L., & Dehaene, S. (2004). Specialization within the ventral stream: The case for the visual word form area. *Neuroimage*, *22*(1), 466–476. https://doi.org/10.1016/j.neuroimage.2003.12.049

Coltheart, M. (2006). Dual route and connectionist models of reading: An overview. *London Review of Education*, *4*(1), 5–17. https://doi.org/10.1080/13603110600574322

Coltheart, M., Curtis, B., Atkins, P., & Haller, M. (1993). Models of reading aloud: Dual-route and parallel-distributed-processing approaches. *Psychological Review*, *100*(4), 589. https://doi.org/10.1037/0033-295X.100.4.589

Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review*, *108*(1), 204. https://doi.org/10.1037//0033-295X.108.1.204

Corballis, M. C. (2017). Language Evolution: A Changing Perspective. *Trends in Cognitive Sciences*, *21*(4), 229–236. https://doi.org/10.1016/j.tics.2017.01.013

Cui, Z., Xia, Z., Su, M., Shu, H., & Gong, G. (2016). Disrupted white matter connectivity underlying developmental dyslexia: A machine learning approach: White Matter Disconnection in Dyslexia. *Human Brain Mapping*, *37*(4), 1443–1458. https://doi.org/10.1002/hbm.23112

De Vos, A., Vanvooren, S., Ghesquière, P., & Wouters, J. (2020). Subcortical auditory neural synchronization is deficient in pre-reading children who develop dyslexia. *Developmental Science*, *23*(6), e12945. https://doi.org/10.1111/desc.12945

Dębska, A., Chyl, K., Dzięgiel, G., Kacprzak, A., Łuniewska, M., Plewko, J., Marchewka, A., Grabowska, A., & Jednoróg, K. (2019). Reading and spelling skills are differentially related to phonological processing: Behavioral and fMRI study. *Developmental Cognitive Neuroscience*, *39*, 100683. https://doi.org/10.1016/j.dcn.2019.100683

Dębska, A., \Luniewska, M., Chyl, K., Banaszkiewicz, A., Żelechowska, A., Wypych, M., Marchewka, A., Pugh, K. R., & Jednoróg, K. (2016). Neural basis of phonological awareness in beginning readers with familial risk of dyslexia—Results from shallow orthography. *Neuroimage*, *132*, 406–416. http://dx.doi.org/10.1016/j.neuroimage.2016.02.063

Deen, B., Richardson, H., Dilks, D. D., Takahashi, A., Keil, B., Wald, L. L., Kanwisher, N., & Saxe, R. (2017). Organization of high-level visual cortex in human infants. *Nature Communications*, *8*(1), 13995. https://doi.org/10.1038/ncomms13995

Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, *56*(2), 384–398. https://doi.org/10.1016/j.neuron.2007.10.004

Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences*, *15*(6), 254–262. https://doi.org/10.1016/j.tics.2011.04.003

Dehaene, S., Cohen, L., Morais, J., & Kolinsky, R. (2015). Illiterate to literate: Behavioural and cerebral changes induced by reading acquisition. *Nature Reviews Neuroscience*, *16*(4), 234–244. https://doi.org/10.1038/nrn3924

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, *9*(7), 335–341. https://doi.org/10.1016/j.tics.2005.05.004

Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Nunes Filho, G., Jobert, A., Dehaene-Lambertz, G., Kolinsky, R., Morais, J., & Cohen, L. (2010). How learning to read changes the cortical networks for vision and language. *Science*, *330*(6009), 1359–1364. https://doi.org/10.1126/science.1194140

Dehaene-Lambertz, G., Monzalvo, K., & Dehaene, S. (2018). The emergence of the visual word form: Longitudinal evolution of category-specific ventral visual areas during reading acquisition. *PLOS Biology*, *16*(3), e2004103. https://doi.org/10.1371/journal.pbio.2004103

Dilnot, J., Hamilton, L., Maughan, B., & Snowling, M. J. (2017). Child and environmental risk factors predicting readiness for learning in children at high risk of dyslexia. *Development and Psychopathology*, *29*(1), 235–244. https://doi.org/10.1017/S0954579416000134

Dimigen, O., Sommer, W., Hohlfeld, A., Jacobs, A. M., & Kliegl, R. (2011). Coregistration of eye movements and EEG in natural reading: Analyses and review. *Journal of Experimental Psychology: General*, *140*(4), 552.

D'Mello, A. M., Centanni, T. M., Gabrieli, J. D., & Christodoulou, J. A. (2020). Cerebellar contributions to rapid semantic processing in reading. *Brain and Language*, *208*, 104828. https://doi.org/10.1016/j.bandl.2020.104828

Eilers, S., Tiffin-Richards, S. P., & Schroeder, S. (2019). Gender Cue Effects in Children's Pronoun Processing: A Longitudinal Eye Tracking Study. *Scientific Studies of Reading*, *23*(6), 509–522. https://doi.org/10.1080/10888438.2019.1617293

Elliott, E. A., Braun, M., Kuhlmann, M., & Jacobs, A. M. (2012). A dual-route cascaded model of reading by deaf adults: Evidence for grapheme to viseme conversion. *Journal of Deaf Studies and Deaf Education*, *17*(2), 227–243.

Enge, A., Friederici, A. D., & Skeide, M. A. (2020). A meta-analysis of fMRI studies of language comprehension in children. *NeuroImage*, 116858. https://doi.org/10.1016/j.neuroimage.2020.116858

Fechino, M., Jacobs, A. M., & Lüdtke, J. (2020). *Following in Jakobson and Lévi-Strauss' footsteps: A neurocognitive poetics investigation of eye movements during the reading of Baudelaire's 'Les Chats'*. https://doi.org/10.16910/JEMR.13.3.4

Forte, A. E., Etard, O., & Reichenbach, T. (2017). The human auditory brainstem response to running speech reveals a subcortical mechanism for selective attention. *ELife*, *6*, e27203. https://doi.org/10.7554/eLife.27203

Fridriksson, J., Yourganov, G., Bonilha, L., Basilakos, A., Ouden, D.-B. D., & Rorden, C. (2016). Revealing the dual streams of speech processing. *Proceedings of the National Academy of Sciences*, *113*(52), 15108–15113. https://doi.org/10.1073/pnas.1614038114

Friederici, A. D. (2011). The Brain Basis of Language Processing: From Structure to Function. *Physiological Reviews*, *91*(4), 1357–1392. https://doi.org/10.1152/physrev.00006.2011

Friedman, N. P., & Robbins, T. W. (2021). The role of prefrontal cortex in cognitive control and executive function. *Neuropsychopharmacology*, 1–18. https://doi.org/10.1016/j.neuroimage.2020.116858

Frith, U. (1986). A developmental framework for developmental dyslexia. *Annals of Dyslexia*, *36*(1), 67–81. https://doi.org/10.1007/BF02648022

Froehlich, E., Liebig, J., Morawetz, C., Ziegler, J. C., Braun, M., Heekeren, H. R., & Jacobs, A. M. (2018). Same same but different: Processing words in the aging brain. *Neuroscience*, *371*, 75–95. https://doi.org/10.1016/j.neuroscience.2017.11.042

Froehlich, E., Liebig, J., Ziegler, J. C., Braun, M., Lindenberger, U., Heekeren, H. R., & Jacobs, A. M. (2016). Drifting through basic subprocesses of reading: A hierarchical diffusion model analysis of age effects on visual word recognition. *Frontiers in Psychology*, *7*, 1863. https://doi.org/10.3389/fpsyg.2016.01863

Gaillard, W. D., Balsamo, L. M., Ibrahim, Z., Sachs, B. C., & Xu, B. (2003). FMRI identifies regional specialization of neural networks for reading in young children. *Neurology*, *60*(1), 94–100. https://doi.org/10.1212/WNL.60.1.94

Glezer, L. S., Jiang, X., & Riesenhuber, M. (2009). Evidence for Highly Selective Neuronal Tuning to Whole Words in the "Visual Word Form Area." *Neuron*, *62*(2), 199–204. https://doi.org/10.1016/j.neuron.2009.03.017

Gluth, S., & Rieskamp, J. (2017). Variability in behavior that cognitive models do not explain can be linked to neuroimaging data. *Journal of Mathematical Psychology*, *76*, 104–116. https://doi.org/10.1016/j.jmp.2016.04.012

Golarai, G., Liberman, A., & Grill-Spector, K. (2015). Experience shapes the development of neural substrates of face processing in human ventral temporal cortex. *Cerebral Cortex*, *27*(2), bhv314. https://doi.org/10.1093/cercor/bhv314

Gomez, J., Barnett, M. A., Natu, V., Mezer, A., Palomero-Gallagher, N., Weiner, K. S., Amunts, K., Zilles, K., & Grill-Spector, K. (2017). Microstructural proliferation in human cortex is coupled with the development of face processing. *Science*, *355*(6320), 68–71. https://doi.org/10.1126/science.aag0311.

Grainger, J., Dufau, S., & Ziegler, J. C. (2016). A Vision of Reading. *Trends in Cognitive Sciences*, *20*(3), 171–179. https://doi.org/10.1016/j.tics.2015.12.008

Grainger, J., & Jacobs, A. M. (1994). A dual read-out model of word context effects in letter perception: Further investigations of the word superiority effect. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(6), 1158. https://psycnet.apa.org/doi/10.1037/0096-1523.20.6.1158

Grainger, J., & Jacobs, A. M. (1996). Orthographic processing in visual word recognition: A multiple read-out model. *Psychological Review*, *103*(3), 518. https://doi.org/10.1037/0033-295X.103.3.518

Grainger, J., Lété, B., Bertand, D., Dufau, S., & Ziegler, J. C. (2012). Evidence for multiple routes in learning to read. *Cognition*, *123*(2), 280–292. https://doi.org/10.1016/j.cognition.2012.01.003

Grainger, J., & Ziegler, J. C. (2011). A Dual-Route Approach to Orthographic Processing. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00054

Grotlüschen, A., Buddeberg, K., Dutz, G., Heilmann, L., & Stammer, C. (2020). Hauptergebnisse und Einordnung zur LEO-Studie 2018–Leben mit geringer Literalität. *LEO 2018: Leben Mit Geringer Literalität*, 13.

Hämäläinen, J. A., Guttorm, T. K., Richardson, U., Alku, P., Lyytinen, H., & Leppänen, P. H. (2013). Auditory event-related potentials measured in kindergarten predict later reading problems at school age. *Developmental Neuropsychology*, *38*(8), 550–566. https://doi.org/10.1080/87565641.2012.718817

Harm, M. W., & Seidenberg, M. S. (1999). Phonology, reading acquisition, and dyslexia: Insights from connectionist models. *Psychological Review*, *106*(3), 491. https://psycnet.apa.org/doi/10.1037/0033-295X.106.3.491

Hawelka, S., Schuster, S., Gagl, B., & Hutzler, F. (2015). On forward inferences of fast and slow readers. An eye movement study. *Scientific Reports*, *5*(1), 1–8. https://doi.org/10.1038/srep08432

Heine, A., Engl, V., Thaler, V., Fussenegger, B., & Jacobs, A. M. (2012). *Neuropsychologie von Entwicklungsstörungen schulischer Fertigkeiten*. Hogrefe Verlag.

Hertrich, I., Dietrich, S., & Ackermann, H. (2016). The role of the supplementary motor area for speech and language processing. *Neuroscience & Biobehavioral Reviews*, *68*, 602–610. https://doi.org/10.1016/j.neubiorev.2016.06.030

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*(5), 393–402. https://doi.org/10.1038/nrn2113

Hickok, G., & Poeppel, D. (2016). Chapter 25—Neural Basis of Speech Perception. *Neurobiology of Language*, 299–310. https://doi.org/10.1016/B978-0-12-407794-2.00025-0

Himmelstoss, N. A., Schuster, S., Hutzler, F., Moran, R., & Hawelka, S. (2020). Co-registration of eye movements and neuroimaging for studying contextual predictions in natural reading. *Language, Cognition and Neuroscience*, *35*(5), 595–612. https://doi.org/10.1080/23273798.2019.1616102

Hoeft, F., Ueno, T., Reiss, A. L., Meyler, A., Whitfield-Gabrieli, S., Glover, G. H., Keller, T. A., Kobayashi, N., Mazaika, P., & Jo, B. (2007). Prediction of children's reading skills using behavioral, functional, and structural neuroimaging measures. *Behavioral Neuroscience*, *121*(3), 602.

Hofmann, M. J., & Jacobs, A. M. (2014). Interactive activation and competition models and semantic context: From behavioral to brain data. *Neuroscience & Biobehavioral Reviews*, *46*, 85–104. https://doi.org/10.1016/j.neubiorev.2014.06.011

Hofmann, M. J., Kuchinke, L., Biemann, C., Tamm, S., & Jacobs, A. M. (2011). Remembering Words in Context as Predicted by an Associative Read-Out Model. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00252

Hofmann, M. J., Müller, L., Rölke, A., Radach, R., & Biemann, C. (2020). Individual corpora predict fast memory retrieval during reading. *ArXiv Preprint.* arXiv:2010.10176

Hornickel, J., Chandrasekaran, B., Zecker, S., & Kraus, N. (2011). Auditory brainstem measures predict reading and speech-in-noise perception in school-aged children. *Behavioural Brain Research*, *216*(2), 597–605. https://dx.doi.org/10.1016%2Fj.bbr.2010.08.051

Hornickel, J., & Kraus, N. (2013). Unstable representation of sound: A biological marker of dyslexia. *Journal of Neuroscience*, *33*(8), 3500–3504. https://doi.org/10.1523/JNEUROSCI.4205-12.2013

Horowitz-Kraus, T., Grainger, M., DiFrancesco, M., Vannest, J., Holland, S. K., & CMIND Authorship Consortium. (2015). Right is not always wrong: DTI and fMRI evidence for the reliance of reading comprehension on language-comprehension networks in the right hemisphere. *Brain Imaging and Behavior*, *9*(1), 19–31. https://doi.org/10.1007/s11682-014-9341-9

Horowitz-Kraus, T., Wang, Y., Plante, E., & Holland, S. K. (2014). Involvement of the right hemisphere in reading comprehension: A DTI study. *Brain Research*, *1582*, 34–44. https://doi.org/10.1016/j.brainres.2014.05.034

Houdé, O., Rossi, S., Lubin, A., & Joliot, M. (2010). Mapping numerical processing, reading, and executive functions in the developing brain: An fMRI meta-analysis of 52 studies including 842 children: Meta-analysis of developmental fMRI data. *Developmental Science*, *13*(6), 876–885. https://doi.org/10.1111/j.1467-7687.2009.00938.x

Houston, S. M., Lebel, C., Katzir, T., Manis, F. R., Kan, E., Rodriguez, G. R., & Sowell, E. R. (2014). Reading skill and structural brain development. *Neuroreport*, *25*(5), 347. https://doi.org/10.1097/WNR.0000000000000121

Hsu, C.-T., Clariana, R., Schloss, B., & Li, P. (2019). Neurocognitive signatures of naturalistic reading of scientific texts: A fixation-related fMRI study. *Scientific Reports, 9*(1), 1–16. https://doi.org/10.1038/s41598-019-47176-7

Hsu, C.-T., Jacobs, A. M., Altmann, U., & Conrad, M. (2015). The magical activation of left amygdala when reading Harry Potter: An fMRI study on how descriptions of supra-natural events entertain and enchant. *PloS One*, *10*(2). https://doi.org/10.1371/journal.pone.0118179

Hsu, C.-T., Jacobs, A. M., & Conrad, M. (2015). Can Harry Potter still put a spell on us in a second language? An fMRI study on reading emotion-laden literature in late bilinguals. *Cortex*, *63*, 282–295. https://doi.org/10.1016/j.cortex.2014.09.002

Huth, A. G., de Heer, W. A., Griffiths, T. L., Theunissen, F. E., & Gallant, J. L. (2016). Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature*, *532*(7600), 453–458. https://doi.org/10.1038/nature17637

Hutzler, F., Braun, M., Võ, M. L.-H., Engl, V., Hofmann, M., Dambacher, M., Leder, H., & Jacobs, A. M. (2007). Welcome to the real world: Validating fixation-related brain potentials for ecologically valid settings. *Brain Research*, *1172*, 124–129. https://doi.org/10.1016/j.brainres.2007.07.025

Jacobs, A. M. (2015a). Towards a neurocognitive poetics model of literary reading. In R. M. Willems (Ed.), *Towards a cognitive neuroscience of natural language use* (pp. 135–159). Cambridge University Press.

Jacobs, A. M. (2015b). Neurocognitive poetics: Methods and models for investigating the neuronal and cognitive-affective bases of literature reception. *Frontiers in Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00186

Jacobs, A. M. (2018). (Neuro-) Cognitive poetics and computational stylistics. *Scientific Study of Literature*, *8*(1), 165–208. https://doi.org/10.1075/ssol.18002.jac

Jacobs, A. M., Hofmann, M. J., & Kinder, A. (2016). On Elementary Affective Decisions: To Like Or Not to Like, That Is the Question. *Frontiers in Psychology*, *7*, 1836. https://doi.org/10.3389/fpsyg.2016.01836

Jacobs, A. M., Lüdtke, J., Kaakinen, J., & Eekhof, L. S. (2019). Eye movements during the reading of narrative and poetic texts.: Symposium 6 at the 20th European Conference on Eye Movement Research (ECEM) in Alicante, 21.8.2019. *Journal of Eye Movement Research*, *12*(7), Article 7. https://doi.org/10.16910/jemr.12.7.9

Jacobs, A. M., Võ, M. L.-H., Briesemeister, B. B., Conrad, M., Hofmann, M. J., Kuchinke, L., Lüdtke, J., & Braun, M. (2015). 10 years of BAWLing into affective and aesthetic processes in reading: What are the echoes? *Frontiers in Psychology*, *6*, 714. http://dx.doi.org/10.3389/fpsyg.2015.00714

Jacobs, A. M., & Willems, R. M. (2018). The Fictive Brain: Neurocognitive Correlates of Engagement in Literature. *Review of General Psychology*, *22*(2), 147–160. https://doi.org/10.1037/gpr0000106

Jansen, H. (2002). *BISC: Bielefelder Screening zur Früherkennung von Lese-Rechtschreibschwierigkeiten*. Hogrefe, Verlag für Psychologie.

Jasińska, K. K., Shuai, L., Lau, A. N. L., Frost, S., Landi, N., & Pugh, K. R. (2021). Functional connectivity in the developing language network in 4-year-old children predicts future reading ability. *Developmental Science*, *24*(2), e13041. https://doi.org/10.1111/desc.13041

Johnson, M. (2001). Functional brain development in humans. *Nature Reviews Neuroscience*, *2*(7), 475–483. https://doi.org/10.1038/35081509

Johnson, M. (2011). Interactive Specialization: A Domain-General Framework for Human Functional Brain Development? *Developmental Cognitive Neuroscience*, *1*, 7–21. https://doi.org/10.1016/j.dcn.2010.07.003

Kaiser, D., Jacobs, A. M., & Cichy, R. M. (2021). Modelling brain representations of abstract concepts. *BioRxiv*. 2021.06.02.446744. https://doi.org/10.1101/2021.06.02.446744

Kandylaki, K. D., & Bornkessel-Schlesewsky, I. (2019). From story comprehension to the neurobiology of language. *Language, Cognition and Neuroscience*, *34*(4), 405–410. https://doi.org/10.1080/23273798.2019.1584679

Karipidis, I. I., Pleisch, G., Brandeis, D., Roth, A., Röthlisberger, M., Schneebeli, M., Walitza, S., & Brem, S. (2018). Simulating reading acquisition: The link between reading outcome and multimodal brain signatures of letter–speech sound learning in prereaders. *Scientific Reports*, *8*(1), 7121. https://doi.org/10.1038/s41598-018-24909-8

Karipidis, I. I., Pleisch, G., Röthlisberger, M., Hofstetter, C., Dornbierer, D., Stämpfli, P., & Brem, S. (2017). Neural initialization of audiovisual integration in prereaders at varying risk for developmental dyslexia: Audiovisual Integration in Prereaders. *Human Brain Mapping*, *38*(2), 1038–1055. https://doi.org/10.1002/hbm.23437

Kelly, C., Leitão, S., Smith-Lock, K., & Heritage, B. (2019). The effectiveness of a classroom-based phonological awareness program for 4–5-year-olds. *International Journal of Speech-Language Pathology*, *21*(1), 101–113. https://doi.org/10.1080/17549507.2017.1400589

Kintsch, W., & Van Dijk, T. A. (1978). Toward a model of text comprehension and production. *Psychological Review*, *85*(5), 363. https://psycnet.apa.org/doi/10.1037/0033-295X.85.5.363

Klassen, R. M., Tze, V. M. C., & Hannok, W. (2013). Internalizing Problems of Adults With Learning Disabilities: A Meta-Analysis. *Journal of Learning Disabilities*, *46*(4), 317–327. https://doi.org/10.1177/0022219411422260

Koelsch, S., Schulze, K., Sammler, D., Fritz, T., Müller, K., & Gruber, O. (2009). Functional architecture of verbal and tonal working memory: An FMRI study. *Human Brain Mapping*, *30*(3), 859–873. https://doi.org/10.1002/hbm.20550

Koyama, M. S., Di Martino, A., Zuo, X.-N., Kelly, C., Mennes, M., Jutagir, D. R., Castellanos, F. X., & Milham, M. P. (2011). Resting-State Functional Connectivity Indexes Reading Competence in Children and Adults. *Journal of Neuroscience*, *31*(23), 8617–8624. https://doi.org/10.1523/JNEUROSCI.4865-10.2011

Krafnick, A. J., Flowers, D. L., Napoliello, E. M., & Eden, G. F. (2011). Gray matter volume changes following reading intervention in dyslexic children. *NeuroImage*, *57*(3), 733–741. https://doi.org/10.1016/j.neuroimage.2010.10.062

Kraus, N., & Chandrasekaran, B. (2010). Music training for the development of auditory skills. *Nature Reviews Neuroscience*, *11*(8), 599–605. https://doi.org/10.1038/nrn2882

Kraus, N., Slater, J., Thompson, E. C., Hornickel, J., Strait, D. L., Nicol, T., & White-Schwoch, T. (2014). Music enrichment programs improve the neural encoding of speech in at-risk children. *Journal of Neuroscience*, *34*(36), 11913–11918. https://doi.org/10.1523/JNEUROSCI.1881-14.2014

Kronbichler, M., Bergmann, J., Hutzler, F., Staffen, W., Mair, A., Ladurner, G., & Wimmer, H. (2007). Taxi vs. Taksi: On Orthographic Word Recognition in the Left Ventral Occipitotemporal Cortex. *Journal of Cognitive Neuroscience*, *19*(10), 1584–1594. https://doi.org/10.1162/jocn.2007.19.10.1584

Kuhlmann, M., Hofmann, M. J., Briesemeister, B. B., & Jacobs, A. M. (2016). Mixing positive and negative valence: Affective-semantic integration of bivalent words. *Scientific Reports*, *6*(1), 30718. https://doi.org/10.1038/srep30718

Kuiken, D., & Jacobs, A. M. (Eds.). (2021). *Handbook of empirical literary studies* (1st ed.). De Gruyter.

Lam, S. S.-Y., White-Schwoch, T., Zecker, S. G., Hornickel, J., & Kraus, N. (2017). Neural stability: A reflection of automaticity in reading. *Neuropsychologia*, *103*, 162–167. https://doi.org/10.1016/j.neuropsychologia.2017.07.023

Landerl, K., Freudenthaler, H. H., Heene, M., De Jong, P. F., Desrochers, A., Manolitsis, G., Parrila, R., & Georgiou, G. K. (2019). Phonological awareness and rapid automatized naming as longitudinal predictors of reading in five alphabetic orthographies with varying degrees of consistency. *Scientific Studies of Reading*, *23*(3), 220–234.

Landerl, K., Ramus, F., Moll, K., Lyytinen, H., Leppänen, P. H. T., Lohvansuu, K., O'Donovan, M., Williams, J., Bartling, J., Bruder, J., Kunze, S., Neuhoff, N., Tóth, D., Honbolygó, F., Csépe, V., Bogliotti, C., Iannuzzi, S., Chaix, Y., Démonet, J.-F., … Schulte-Körne, G. (2013). Predictors of developmental dyslexia in European orthographies with varying complexity: Cross-linguistic predictors of dyslexia. *Journal of Child Psychology and Psychiatry*, *54*(6), 686–694. https://doi.org/10.1111/jcpp.12029

Lehmann, A., & Schönwiesner, M. (2014). Selective attention modulates human auditory brainstem responses: Relative contributions of frequency and spatial cues. *PloS One*, *9*(1), e85442. https://doi.org/10.1371/journal.pone.0085442

Lenhard, W., & Schneider, W. (2006). *Ein Leseverständnistest für Erst-und Sechstklässler: ELFE 1-6*. Hogrefe Göttingen.

Leppänen, Hämäläinen, J. A., Guttorm, T. K., Eklund, K. M., Salminen, H., Tanskanen, A., Torppa, M., Puolakanaho, A., Richardson, U., & Pennala, R. (2012). Infant brain responses associated with reading-related skills before school and at school age. *Neurophysiologie Clinique/Clinical Neurophysiology*, *42*(1–2), 35–41. https://doi.org/10.1016/j.neucli.2011.08.005

Li, H., Kepinska, O., Caballero, J., Zekelman, L., Marks, R., Uchikoshi, Y., Kovelman, I., & Hoeft, F. (2021). Decoding the role of the cerebellum in the early stages of reading acquisition. *Cortex*, *141*. https://doi.org/10.1016/j.cortex.2021.02.033

Liberman, I. Y., Shankweiler, D., Fischer, F. W., & Carter, B. (1974). Explicit syllable and phoneme segmentation in the young child. *Journal of Experimental Child Psychology*, *18*(2), 201–212. https://doi.org/10.1016/0022-0965(74)90101-5

Liebig, J., Friederici, A. D., Neef, N. E., Friederici, A. D., Emmrich, F., Brauer, J., Wilcke, A., Neef, N. E., Boltze, J., Skeide, M., Kirsten, H., Schaadt, G., Müller, B., Kraft, I., Czepezauer, I., & Dörr, L. (2020). Auditory brainstem measures and genotyping boost the prediction of literacy: A longitudinal study on early markers of dyslexia. *Developmental Cognitive Neuroscience*, *46*, 100869. https://doi.org/10.1016/j.dcn.2020.100869

Liebig, J., Friederici, A. D., & Neef, N. E. (2021). Erratum to "Auditory brainstem measures and genotyping boost the prediction of literacy: A longitudinal study on early markers of dyslexia" [Dev. Cognit. Neurosci. 46 (2020) 100869]. *Developmental Cognitive Neuroscience*, *48*, 100889. https://doi.org/10.1016/j.dcn.2020.100889

Liebig, J., Froehlich, E., Morawetz, C., Braun, M., Jacobs, A. M., Heekeren, H. R., & Ziegler, J. C. (2017). Neurofunctionally dissecting the reading system in children. *Developmental Cognitive Neuroscience*, *27*, 45–57. https://doi.org/10.1016/j.dcn.2017.07.002

Liebig, J., Froehlich, E., Sylvester, T., Braun, M., Heekeren, H. R., Ziegler, J. C., & Jacobs, A. M. (2021). Neural processing of vision and language in kindergarten is associated with prereading skills and predicts future literacy. *Human Brain Mapping*. https://doi.org/10.1002/hbm.25449

Liu, X., Gao, Y., Di, Q., Hu, J., Lu, C., Nan, Y., Booth, J. R., & Liu, L. (2018). Differences between child and adult large-scale functional brain networks for reading tasks. *Human Brain Mapping*, *39*(2), 662–679. https://doi.org/10.1002/hbm.23871

Lochy, A., Van Reybroeck, M., & Rossion, B. (2016). Left cortical specialization for visual letter strings predicts rudimentary knowledge of letter-sound association in preschoolers. *Proceedings of the National Academy of Sciences*, *113*(30), 8544–8549. http://datadryad.org/resource/doi:10.5061/dryad.v54jq

Lüdtke, J., Froehlich, E., Jacobs, A. M., & Hutzler, F. (2019). The SLS-Berlin: Validation of a German Computer-Based Screening Test to Measure Reading Proficiency in Early and Late Adulthood. *Frontiers in Psychology*, *10*, 1682. https://doi.org/10.3389/fpsyg.2019.01682

Łuniewska, M., Chyl, K., Dębska, A., Banaszkiewicz, A., Żelechowska, A., Marchewka, A., Grabowska, A., & Jednoróg, K. (2019). Children With Dyslexia and Familial Risk for Dyslexia Present Atypical Development of the Neuronal Phonological Network. *Frontiers in Neuroscience*, *0*. https://doi.org/10.3389/fnins.2019.01287

Lyytinen, H., Erskine, J., Hämäläinen, J., Torppa, M., & Ronimus, M. (2015). Dyslexia—early identification and prevention: Highlights from the Jyväskylä longitudinal study of dyslexia. *Current Developmental Disorders Reports*, *2*(4), 330–338. https://doi.org/10.1007/s40474-015-0067-1

Marks, R. A., Kovelman, I., Kepinska, O., Oliver, M., Xia, Z., Haft, S. L., Zekelman, L., Duong, P., Uchikoshi, Y., Hancock, R., & Hoeft, F. (2019). Spoken language proficiency predicts print-speech convergence in beginning readers. *NeuroImage*, *201*, 116021. https://doi.org/10.1016/j.neuroimage.2019.116021

Martin, A., Schurz, M., Kronbichler, M., & Richlan, F. (2015). Reading in the brain of children and adults: A meta-analysis of 40 functional magnetic resonance imaging studies: Reading in the Brain of Children and Adults. *Human Brain Mapping*, *36*(5), 1963–1981. https://doi.org/10.1002/hbm.22749

Mayringer, H., & Wimmer, H. (2008). *SLS 1-4: Salzburger Lese-Screening für die Klassenstufen 1-4*. Huber.

McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, *7*(7), 293–299. https://doi.org/10.1016/S1364-6613(03)00134-7

McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: I. An account of basic findings. *Psychological Review*, *88*(5), 375. https://psycnet.apa.org/doi/10.1037/0033-295X.88.5.375

Menon, V., & D'Esposito, M. (2021). The role of PFC networks in cognitive control and executive function. *Neuropsychopharmacology*, 1–14. https://doi.org/10.1038/s41386-021-01152-w

Moll, K., Kunze, S., Neuhoff, N., Bruder, J., & Schulte-Körne, G. (2014). Specific Learning Disorder: Prevalence and Gender Differences. *PLOS ONE*, *9*(7), e103537. https://doi.org/10.1371/journal.pone.0103537

Moll, K., & Landerl, K. (2010). *SLRT-II: Lese-und Rechtschreibtest; Weiterentwicklung des Salzburger Lese-und Rechtschreibtests (SLRT)*. Huber.

Moll, K., Ramus, F., Bartling, J., Bruder, J., Kunze, S., Neuhoff, N., Streiftau, S., Lyytinen, H., Leppänen, P. H., Lohvansuu, K., & others. (2014). Cognitive mechanisms underlying reading and spelling development in five European orthographies. *Learning and Instruction*, *29*, 65–77. http://dx.doi.org/10.1016/j.learninstruc.2013.09.003

Monzalvo, K., & Dehaene-Lambertz, G. (2013). How reading acquisition changes children's spoken language network. *Brain and Language*, *127*(3), 356–365. http://dx.doi.org/10.1016/j.bandl.2013.10.009

Monzalvo, K., Fluss, J., Billard, C., Dehaene, S., & Dehaene-Lambertz, G. (2012). Cortical networks for vision and language in dyslexic and normal children of variable socio-economic status. *NeuroImage*, *61*(1), 258–274. https://doi.org/10.1016/j.neuroimage.2012.02.035

Morken, F., Helland, T., Hugdahl, K., & Specht, K. (2017). Reading in dyslexia across literacy development: A longitudinal study of effective connectivity. *NeuroImage*, *144*, 92–100. https://doi.org/10.1016/j.neuroimage.2016.09.060

Moulton, E., Bouhali, F., Monzalvo, K., Poupon, C., Zhang, H., Dehaene, S., Dehaene-Lambertz, G., & Dubois, J. (2019). Connectivity between the visual word form area and the parietal lobe improves after the first year of reading instruction: A longitudinal MRI study in children. *Brain Structure and Function*, *224*(4), 1519–1536. https://doi.org/10.1007/s00429-019-01855-3

Neef, N. E., Müller, B., Liebig, J., Schaadt, G., Grigutsch, M., Gunter, T. C., Wilcke, A., Kirsten, H., Skeide, M. A., & Kraft, I. (2017). Dyslexia risk gene relates to representation of sound in the auditory brainstem. *Developmental Cognitive Neuroscience*, *24*, 63–71. https://doi.org/10.1016/j.dcn.2017.01.008

Neef, N. E., Schaadt, G., & Friederici, A. D. (2017). Auditory brainstem responses to stop consonants predict literacy. *Clinical Neurophysiology*, *128*(3), 484–494. https://doi.org/10.1016/j.clinph.2016.12.007

Nordt, M., Gomez, J., Natu, V., Jeska, B., Barnett, M., & Grill-Spector, K. (2019). Learning to Read Increases the Informativeness of Distributed Ventral Temporal Responses. *Cerebral Cortex*, *29*(7), 3124–3139. https://doi.org/10.1093/cercor/bhy178

Nordt, M., Gomez, J., Natu, V. S., Rezai, A. A., Finzi, D., Kular, H., & Grill-Spector, K. (2021). Cortical recycling in high-level visual cortex during childhood development. *Nature Human Behaviour*, 1–12. https://doi.org/10.1038/s41562-021-01141-5

Norton, E. S., & Wolf, M. (2012). Rapid automatized naming (RAN) and reading fluency: Implications for understanding and treatment of reading disabilities. *Annual Review of Psychology*, *63*, 427–452. https://doi.org/10.1146/annurev-psych-120710-100431

OECD. (2006). *Messages from PISA 2000*. OECD. https://doi.org/10.1787/9789264018761-en

OECD. (2021). *21st-century readers: Developing literacy skills in a digital world*. PISA, OECD Publishing.

Olulade, O. A., Flowers, D. L., Napoliello, E. M., & Eden, G. F. (2015). Dyslexic children lack word selectivity gradients in occipito-temporal and inferior frontal cortex. *NeuroImage: Clinical*, *7*, 742–754. https://doi.org/10.1016/j.nicl.2015.02.013

Ozernov-Palchik, O., & Gaab, N. (n.d.). *Tackling the Early Identification of Dyslexia with the Help of Neuroimaging*. 1.

Ozernov-Palchik, O., & Gaab, N. (2016). Tackling the 'dyslexia paradox': Reading brain and behavior for early markers of developmental dyslexia: Tackling the 'dyslexia paradox.' *Wiley Interdisciplinary Reviews: Cognitive Science*, *7*(2), 156–176. https://doi.org/10.1002/wcs.1383

Ozernov-Palchik, O., Norton, E. S., Wang, Y., Beach, S. D., Zuk, J., Wolf, M., Gabrieli, J. D., & Gaab, N. (2019). The relationship between socioeconomic status and white matter microstructure in pre-reading children: A longitudinal investigation. *Human Brain Mapping*, *40*(3), 741–754. https://doi.org/10.1002/hbm.24407

Partanen, M., Kim, D. H. C., Rauscher, A., Siegel, L. S., & Giaschi, D. E. (2021). White matter but not grey matter predicts change in reading skills after intervention. *Dyslexia*, *27*(2), 224–244. https://doi.org/10.1002/dys.1668

Pavlidou, E. V., & Bogaerts, L. (2019). Implicit statistical learning across modalities and its relationship with reading in childhood. *Frontiers in Psychology*, *10*, 1834. https://doi.org/10.3389/fpsyg.2019.01834

Perfetti, C. A., Beck, I., Bell, L. C., & Hughes, C. (1987). Phonemic knowledge and learning to read are reciprocal: A longitudinal study of first grade children. *Merrill-Palmer Quarterly (1982-)*, 283–319.

Perry, C., Ziegler, J. C., & Zorzi, M. (2007). Nested incremental modeling in the development of computational theories: The CDP+ model of reading aloud. *Psychological Review*, *114*(2), 273–315. https://doi.org/10.1037/0033-295X.114.2.273

Perry, C., Ziegler, J. C., & Zorzi, M. (2010). Beyond single syllables: Large-scale modeling of reading aloud with the Connectionist Dual Process (CDP++) model. *Cognitive Psychology*, *61*(2), 106–151. http://dx.doi.org/10.1016/j.cogpsych.2010.04.001

Perry, C., Zorzi, M., & Ziegler, J. C. (2019). Understanding Dyslexia Through Personalized Large-Scale Computational Models. *Psychological Science*, *30*(3), 386–395. https://doi.org/10.1177/0956797618823540

Pessoa, L. (2018). Emotion and the interactive brain: Insights from comparative neuroanatomy and complex systems. *Emotion Review*, *10*(3), 204–216. https://doi.org/10.1177%2F1754073918765675

Petermann, F., & Petermann, U. (2008). HAWIK-iv. *Kindheit Und Entwicklung*, *17*(2), 71–75.

Petermann, F., & Petermann, U. (2014). *Wechsler intelligence scale for children-: Manual 1: Grundlagen, Testauswertung und Interpretation: Übersetzung und Adaptation der WISC-IV von David Wechsler*. Pearson.

Phan, T. V., Sima, D., Smeets, D., Ghesquière, P., Wouters, J., & Vandermosten, M. (2021). Structural brain dynamics across reading development: A longitudinal MRI study from kindergarten to grade 5. *Human Brain Mapping*. https://doi.org/10.1002/hbm.25560

Pleisch, G., Karipidis, I. I., Brauchli, C., Röthlisberger, M., Hofstetter, C., Stämpfli, P., Walitza, S., & Brem, S. (2019). Emerging neural specialization of the ventral occipitotemporal cortex to characters through phonological association learning in preschool children. *NeuroImage*, *189*, 813–831. https://doi.org/10.1016/j.neuroimage.2019.01.046

Plewko, J., Chyl, K., Bola, Ł., Łuniewska, M., Dębska, A., Banaszkiewicz, A., Wypych, M., Marchewka, A., van Atteveldt, N., & Jednoróg, K. (2018). Letter and Speech Sound Association in Emerging Readers With Familial Risk of Dyslexia. *Frontiers in Human Neuroscience*, *12*, 393. https://doi.org/10.3389/fnhum.2018.00393

Poeppel, D., Emmorey, K., Hickok, G., & Pylkkanen, L. (2012). Towards a New Neurobiology of Language. *Journal of Neuroscience*, *32*(41), 14125–14131. https://doi.org/10.1523/JNEUROSCI.3244-12.2012

Preston, J. L., Molfese, P. J., Frost, S. J., Mencl, W. E., Fulbright, R. K., Hoeft, F., Landi, N., Shankweiler, D., & Pugh, K. R. (2016). Print-speech convergence predicts future reading outcomes in early readers. *Psychological Science*, *27*(1), 75–84. https://doi.org/10.1177/0956797615611921

Price, C. J. (2012). A review and synthesis of the first 20years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage*, *62*(2), 816–847. https://doi.org/10.1016/j.neuroimage.2012.04.062

Price, C. J. (2018). The evolution of cognitive models: From neuropsychology to neuroimaging and back. *Cortex*, *107*, 37–49. https://dx.doi.org/10.1016%2Fj.cortex.2017.12.020

Price, C. J., & Devlin, J. T. (2003). The myth of the visual word form area. *NeuroImage*, *19*(3), 473–481. https://doi.org/10.1016/S1053-8119(03)00084-3

Price, C. J., & Devlin, J. T. (2011). The interactive account of ventral occipitotemporal contributions to reading. *Trends in Cognitive Sciences*, *15*(6), 246–253. http://dx.doi.org/10.1016/j.tics.2011.04.001

Protopapas, A., Orfanidou, E., Taylor, J. S. H., Karavasilis, E., Kapnoula, E. C., Panagiotaropoulou, G., Velonakis, G., Poulou, L. S., Smyrnis, N., & Kelekis, D. (2016). Evaluating cognitive models of visual word recognition using fMRI: Effects of lexical and sublexical variables. *NeuroImage*, *128*, 328–341. https://doi.org/10.1016/j.neuroimage.2016.01.013

Pugh, K. R., Landi, N., Preston, J. L., Mencl, W. E., Austin, A. C., Sibley, D., Fulbright, R. K., Seidenberg, M. S., Grigorenko, E. L., Constable, R. T., Molfese, P., & Frost, S. J. (2013). The relationship between phonological and auditory processing and brain organization in beginning readers. *Brain and Language*, *125*(2), 173–183. https://doi.org/10.1016/j.bandl.2012.04.004

Pugh, K. R., Mencl, W. E., Jenner, A. R., Katz, L., Frost, S. J., Lee, J. R., Shaywitz, S. E., & Shaywitz, B. A. (2000). Functional neuroimaging studies of reading and reading disability (developmental dyslexia). *Mental Retardation and Developmental Disabilities Research Reviews*, *6*(3), 207–213. https://doi.org/10.1002/1098-2779

Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., Constable, R. T., Skudlarski, P., Fulbright, R. K., Bronen, R. A., Shankweiler, D. P., Katz, L., Fletcher, J. M., & Gore, J. C. (1996). Cerebral organization of component processes in reading. *Brain*, *119*(4), 1221–1238. https://doi.org/10.1093/brain/119.4.1221

Rae, C. L., Hughes, L. E., Anderson, M. C., & Rowe, J. B. (2015). The Prefrontal Cortex Achieves Inhibitory Control by Facilitating Subcortical Motor Pathway Connectivity. *Journal of Neuroscience*, *35*(2), 786–794. https://doi.org/10.1523/JNEUROSCI.3093-13.2015

Raizada, R. D. S., & Poldrack, R. A. (2007). Selective Amplification of Stimulus Differences during Categorical Processing of Speech. *Neuron*, *56*(4), 726–740. https://doi.org/10.1016/j.neuron.2007.11.001

Raschle, N., Chang, M., & Gaab, N. (2011). Structural brain alterations associated with dyslexia predate reading onset. *Neuroimage*, *57*(3), 742–749. https://doi.org/10.1016/j.neuroimage.2010.09.055

Raschle, N., Zuk, J., & Gaab, N. (2012). Functional characteristics of developmental dyslexia in left-hemispheric posterior brain regions predate reading onset. *Proceedings of the National Academy of Sciences*, *109*(6), 2156–2161.

Rauschecker, J. P. (2018). Where, When, and How: Are they all sensorimotor? Towards a unified view of the dorsal pathway in vision and audition. *Cortex*, *98*, 262–268. https://doi.org/10.1016/j.cortex.2017.10.020

Richardson, U., & Lyytinen, H. (2014). The GraphoGame method: The theoretical and methodological background of the technology-enhanced learning environment for learning to read. *Human Technology*, *10*(1). https://doi.org/10.17011/ht/urn.201405281859</a

Richlan, F. (2012). Developmental dyslexia: Dysfunction of a left hemisphere reading network. *Frontiers in Human Neuroscience*, *6*. https://doi.org/10.3389/fnhum.2012.00120

Richlan, F. (2014). Functional neuroanatomy of developmental dyslexia: The role of orthographic depth. *Frontiers in Human Neuroscience*, *0*. https://doi.org/10.3389/fnhum.2014.00347

Richlan, F. (2019). The functional neuroanatomy of letter-speech sound integration and its relation to brain abnormalities in developmental dyslexia. *Frontiers in Human Neuroscience*, *13*, 21. https://doi.org/10.3389/fnhum.2019.00021

Richlan, F., Kronbichler, M., & Wimmer, H. (2009). Functional abnormalities in the dyslexic brain: A quantitative meta-analysis of neuroimaging studies. *Human Brain Mapping*, *30*(10), 3299–3308. https://doi.org/10.1002/hbm.20752

Richlan, F., Kronbichler, M., & Wimmer, H. (2011). Meta-analyzing brain dysfunctions in dyslexic children and adults. *NeuroImage*, *56*(3), 1735–1742. https://doi.org/10.1016/j.neuroimage.2011.02.040

Richlan, F., Sturm, D., Schurz, M., Kronbichler, M., Ladurner, G., & Wimmer, H. (2010). A Common Left Occipito-Temporal Dysfunction in Developmental Dyslexia and Acquired Letter-By-Letter Reading? *PLoS ONE*, *5*(8), e12073. https://doi.org/10.1371/journal.pone.0012073

Rodd, J. M., Vitello, S., Woollams, A. M., & Adank, P. (2015). Localising semantic and syntactic processing in spoken and written language comprehension: An Activation Likelihood Estimation meta-analysis. *Brain and Language*, *141*, 89–102. https://doi.org/10.1016/j.bandl.2014.11.012

Rueckl, J. G., Paz-Alonso, P. M., Molfese, P. J., Kuo, W.-J., Bick, A., Frost, S. J., Hancock, R., Wu, D. H., Mencl, W. E., & Duñabeitia, J. A. (2015). Universal brain signature of proficient reading: Evidence from four contrasting languages. *Proceedings of the National Academy of Sciences*, *112*(50), 15510–15515. https://doi.org/10.1073/pnas.1509321112

Rumelhart, D. E., & McClelland, J. L. (1982). An interactive activation model of context effects in letter perception: II. The contextual enhancement effect and some tests and extensions of the model. *Psychological Review*, *89*(1), 60. https://psycnet.apa.org/doi/10.1037/0033-295X.89.1.60

Rüsseler, J., Boltzmann, M., & Grosche, M. (2019). Funktionaler Analphabetismus in Deutschland – Größenordnung, Ursachen, Interventionen. *Zeitschrift Für Neuropsychologie*, *30*(2), 87–95. https://doi.org/10.1024/1016-264X/a000253

Saiz-Alía, M., & Reichenbach, T. (2020). Computational modeling of the auditory brainstem response to continuous speech. *Journal of Neural Engineering*, *17*(3), 036035. https://doi.org/10.1088/1741-2552/ab970d

Sandak, R., Mencl, W. E., Frost, S. J., & Pugh, K. R. (2004). The Neurobiological Basis of Skilled and Impaired Reading: Recent Findings and New Directions. *Scientific Studies of Reading*, *8*(3), 273–292. https://doi.org/10.1207/s1532799xssr0803_6

Saygin, Z. M., Osher, D. E., Norton, E. S., Youssoufian, D. A., Beach, S. D., Feather, J., Gaab, N., Gabrieli, J. D., & Kanwisher, N. (2016). Connectivity precedes function in the development of the visual word form area. *Nature Neuroscience*, *19*(9), 1250–1255. https://dx.doi.org/10.1038%2Fnn.4354

Schaadt, G., Männel, C., van der Meer, E., Pannekamp, A., Oberecker, R., & Friederici, A. D. (2015). Present and past: Can writing abilities in school children be associated with their auditory discrimination capacities in infancy? *Research in Developmental Disabilities*, *47*, 318–333. https://doi.org/10.1016/j.ridd.2015.10.002

Schauenburg, G., Aryani, A., Hsu, C.-T., Schröder, T., Conrad, M., von Scheve, C., & Jacobs, A. M. (2021). Conflict Detection In Affective Language Content: Affective Incongruency In Semantically Correct Sentences Describing Social Interactions Activates The Anterior Cingulate Cortex. *Research Square Platform LLC.* https://doi.org/10.21203/rs.3.rs-549518/v1

Schrott, R., & Jacobs, A. M. (2011). *Gehirn und Gedicht: Wie wir unsere Wirklichkeiten konstruieren* (2nd ed.). Carl Hanser Verlag GmbH & Co. KG.

Schulte-Körne, G., Deimel, W., Jungermann, M., & Remschmidt, H. (2003). Nachuntersuchung einer Stichprobe von lese-rechtschreibgestörten Kindern im Erwachsenenalter. *Zeitschrift Für Kinder- Und Jugendpsychiatrie Und Psychotherapie*, *31*(4), 267–276. https://doi.org/10.1024/1422-4917.31.4.267

Schurz, M., Sturm, D., Richlan, F., Kronbichler, M., Ladurner, G., & Wimmer, H. (2010). A dual-route perspective on brain activation in response to visual words: Evidence for a length by lexicality interaction in the visual word form area (VWFA). *NeuroImage*, *49*(3), 2649–2661. https://doi.org/10.1016/j.neuroimage.2009.10.082

Schuster, S., Hawelka, S., Himmelstoss, N. A., Richlan, F., & Hutzler, F. (2020). The neural correlates of word position and lexical predictability during sentence reading: Evidence from fixation-related fMRI. *Language, Cognition and Neuroscience*, *35*(5), 613–624. https://doi.org/10.1080/23273798.2019.1575970

Schuster, S., Himmelstoss, N. A., Hutzler, F., Richlan, F., Kronbichler, M., & Hawelka, S. (2021). Cloze enough? Hemodynamic effects of predictive processing during natural reading. *NeuroImage*, *228*, 117687. https://doi.org/10.1016/j.neuroimage.2020.117687

Scolari, M., Seidl-Rathkopf, K. N., & Kastner, S. (2015). Functions of the human frontoparietal attention network: Evidence from neuroimaging. *Current Opinion in Behavioral Sciences*, *1*, 32–39. https://doi.org/10.1016/j.cobeha.2014.08.003

Sekiyama, K., & Burnham, D. (2008). Impact of language on development of auditory-visual speech perception. *Developmental Science*, *11*(2), 306–320. https://doi.org/10.1111/j.1467-7687.2008.00677.x

Sestieri, C., Shulman, G. L., & Corbetta, M. (2017). The contribution of the human posterior parietal cortex to episodic memory. *Nature Reviews. Neuroscience*, *18*(3), 183–192. https://doi.org/10.1038/nrn.2017.6

Share, D. L. (1995). Phonological recoding and self-teaching: Sine qua non of reading acquisition. *Cognition*, *55*(2), 151–218. https://doi.org/10.1016/0010-0277(94)00645-2

Shaywitz, S. E., Shaywitz, B. A., Pugh, K. R., Fulbright, R. K., Constable, R. T., Mencl, W. E., Shankweiler, D. P., Liberman, A. M., Skudlarski, P., & Fletcher, J. M. (1998). Functional disruption in the organization of the brain for reading in dyslexia. *Proceedings of the National Academy of Sciences*, *95*(5), 2636–2641. https://doi.org/10.1073/pnas.95.5.2636

Shenhav, A., Botvinick, M. M., & Cohen, J. D. (2013). The Expected Value of Control: An Integrative Theory of Anterior Cingulate Cortex Function. *Neuron*, *79*(2), 217–240. https://doi.org/10.1016/j.neuron.2013.07.007

Skeide, M. A., & Friederici, A. D. (2016). The ontogeny of the cortical language network. *Nature Reviews Neuroscience*, *17*(5), 323–332. https://doi.org/10.1038/nrn.2016.23

Skeide, M. A., Kumar, U., Mishra, R. K., Tripathi, V. N., Guleria, A., Singh, J. P., Eisner, F., & Huettig, F. (2017). Learning to read alters cortico-subcortical cross-talk in the visual system of illiterates. *Science Advances*, *3*(5), e1602612. https://doi.org/10.1126/sciadv.1602612

Skoe, E., & Kraus, N. (2010). Auditory brainstem response to complex sounds: A tutorial. *Ear and Hearing*, *31*(3), 302. https://dx.doi.org/10.1097%2FAUD.0b013e3181cdb272

Skoe, E., Krizman, J., Spitzer, E., & Kraus, N. (2013). The auditory brainstem is a barometer of rapid auditory learning. *Neuroscience*, *243*, 104–114. https://doi.org/10.1016/j.neuroscience.2013.03.009

Smith, G. J., Booth, J. R., & McNorgan, C. (2018). Longitudinal Task-Related Functional Connectivity Changes Predict Reading Development. *Frontiers in Psychology*, *9*. https://doi.org/10.3389/fpsyg.2018.01754

Snowling, M. J., Hulme, C., & Nation, K. (2020). Defining and understanding dyslexia: Past, present and future. *Oxford Review of Education*, *46*(4), 501–513. https://doi.org/10.1080/03054985.2020.1765756

Stock, C., & Schneider, W. (2008). *DERET 1-2+: Deutscher Rechtschreibtest für das erste und zweite Schuljahr*. Beltz.

Sylvester, T., Braun, M., Schmidtke, D., & Jacobs, A. M. (2016). The Berlin Affective Word List for Children (kidBAWL): Exploring Processing of Affective Lexical Semantics in the Visual and Auditory Modalities. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.00969

Sylvester, T., Liebig, J., & Jacobs, A. M. (2021a). Neural correlates of affective contributions to lexical decisions in children and adults. *Scientific Reports*, *11*(1), 945. https://doi.org/10.1038/s41598-020-80359-1

Sylvester, T., Liebig, J., & Jacobs, A. M. (2021b). Neuroimaging of valence decisions in children and adults. *Developmental Cognitive Neuroscience*, *48*, 100925. https://doi.org/10.1016/j.dcn.2021.100925

Szwed, M., Cohen, L., Qiao, E., & Dehaene, S. (2009). The role of invariant line junctions in object and visual word recognition. *Vision Research*, *49*(7), 718–725. https://doi.org/10.1016/j.visres.2009.01.003

Taylor, J. S. H., Davis, M. H., & Rastle, K. (2019). Mapping visual symbols onto spoken language along the ventral visual stream. *Proceedings of the National Academy of Sciences*, *116*(36), 17723–17728. https://doi.org/10.1073/pnas.1818575116

Taylor, J. S. H., Rastle, K., & Davis, M. H. (2013). Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies. *Psychological Bulletin*, *139*(4), 766–791. https://doi.org/10.1037/a0030266

Tecoulesco, L., Skoe, E., & Naigles, L. R. (2020). Phonetic discrimination mediates the relationship between auditory brainstem response stability and syntactic performance. *Brain and Language*, *208*, 104810. https://doi.org/10.1016/j.bandl.2020.104810

Tiffin-Richards, S. P., & Schroeder, S. (2020). Context facilitation in text reading: A study of children's eye movements. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *46*(9), 1701. http://dx.doi.org/10.1037/xlm0000834

Torgesen, J. K., Wagner, R. K., & Rashotte, C. A. (1994). Longitudinal studies of phonological processing and reading. *Journal of Learning Disabilities*, *27*(5), 276–286. https://doi.org/10.1177%2F002221949402700503

Truong, D. T., Che, A., Rendall, A. R., Szalkowski, C. E., LoTurco, J. J., Galaburda, A. M., & Holly Fitch, R. (2014). Mutation of Dcdc2 in mice leads to impairments in auditory processing and memory ability. *Genes, Brain and Behavior*, *13*(8), 802–811. https://dx.doi.org/10.1111%2Fgbb.12170

Turkeltaub, P. E., Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-Analysis of the Functional Neuroanatomy of Single-Word Reading: Method and Validation. *NeuroImage*, *16*(3), 765–780. https://doi.org/10.1006/nimg.2002.1131

Turkeltaub, P. E., Gareau, L., Flowers, D. L., Zeffiro, T. A., & Eden, G. F. (2003). Development of neural mechanisms for reading. *Nature Neuroscience*, *6*(7), 767–773. https://doi.org/10.1038/nn1065

Usée, F., Jacobs, A. M., & Lüdtke, J. (2020). From Abstract Symbols to Emotional (In-) Sights: An Eye Tracking Study on the Effects of Emotional Vignettes and Pictures. *Frontiers in Psychology*, *11*, 905. https://doi.org/10.3389/fpsyg.2020.00905

Van Atteveldt, N., Blau, V. C., Blomert, L., & Goebel, R. (2010). FMR-adaptation indicates selectivity to audiovisual content congruency in distributed clusters in human superior temporal cortex. *BMC Neuroscience*, *11*(1), 11. https://doi.org/10.1186/1471-2202-11-11

Van de Walle de Ghelcke, A., Rossion, B., Schiltz, C., & Lochy, A. (2020). Developmental changes in neural letter-selectivity: A 1-year follow-up of beginning readers. *Developmental Science*, *24*(1), e12999. https://doi.org/10.1111/desc.12999

van der Kant, A., Männel, C., Paul, M., Friederici, A. D., Höhle, B., & Wartenburger, I. (2020). Linguistic and non-linguistic non-adjacent dependency learning in early development. *Developmental Cognitive Neuroscience*, *45*, 100819. https://doi.org/10.1016/j.dcn.2020.100819

van der Mark, S., Bucher, K., Maurer, U., Schulz, E., Brem, S., Buckelmüller, J., Kronbichler, M., Loenneker, T., Klaver, P., Martin, E., & Brandeis, D. (2009). Children with dyslexia lack multiple specializations along the visual word-form (VWF) system. *NeuroImage*, *47*(4), 1940–1949. https://doi.org/10.1016/j.neuroimage.2009.05.021

Vander Stappen, C., & Reybroeck, M. V. (2018). Phonological Awareness and Rapid Automatized Naming Are Independent Phonological Competencies With Specific Impacts on Word Reading and Spelling: An Intervention Study. *Frontiers in Psychology*, *9*, 320. https://doi.org/10.3389/fpsyg.2018.00320

Vanderauwera, J., Vandermosten, M., Dell'Acqua, F., Wouters, J., & Ghesquière, P. (2015). Disentangling the relation between left temporoparietal white matter and reading: A spherical deconvolution tractography study. *Human Brain Mapping*, *36*(8), 3273–3287. https://doi.org/10.1002/hbm.22848

Vandermosten, M., Hoeft, F., & Norton, E. S. (2016). Integrating MRI brain imaging studies of pre-reading children with current theories of developmental dyslexia: A review and quantitative meta-analysis. *Current Opinion in Behavioral Sciences*, *10*, 155–161. https://doi.org/10.1016/j.cobeha.2016.06.007

Vassena, E., Deraeve, J., & Alexander, W. H. (2020). Surprise, value and control in anterior cingulate cortex during speeded decision-making. *Nature Human Behaviour*, *4*(4), 412–422. https://doi.org/10.1038/s41562-019-0801-5

Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical Coding of Letter Strings in the Ventral Stream: Dissecting the Inner Organization of the Visual Word-Form System. *Neuron*, *55*(1), 143–156. https://doi.org/10.1016/j.neuron.2007.05.031

Walenski, M., Europa, E., Caplan, D., & Thompson, C. K. (2019). Neural networks for sentence comprehension and production: An ALE-based meta-analysis of neuroimaging studies. *Human Brain Mapping*, *40*(8), 2275–2304. https://doi.org/10.1002/hbm.24523

Wang, J., Deng, Y., & Booth, J. R. (2019). Automatic semantic influence on early visual word recognition in the ventral occipito-temporal cortex. *Neuropsychologia*, *133*, 107188. https://doi.org/10.1016/j.neuropsychologia.2019.107188

Wang, J., Joanisse, M. F., & Booth, J. R. (2020a). Neural representations of phonology in temporal cortex scaffold longitudinal reading gains in 5-to 7-year-old children. *NeuroImage*, *207*, 116359.

Wang, J., Joanisse, M. F., & Booth, J. R. (2020b). Letter fluency in 7-8-year-old children is related to the anterior, but not posterior, ventral occipito-temporal cortex during an auditory phonological task. *Developmental Cognitive Neuroscience*, *47*, 100898. https://doi.org/10.1016/j.dcn.2020.100898

Wang, J., Pines, J., Joanisse, M., & Booth, J. R. (2021). Reciprocal relations between reading skill and the neural basis of phonological awareness in 7- to 9-year-old children. *NeuroImage*, 118083. https://doi.org/10.1016/j.neuroimage.2021.118083

Wang, J., Yamasaki, B., Weiss, Y., & Booth, J. R. (2021). Both frontal and temporal cortex exhibit phonological and semantic specialization during spoken language processing in 7- to 8-year-old children. *Human Brain Mapping*. https://doi.org/10.1002/hbm.25450

Wanzek, J., Stevens, E. A., Williams, K. J., Scammacca, N., Vaughn, S., & Sargent, K. (2018). Current evidence on the effects of intensive early reading interventions. *Journal of Learning Disabilities*, *51*(6), 612–624. https://doi.org/hDttOpsI://1d0o.i.1o1rg7/71/00.10127272/010924212189747158171750110

Weiss, B., Knakker, B., & Vidnyánszky, Z. (2016). Visual processing during natural reading. *Scientific Reports*, *6*(1), 26902. https://doi.org/10.1038/srep26902

Weiß, R. H., & Weiß, H. R. (2006). Cft 20-r. *Grundintelligenztest Skala*, *2*.

Weiss-Croft, L. J., & Baldeweg, T. (2015). Maturation of language networks in children: A systematic review of 22years of functional MRI. *NeuroImage*, *123*, 269–281. https://doi.org/10.1016/j.neuroimage.2015.07.046

Welcome, S. E., & Joanisse, M. F. (2012). Individual differences in skilled adult readers reveal dissociable patterns of neural activity associated with component processes of reading. *Brain and Language*, *120*(3), 360–371. https://doi.org/10.1016/j.bandl.2011.12.011

White-Schwoch, T., & Kraus, N. (2013). Physiologic discrimination of stop consonants relates to phonological skills in pre-readers: A biomarker for subsequent reading ability? *Frontiers in Human Neuroscience*, *7*, 899. https://doi.org/10.3389/fnhum.2013.00899

White-Schwoch, T., Woodruff Carr, K., Thompson, E. C., Anderson, S., Nicol, T., Bradlow, A. R., Zecker, S. G., & Kraus, N. (2015). Auditory Processing in Noise: A Preschool Biomarker for Literacy. *PLoS Biology*, *13*(7), 1–17. https://doi.org/10.1371/journal.pbio.1002196

Wißmann, J., Heine, A., Handl, P., & Jacobs, A. M. (2013). Förderung von Kindern mit isolierter Rechenschwäche und kombinierter Rechen-und Leseschwäche: Evaluation eines numerischen Förderprogramms für Grundschüler. *Lernen Und Lernstörungen*.

Xue, S., Jacobs, A. M., & Lüdtke, J. (2020). What Is the Difference? Rereading Shakespeare's Sonnets—An Eye Tracking Study. *Frontiers in Psychology*, *11*, 421.

Xue, S., Lüdtke, J., Sylvester, T., & Jacobs, A. M. (2019). Reading Shakespeare sonnets: Combining quantitative narrative analysis and predictive modeling - an eye tracking study. *Journal of Eye Movement Research, 12*(5). https://doi.org/10.16910/JEMR.12.5.2

Yamada, Y., Stevens, C., Dow, M., Harn, B. A., Chard, D. J., & Neville, H. J. (2011). Emergence of the neural network for reading in five-year-old beginning readers of different levels of pre-literacy abilities: An fMRI study. *NeuroImage*, *57*(3), 704–713. https://doi.org/10.1016/j.neuroimage.2010.10.057

Yeatman, J. D., Ben-Shachar, M., Glover, G. H., & Feldman, H. M. (2010). Individual differences in auditory sentence comprehension in children: An exploratory event-related functional magnetic resonance imaging investigation. *Brain and Language*, *114*(2), 72–79. https://doi.org/10.1016/j.bandl.2009.11.006

Yu, X., Raney, T., Perdue, M. V., Zuk, J., Ozernov-Palchik, O., Becker, B. L. C., Raschle, N. M., & Gaab, N. (2018). Emergence of the neural network underlying phonological processing from the prereading to the emergent reading stage: A longitudinal study. *Human Brain Mapping*, *39*(5), 2047–2063. https://doi.org/10.1002/hbm.23985

Zhao, L., Chen, C., Shao, L., Wang, Y., Xiao, X., Chen, C., Yang, J., Zevin, J., & Xue, G. (2017). Orthographic and Phonological Representations in the Fusiform Cortex. *Cerebral Cortex*, *27*(11), 5197–5210. https://doi.org/10.1093/cercor/bhw300

Ziegler, J. C., Bertrand, D., Tóth, D., Csépe, V., Reis, A., Faísca, L., Saine, N., Lyytinen, H., Vaessen, A., & Blomert, L. (2010). Orthographic depth and its impact on universal predictors of reading a cross-language investigation. *Psychological Science*. https://doi.org/10.1177/0956797610363406

Ziegler, J. C., Castel, C., Pech-Georgel, C., George, F., Alario, F.-X., & Perry, C. (2008). Developmental dyslexia and the dual route model of reading: Simulating individual differences and subtypes. *Cognition*, *107*(1), 151–178. https://doi.org/10.1016/j.cognition.2007.09.004

Ziegler, J. C., & Goswami, U. (2005). Reading Acquisition, Developmental Dyslexia, and Skilled Reading Across Languages: A Psycholinguistic Grain Size Theory. *Psychological Bulletin*, *131*(1), 3–29. https://doi.org/10.1037/0033-2909.131.1.3

Ziegler, J. C., Pech-Georgel, C., George, F., & Lorenzi, C. (2009). Speech-perception-in-noise deficits in dyslexia. *Developmental Science*, *12*(5), 732–745. https://doi.org/10.1111/j.1467-7687.2009.00817.x

Ziegler, J. C., Perry, C., & Zorzi, M. (2014). Modelling reading development through phonological decoding and self-teaching: Implications for dyslexia. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1634), 20120397. https://doi.org/10.1098/rstb.2012.0397

Ziegler, J. C., Perry, C., & Zorzi, M. (2020). Learning to Read and Dyslexia: From Theory to Intervention Through Personalized Computational Models. *Current Directions in Psychological Science*, 096372142091587. https://doi.org/10.1177/0963721420915873

Supplementary Material

Study II (Liebig et al., 2021)

Prediction of reading comprehension and spelling

Preprocessing. For the additional analysis I used the preprocessed data of the original publication (Liebig et al., 2021).

Analysis. To compare the results of Study II and Study II I performed additional regression analyses for reading comprehension (ELFE) and spelling (DERET) targeted in Liebig et al. (2020, Study II). Analogous to the original publication (Liebig et al., 2021) I computed additional simple regressions of the baseline contrasts (faces, written words, spoken words) and the differential contrast (faces > [houses, written words]) to predict future literacy. The initial cluster forming threshold was set to $p < .001$ and $p < .05$ FWE-corrected on cluster level. Results were additionally controlled for the number of regressions (4 contrasts x 2 literacy tasks) at $p < .006$.

Results. None of the contrasts significantly predicted reading comprehension or spelling.

Study III (Liebig et al., 2020)

Concurrent gene-brain-behavior relationships

Analysis. To explore the concurrent relationship of environmental-demographic factors, the targeted risk-variants of *DCDC2* and *KIAA0319* and the auditory brainstem response to speech (first component of the principal component analysis, see Liebig et al., 2020), I set up additional multiple regressions. These were set up according to the original publication (Liebig et al., 2020) with the z-standardized values of RAN (mean of the two subtests objects and colors; BISC; Jansen, 2002) and phonological awareness (sound-to-word matching; BISC; Jansen, 2002) as outcome. Model goodness of fit of the different models was tested with the likelihood ratio test.

Results. The environmental demographic-model explained 15 % variance of RAN ($R^2 = .15$, adj. $R^2 = .09$, $F_{(5,68)} = 2.4$, $p < .05$). The effect was driven by non-verbal intelligence (see Table S1). Then genetic information was added, but this did not significantly change the prediction (*DEMO/DCDC2:* $R^2 = .191$, adj. $R^2 = .063$, $F_{(10, 63)} = 1.49$, $p = .16$; *DEMO/KIAA0319:* $R^2 = .194$, adj. $R^2 = .066$, $F_{(10, 63)} = 1.51$, $p = .6$). Likewise, the genetic information did not significantly improve the models (*DEMO/DCDC2*: $\chi^2(5) = 5.69$, p= .59; *DEMO/KIAA0319*: χ^2 (5) = 3.90, p= .56). In a last step, the auditory brainstem response was added to the two genetic models. The full models could explain 25 % and 24 % of variance (*DEMO/DCDC2/ABR:* $R^2 = .247$, adj. $R^2 = .114$, $F_{(11, 62)} = 1.85$, $p = .06$; *DEMO/KIAA0319/ABR:* $R^2 = .249$, adj. $R^2 = .116$, $F_{(11, 62)} = 1.87$, $p = .06$). Although the models did not reach significance, model comparison showed that the full model was more suitable (*DEMO/DCDC2/ABR:* $X^2_{(1)}$ = 5.33, p< .05; *DEMO/KIAA0319/ABR:* $\chi^2_{(1)}$ = 5.27, p< .05). A similar pattern emerged for phonological awareness: The basic model explained 15 % variance (R^2 = .149, adj. R^2 = .09, $F_{(5,68)}$ = 2.4, *p*< .05). Again, adding the genetic information did not significantly enhance the prediction of phonological awareness (*DEMO/DCDC2:* R^2 = .225, adj. R^2 = .103, $F_{(10, 63)}$ = 1.85, *p*= .07; *DEMO/KIAA0319:* R^2 = .197, adj. R^2 = .071, $F_{(10, 63)}$ = 1.57, *p*= .14). This was also confirmed by the likelihood test (DEMO/DCDC2: $X^2_{(5)}$ = 7.0, *p*= .2; DEMO/KIAA0319: $\chi^2_{(5)}$ = 4.35, *p*= .5). In combination with the auditory brainstem response the *DCDC2* model explained 27 % and the *KIAA0319* model explained 24 % of variance in phonological awareness (*DEMO/DCDC2/ABR:* R^2 = .274, adj. R^2 = .147, $F_{(11, 62)}$ = 2.126, *p*< .05, model comparison: $\chi^2_{(1)}$= 4.94, p<.05; ; *DEMO/KIAA0319/ABR:* R^2 = .236, adj. R^2 = .103, $F_{(11, 62)}$ = 1.78, *p*= .08, model comparison: $\chi^2_{(1)}$= 3.82, *p*= .05).The results of the models are shown in detail in Table S1 and S2 below.

Prediction of reading fluency by genotypes and auditory brainstem response

***Analysis**.* In last series of analysis, I tested whether the multifactorial model could predict future reading fluency. For that, the mean of single word and pseudoword reading of the SLRT was taken. The data was only available for a subsample of 53 children.

***Results**.* The basic demographic-environmental model explained 27 % of variance in reading fluency (R^2 = .270, adj. R^2 = .194, $F_{(5,48)}$ = 3.56, *p*< .01). Similar to spelling, the DCDC2 genetic model did significantly improve prediction ($\chi^2_{(5)}$ = 15.9, p< .01), while adding KIAA0319 did not change the model fit ($\chi^2_{(5)}$ = 6.81, p= .2). The DCDC2 genetic model explained 46 % of variance in reading fluency (R^2 = .456, adj. R^2 = .330, $F_{(11, 43)}$ = *3.61,, p*< .01), the KIAA0319 model 36 % (R^2 = .360, adj. R^2 = .207, $F_{(11, 43)}$ = *2.39, p*< .05). Adding the information of the auditory brainstem response did not improve the prediction: *DEMO/DCDC2/ABR:* R^2 = .457, adj. R^2 = .315, $F_{(11, 42)}$ = *3.22, p*< .01, model comparison: $\chi^2_{(1)}$ = .09, p= .7; *DEMO/KIAA0319/ABR:* R^2 = 360, adj. R^2 = .192 , $F_{(11, 42)}$ = *2.15, p*< .05, model comparison: $\chi^2_{(1)}$ = .24, p= .6). The detailed results are shown in Table S3.

Table S1. Concurrent brain-behavior relationship with rapid automatized naming.

Coefficient	*Estimate*	*SE*	*t*	*p*	Coefficient	*Estimate*	*SE*	*t*	*p*
Demographic-environmental model									
(Intercept)	-0.063538	0.155395	-0.409	0.684					
Age	-0.049727	0.10014	-0.497	0.621					
Sex	0.294014	0.18452	1.593	0.116					
non-verbal IQ	**0.018861**	**0.008111**	**2.325**	**0.023**					
FHD	-0.173941	0.18105	-0.961	0.34					
PE	0.08435	0.091278	0.924	0.359					
Genetic Models									
DCDC2					KIAA0319				
rs807724	-0.342245	0.253329	-1.351	0.1815	rs2179515	-0.180971	0.250798	-0.722	0.4733
rs1087266	-0.091345	0.167184	-0.546	0.5867	rs6935076flipflop	-0.001455	0.248414	-0.006	0.9953
rs793842	0.343161	0.237222	1.447	0.153	rs761100	-0.016299	0.332225	-0.049	0.9610
rs1091047	-0.197635	0.252702	-0.782	0.4371	rs2143340	0.458934	0.306441	1.498	0.1393
rs6922023	0.037525	0.203547	0.184	0.8543	rs3212236	-0.332446	0.395067	-0.841	0.4033
Auditory Brainstem Models									
ABR PC1	**0.197097**	**0.09163**	**2.151**	**0.0354**	**ABR PC1**	**0.1967**	**0.091957**	**2.139**	**0.0364**

Note. SE = standard error, *t* = t-value, *p* = *p*-value, non-verbal IQ = non-verbal intelligence, FHD = family history of dyslexia, PE = parental education, ABR PC1 = first component of auditory brainstem response features.

Table S2. Concurrent brain-behavior relationship with phonological awareness.

Coefficient	*Estimate*	*SE*	*t*	*p*	Coefficient	*Estimate*	*SE*	*t*	*p*
Demographic-environmental model									
(Intercept)	-0.07712	0.19229	-0.401	0.6896					
Age	-0.16559	0.1232	-1.344	0.1833					
Sex	0.20173	0.22791	0.885	0.3792					
non-verbal IQ	**0.02361**	**0.01003**	**2.354**	**0.0214**					
FHD	-0.048	0.22287	-0.215	0.8301					
PE	0.22177	0.11307	1.961	0.0539					
Genetic Models									
DCDC2					KIAA0319				
rs807724	0.48402	0.30691	1.577	0.1197	rs2179515	-0.430011	0.316262	-1.36	0.1787
rs1087266	-0.36644	0.19982	-1.834	0.0713	rs6935076flipflop	0.197335	0.314493	0.627	0.5326
rs793842	-0.13397	0.2874	-0.466	0.6427	rs761100	-0.408187	0.420889	-0.97	0.3358
rs1091047	0.03948	0.30622	0.129	0.8978	rs2143340	0.506552	0.388951	1.302	0.1975
rs6922023	-0.27811	0.24648	-1.128	0.2634	rs3212236	-0.504852	0.498406	-1.013	0.3149
Auditory Brainstem Models									
ABR PC1	**0.22761**	**0.10987**	**2.072**	**0.0424**	ABR PC1	0.20582	0.11346	1.814	0.0744

Note. SE = standard error, *t* = *t*-value, *p* = *p*-value, non-verbal IQ = non-verbal intelligence, FHD = family history of dyslexia, P E= parental education, ABR PC1 = first component of auditory brainstem response features.

Table S3. Prediction of reading fluency.

Coefficient	*Estimate*	*SE*	*t*	*p*	Coefficient	*Estimate*	*SE*	*t*	*p*
Demographic-environmental model									
(Intercept)	54.5737	7.4	7.375	1.96E-09					
Age	**-12.352**	**5.7228**	**-2.158**	**0.03593**					
Sex	-4.3352	6.8819	-0.63	0.53171					
non-verbal IQ	0.4929	0.281	1.754	0.08573					
FHD	-0.9123	6.8027	-0.134	0.89387					
PE	**9.8718**	**3.3779**	**2.922**	**0.00528**					
Genetic Models									
DCDC2					KIAA0319				
rs807724	**-28.2921**	**8.6078**	**-3.287**	**0.002023**	rs2179515	8.2622	9.8327	0.84	0.4054
rs1087266	9.8117	5.9062	1.661	0.103936	rs6935076flipflop	-16.1402	9.0765	-1.778	0.08244
rs793842	**25.3922**	**7.7677**	**3.269**	**0.002128**	rs761100	18.226	12.8049	1.423	0.16185
rs1091047	-14.2206	8.3366	-1.706	0.09526	rs2143340	18.5323	15.1774	1.221	0.22872
rs6922023	4.4151	6.6803	0.661	0.512196	rs3212236	0.2176	17.2057	0.013	0.98997
Auditory Brainstem Models									
ABR PC1	0.7988	2.9805	0.268	0.790011	ABR PC1	-1.60857	3.71058	-0.434	0.66686

Note. SE = standard error, *t* = *t*-value, *p* = *p*-value, non-verbal IQ = non-verbal intelligence, FHD = family history of dyslexia, PE = parental education, ABR PC1 = first component of auditory brainstem response features.

Study I (Liebig et al., 2017) and Study II (Liebig et al., 2021)

Prediction of component processes of reading by preliterate regions of interest

Analysis. First and second level general linear models were computed according to Liebig et al. (2017). The results were masked with the ROIs extracted from Liebig et al. (2021). The reading-sensitive preliterate ROIs consisted of: left and right FuG, IOG/MTG, STG/SMG, precuneus/SPL, and PRG (see Liebig et al., 2021, Table 2 and 3, for peak locations and cluster size). For all contrasts an initial cluster forming threshold of $p< .001$ was used and FWE-corrected of $p< .05$ corrected for multiple testing is reported.

On the group level several regressions were performed with reading fluency (SLRT) and reading comprehension (SLS). Again, results were masked with the ROIs extracted from Liebig et al. (2021).

Results. Are described in the summary of Study II (Follow Up Analyses).

Appendix

I. Deutsche Zusammenfassung

Wenn ein Kind lesen lernt, führt dies zu fundamentalen strukturellen und funktionalen Veränderungen im Gehirn (Dehaene et al., 2015). Bei erwachsenen, geschulten Leserinnen und Lesern sind die zahlreichen Subprozesse der Einzelworterkennung primär drei neuronalen Routen zugeordnet: Die dorsale Route des temporo-parietalen Kortex wird mit indirektem Lesen durch phonologisches Dekodieren assoziiert. Die direkte ganzheitliche Worterkennung wird mit der ventralen Route des temporalen Kortex assoziiert. Beide Leserouten enden in der dritten frontalen Route, in der die semantische Analyse und die Integration der Subprozesse erfolgt. Die frontale Route, hier vor allem der IFG, wird außerdem mit verschiedensten sprachlichen und nicht-sprachlichen Funktionen assoziiert (Froehlich et al., 2018; Price, 2012; Welcome & Joanisse, 2012). Bei Kindern hingegen sind die neuronalen Veränderungen, die die Leseentwicklung charakterisieren, bisher noch nicht allumfassend erforscht. Das übergeordnete Ziel der vorliegenden Dissertation ist es daher, das Zusammenspiel der Routen bei lesenden Kindern sowie die neuronalen Voraussetzungen kurz vor dem Leseerwerb zu untersuchen.

Im Mittelpunkt der ersten Studie (Liebig et al., 2017) stehen die zentralen Subprozessen des Einzelwortlesens. Diese umfassen sublexikalisches Dekodieren, orthographische und phonologische Analyse sowie die lexikalisch-semantische Verarbeitung. Mittels funktioneller Magnet-Resonanz-Tomographie (fMRT) wurden diese Prozesse systematisch bei neun bis 13-jährigen Kindern und Jugendlichen untersucht. Der Fokus liegt auf folgenden zwei Aspekten:

1.) Charakterisierung der neuronalen Korrelate der zentralen Subprozesse der Einzelworterkennung bei flüssig lesenden Kindern.
2.) Zusammenspiel und Differenzierung der Subprozesse innerhalb der drei Leserouten nach fünf bis acht Jahren Leseerfahrung.

In Studie zwei und drei (Liebig et al., 2020; Liebig, Froehlich, et al., 2021) wird mittels longitudinal angelegter Studien die Leseentwicklung vom Ende des Kindergartens bis zum Ende der zweiten Klasse verfolgt. Im Querschnittsvergleich wurden die neuronalen Korrelate in Bezug auf zwei der wichtigsten kognitiv-linguistischen Vorläuferfähigkeiten untersucht: Phonologische Bewusstheit und schnelles, automatisiertes Benennen von Objekten (engl.: rapid automatized naming, RAN). Am Ende der zweiten Klasse wurde die Lese- und Schreibleistung dann retrospektiv mit der Gehirnfunktion vor der Einschulung in Verbindung gesetzt. Sprich, es wurde überprüft, ob die Hirnaktivität im Kindergartenalter die zukünftige Leseleistung vorhersagen kann. Die beiden primären Ziele der Studien sind wie folgt zusammenzufassen:

1.) Untersuchung der neuronalen Korrelate kognitiv-linguistischer Vorläuferfähigkeiten des späteren Leseerwerbs.
2.) Untersuchung der neuronalen Aktivität im Kindergartenalter als biologischer Prädiktor der zukünftigen Leseleistung.

In Liebig et al. (2021) wird diesen Fragen auf der kortikalen Ebene nachgegangen. Unter Verwendung eines passiven fMRT Paradigmas wurden die visuellen und auditiven neuronalen Systeme mit sprachlichem und nicht-sprachlichem Material bei jungen Kindern untersucht. Die neuronale Aktivität wurde dann mit den erbrachten Leistungen in den Tests zur Phonologischen Bewusstheit und RAN korreliert. Hier ergibt sich folgendes Bild: Interindividuelle Unterschiede in der neuronalen Antwort auf Gesichter, geschriebene und gehörte Wörter korreliert mit RAN. Die sensitiven Regionen liegen ausschließlich in den drei zukünftigen Leserouten. Des Weiteren prädizieren die neuronalen Korrelate der Verarbeitung von Gesichtern in der ventralen Route die zukünftige Leseleistung der Kinder. Die Ergebnisse reihen sich in eine wachsende Zahl longitudinaler Studien ein, die ebenfalls einen systematischen Zusammenhang zwischen der neuronalen Aktivität in den zukünftigen Leserouten vor dem Leseerwerb und der späteren Leseleistung zeigen (Chyl et al., 2021). Aufgrund einiger Besonderheiten tragen die Ergebnisse der zweiten empirischen Studie der Dissertation zum Erkenntnisgewinn in dem Bereich der neurokognitiven Leseforschung wie folgt bei: Erstens ermöglicht das verwendete passive fMRT Paradigma eine objektive Messung der neuronalen Aktivität, die nicht, wie in anderen Studien, durch die Schwierigkeit der zu lösenden Aufgabe konfundiert ist. Zweitens, zeigen sich lese-relevante interindividuelle Unterschiede in verschiedenen Modalitäten und auch bei nicht-sprachlicher Gesichtserkennung. Die enge Beziehung zwischen der Verarbeitung von Gesichtern und Lesen wurde bereits für ältere Kinder mit und ohne Dyslexie (Monzalvo et al., 2012) und auch in den ersten Phasen des Leseerwerbs (Dehaene-Lambertz et al., 2018) gezeigt. In Liebig et al. (2021) wird dieser Zusammenhang nun auch für jüngere Kinder vor dem Leseerwerb gefunden. Zusammenfassend weisen die Ergebnisse darauf hin, dass sich die neuronalen Voraussetzungen für einen (erfolgreichen) Leseerwerb bei Kindergartenkindern eindeutig unterscheiden und, dass diese den Leseerwerb signifikant beeinflussen.

In Liebig et al. (2020) liegt der Fokus auf der subkortikalen Gehirnantwort auf der Ebene des auditiven Hirnstamms. Anstatt sich ausschließlich der Beziehung zwischen Gehirn und Verhalten zu widmen, werden mehr-faktorielle Modelle aufgesetzt. Konkret, werden demographische und Umweltfaktoren, genetische Varianten bekannter Dyslexiegene (*KIAA0319, DCDC2*), und das Hirnstammsignal gesprochener Silben in die Modelle aufgenommen. Von besonderem Interesse für die vorliegende Dissertation ist der Einfluss der Repräsentation von gesprochener Sprache im Hirnstamm. Im auditiven Hirnstamm wird das Sprachsignal für die weitere Analyse im Kortex vorverarbeitet. Das Signal des Hirnstamms bildet dabei die akustischen Wellen sehr exakt ab. Frühere Untersuchungen konnten feststellen, dass sich die Präzision des Signals in Abhängigkeit der Leseleistung unterscheidet (Neef, Schaadt, et al., 2017). Die Ergebnisse der dritten empirischen Studie der vorliegenden Dissertation zeichnen ein gemischtes Bild. In der Quer-schnittsanalyse zeigt sich eine signifikante Beziehung zwischen dem Hirnstammsignal und den interindividuellen Unterschieden in der Phonologischen Bewusstheit und RAN. Longitudinal sagt die Genauigkeit des Hirnstammsignals lediglich die Schreibleistung signifikant vorher. Somit belegen auch die Ergebnisse dieser Dissertationsstudie interindividuelle Unterschiede in den (sub-kortikalen) neuronalen Voraussetzungen des Leseerwerbs, vor allem in der querschnittlichen Untersuchung. Im Vergleich zur kortikalen Verarbeitung in den zukünftigen Leserouten scheint das Hirnstammsignal jedoch als potenzieller objektiver biologischer Marker der zukünftigen Leseleistung weniger gut geeignet.

In der vorliegenden Dissertationsschrift werden die Ergebnisse der drei empirischen Studien ausführlich diskutiert und weiterführende Anwendungsbeispiele illustriert. So könnten vor allem die Ergebnisse der ersten Studie dabei helfen komputationale und kognitive Modelle des Lesens zu verfeinern. Die Ergebnisse der letzten beiden Studien implizieren, dass eine präventive Therapie die beobachteten Leistungsunterschiede schon vor der Einschulung abmildern könnte. Die Diagnose und Therapie von Leseschwierigkeiten, die aktuell oftmals erst am Ende der zweiten Klasse starten, müsste dafür grundlegend erneuert werden.

Im letzten Teil der Dissertation, stelle ich basierend auf dem einflussreichen Modell von Pugh et al. (2000), den Entwurf für ein überarbeitetes neurokognitives Modell der Leseentwicklung vor.

II. Eidesstattliche Erklärung

Hiermit erkläre ich, die vorliegende Dissertation selbstständig verfasst und ohne unerlaubte Hilfe angefertigt habe.

Alle Hilfsmittel, die verwendet wurden, habe ich angegeben. Die Dissertation ist in keinem früheren Promotionsverfahren angenommen oder abgelehnt worden.

Berlin, den 18.10.2021

Johanna Liebig

III. List of Publications

Peer-reviewed First Author Journal Articles - Published

Liebig, J., Froehlich, E., Sylvester, T., Braun, M., Heekeren, H. R., Ziegler, J. C, & Jacobs, A. M., (2021). Neural processing of vision and language in kindergarten is associated with prereading skills and predicts future literacy. *Human Brain Mapping,* 2021, 1-17. https://doi.org/10.1002/hbm.25449
(Study II)

Liebig, J., Friederici, A., & Neef, N. (2020). Auditory brainstem measures and genotyping boost the prediction of literacy: A longitudinal study on early markers of dyslexia. *Developmental Cognitive Neuroscience*, 46, 100869. https://doi.org/10.1016/j.dcn.2020.100869

Liebig, J., LEGASCREEN Consortium, Friederici, A. D., Neef, N. E. (2021). Erratum to "Auditory brainstem measures and genotyping boost the prediction of literacy: A longitudinal study on early markers of dyslexia" [Dev. Cognit. Neurosci. 46 (2020) 100869]. *Developmental Cognitive Neuroscience*, *48*. https://doi.org/10.1016/j.dcn.2020.100869
(Study III)

Liebig, J., Froehlich, E., Morawetz, C., Braun, M., Jacobs, A. M., Heekeren, H. R., & Ziegler, J. C. (2017). Neurofunctionally dissecting the reading system in children. *Developmental Cognitive Neuroscience, 27*, 45-57. https://doi.org/10.1016/j.dcn.2017.07.002
(Study I)

Further Peer-reviewed Journal Articles – Published

Sylvester, T., **Liebig, J**., & Jacobs, A. M. (2021). Neural correlates of affective contributions to lexical decisions in children and adults. *Scientific Reports*, *11*(1), 1-11. https://doi.org/10.1038/s41598-020-80359-1

Sylvester, T., **Liebig, J**., & Jacobs, A. M. (2021). Neuroimaging of valence decisions in children and adults. *Developmental Cognitive Neuroscience*, *48*, 100925. https://doi.org/10.1016/j.dcn.2021.100925

Froehlich, E., **Liebig, J**., Morawetz, C., Ziegler, J. C., Braun, M., Heekeren, H. R., & Jacobs, A. M. (2018). Same same but different: processing words in the aging brain. *Neuroscience*, *371*, 75-95. https://doi.org/10.1016/j.neuroscience.2017.11.042

Neef, N. E., Müller, B., **Liebig, J.**, Schaadt, G., Grigutsch, M., Gunter, T. C., Wilcke, A., Kirsten, H., Skeide, M. A., Kraft, I., Kraus, N., Emmrich, F., Brauer, J., Boltze, J., & Friederici, A. D. (2017). Dyslexia risk gene relates to representation of sound in the auditory brainstem. *Developmental Cognitive Neuroscience*, 24, 63–71. https://doi.org/10.1016/j.dcn.2017.01.008

Froehlich, E**., Liebig, J**., Ziegler, J. C., Braun, M., Lindenberger, U., Heekeren, H. R., & Jacobs, A. M. (2016). Drifting through basic subprocesses of reading: a hierarchical diffusion model analysis of age effects on visual word recognition. *Frontiers in Psychology*, *7*, 1863. https://doi.org/*10.3389/fpsyg.2016.01863*

IV. Original Publications

Study I

For Copyright reasons the original publication is not included in this PDF.

Please access the publiation via the DOI provided below.

Liebig, J., Froehlich, E., Morawetz, C., Braun, M., Jacobs, A. M., Heekeren, H. R., & Ziegler, J. C. (2017). Neurofunctionally dissecting the reading system in children. *Developmental Cognitive Neuroscience, 27*, 45-57. https://doi.org/10.1016/j.dcn.2017.07.002

Study II

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Please access the publiation via the DOI provided below.

Liebig, J., Froehlich, E., Sylvester, T., Braun, M., Heekeren, H. R., Ziegler, J. C, & Jacobs, A. M., (2021). Neural processing of vision and language in kindergarten is associated with prereading skills and predicts future literacy. *Human Brain Mapping,* 2021, 1-17. https://doi.org/10.1002/hbm.25449

Study III

Liebig, J., Friederici, A. D., & Neef, N., LEGASCREEN Consortium (2020). Auditory brainstem measures and genotyping boost the prediction of literacy: A longitudinal study on early markers of dyslexia. *Developmental Cognitive Neuroscience*, 46, 100869. https://doi.org/10.1016/j.dcn.2020.100869

Liebig, J., LEGASCREEN Consortium, Friederici, A. D., & Neef, N. E. (2021). Erratum to “Auditory brainstem measures and genotyping boost the prediction of literacy: A longitudinal study on early markers of dyslexia” [Dev. Cognit. Neurosci. 46 (2020) 100869]. *Developmental Cognitive Neuroscience*, 48, 100889. https://doi.org/10.1016/j.dcn.2020.100889