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Review

Exploring the neurobiology of reading through non-invasive brain stimulation: A review

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ABSTRACT

Non-invasive brain stimulation (NIBS) has gained increasing popularity as a modulatory tool for drawing causal inferences and exploring task-specific network interactions. Yet, a comprehensive synthesis of reading-related NIBS studies is still missing. We fill this gap by synthesizing the results of 78 NIBS studies investigating the causal involvement of brain regions for reading processing, and then link these results to a neurobiological model of reading. The included studies provide evidence for a functional-anatomical double dissociation for phonology versus semantics during reading-related processes within left inferior frontal and parietal areas. Additionally, the posterior parietal cortex and the anterior temporal lobe are identified as critical regions for reading-related processes. Overall, the findings provide some evidence for a dual-stream neurobiological model of reading, in which a dorsal stream (left temporo-parietal and inferior frontal areas) processes unfamiliar words and pseudowords, and a ventral stream (left occipito-temporal and inferior frontal areas, with assistance from the angular gyrus and the anterior temporal lobe) processes known words. However, individual differences in reading abilities and strategies, as well as differences in stimulation parameters, may impact the neuromodulatory effects induced by NIBS. We emphasize the need to investigate task-specific network interactions in future studies by combining NIBS with neuroimaging.

1. Introduction

The development of non-invasive brain stimulation (NIBS) techniques has substantially enriched our understanding of human brain function across the past decades. An increasing number of studies have used different NIBS protocols in various research disciplines, spanning electrophysiological applications, studies of human cognition and the treatment of neurological and psychiatric disorders (e.g., depression, schizophrenia, epilepsy, stroke) (Fertonani & Miniussi, 2017; Sandrini, Umiltà, & Rusconi, 2011; Terranova et al., 2019). While neuroimaging only provides correlational evidence for structure—function relationships, NIBS allows to probe not only the causal relevance of a given brain region for a function

of interest, but also the interaction between several nodes in larger brain networks.

One intriguing domain is the neurobiology of reading. Although NIBS is an ideal tool to explore the underlying reading network and deepen our understanding of the contribution of the core reading areas to reading processing, few studies have addressed these topics so far. While the use of NIBS in the study of language has been discussed in several previous reviews (Devlin & Watkins, 2007; Hartwigsen, 2015, 2016), a comprehensive overview of the modulation of the reading network(s) is still missing. Furthermore, research exploring the potential of NIBS to alleviate symptoms of reading impairments is still in its infancy and only a handful of studies have been conducted to date. The aim of the present review is to synthesize the results of all hitherto conducted reading-related NIBS studies to provide insight into the neurobiology of reading and identify challenges and avenues for future research. One of these future avenues for research is the potential of different NIBS protocols to modulate reading processing in impaired readers.

1.1.   Basic principles of NIBS protocols

NIBS is currently the only approach that allows to actively and non-invasively interfere with brain function in healthy human participants and has hence reshaped the way we explore brain-behavior relations (Valero-Cabré, Amengual, Stengel, Pascual-Leone, & Coubard, 2017). The main idea behind NIBS is to transiently modify neural activity to probe causal structure—function relationships, investigate functional network interactions and plasticity in cortical networks, and alter behavior (e.g., augment skill acquisition) to improve cognitive and motor function (Hartwigsen, 2016; Pascual-Leone, Walsh, & Rothwell, 2000). The two most widely applied NIBS methods are transcranial magnetic stimulation (TMS) and transcranial direct current stimulation (tDCS) (for reviews, see Bestmann, 2008; Nitsche & Paulus, 2000; Siebner, Hartwigsen, Kassuba, & Rothwell, 2009; Stagg & Nitsche, 2011; Walsh & Cowey, 2000).

In brief, TMS uses a strong, relatively focal, rapidly changing magnetic field that induces electrical currents in the brain tissue under the coil, and can elicit action potentials in axons of the cortex and in subcortical white matter, which leads to the release of neurotransmitters at terminal synapses (Priori, Hallett, & Rothwell, 2009; Ridding & Rothwell, 2007). TMS may be applied as single pulses, paired pulses or short trains (repetitive TMS/rTMS) before (offline TMS) or during a task (online TMS) (for details, see Valero-Cabré et al., 2017). Two of the most widely used rTMS protocols are 1 Hz stimulation and (continuous) theta burst stimulation (cTBS; for details, see Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). Depending on the stimulation duration and the specific protocol, offline rTMS may outlast the stimulation for 30–60 min (e.g., Parkin, Ekhtiari, & Walsh, 2015; Siebner & Rothwell, 2003), allowing for a long-lasting modulation of cortical activity that can be mapped with neuroimaging techniques (Siebner et al., 2009). The specific stimulation protocol and its (complex) interaction with the cognitive process at hand determines the outcome of the stimulations. Inhibitory stimulation has been repeatedly reported to result in a decrease of

brain activation in the targeted area and potentially also in remote, connected regions, which can be mapped with functional neuroimaging techniques (for reviews, see Hartwigsen, 2016; Hartwigsen & Volz, 2021). In contrast, the direction of the modulatory effect of facilitatory stimulation protocols on task-related activity is less clear. Indeed, facilitatory protocols also often result in decreases in task-related activity, which is usually interpreted as more efficient task processing, especially in challenging learning or memory tasks (see Fiori, Kunz, Kuhnke, Marangolo, & Hartwigsen, 2018, or Holland et al., 2011 for examples in the language domain). Aside from these local effects, both stimulation protocols may further induce up- or down-regulation of homologous or tightly connected regions, but the direction of such effects remains largely unexplored (Bergmann & Hartwigsen, 2020).

Aside from TMS, transcranial electrical stimulation (tES) methods, including tDCS, tACS (transcranial alternating stimulation) and — less frequently — tRNS (transcranial random noise stimulation), are also used to modulate brain function and induce plasticity. The majority of tES studies in the field of cognition rely on tDCS (Fertonani & Miniussi, 2017; Sandrini et al., 2011). tES delivers weak direct electrical currents (1–2 mA) through electrodes placed on the scalp (Michael A. Nitsche & Paulus, 2011). In tDCS, these currents are expected to slightly modulate the resting membrane potential of cortical neurons, thereby increasing or decreasing the likelihood of spontaneous or task-evoked firing (Priori et al., 2009), which may alter neuronal activity and behavior. A common assumption is that anodal tDCS increases the overall activity in a brain region while cathodal tDCS decreases it, which should in turn map onto the respective behavioral consequences (i.e., improvement versus disruption) for both online and offline application of tDCS (Krause, Márquez-Ruiz, & Cohen Kadosh, 2013). tACS and tRNS, on the other hand, are used to entrain or modulate specific neuronal oscillations in the brain using alternating currents. The major difference between both approaches is that tRNS uses currents alternating at random frequencies (Reed & Cohen Kadosh, 2018). Relative to TMS, tES techniques are cheaper and easier to apply. Moreover, they are also less prone to severe side effects than TMS and thus more suited for simultaneous combinations with behavioral interventions for training and therapy. However, given the lower focality of tES, direct structure—function relationships are harder to establish (Seibt, Brunoni, Huang, & Bikson, 2015).

1.2.   The neurobiology of reading

Becoming literal is a crucial milestone in human development as literacy provides not only the key to education, employment, and social contacts, but also to well-being and mental health. However, despite the growing interest in the neurobiology of reading and impairments thereof, we are still far from fully understanding its neuroanatomical and neurofunctional bases and developing effective intervention techniques to treat reading impairments (e.g., through neuromodulation of reading networks). Especially the latter is an area of applied research that has seen behavioral studies flourish over the past years, whereas methods targeting the brain directly have been neglected (van den Noort, Struys, & Bosch, 2015).

It is generally believed that learning to read establishes a new visual interface into language and modifies the processing of spoken language by developing the phonological areas of the brain through strengthening of the anatomical and functional links between phonemic and graphical representations and the enhancement of phonological coding (Dehaene, Cohen, Morais, & Kolinsky, 2015). In the past decades, neuroimaging has been predominantly used to investigate the neural correlates of reading, focusing on exploring the trajectory of brain activation patterns during literacy acquisition in typically-developing and disabled readers (e.g., Martin, Kronbichler, & Richlan, 2016; Pugh et al., 2001; Richlan, Kronbichler, & Wimmer, 2009; Shaywitz et al., 2002). The highly intertwined, and mostly universal reading network in the human brain comprises three core circuits, namely a left inferior frontal, a left dorsal temporo-parietal, and a left ventral occipito-temporal circuit (Pugh et al., 2001). The specific contributions of these regions as determined by neuroimaging studies are as follows (Kearns, Hancock, Hoeft, Pugh, & Frost, 2019): the posterior inferior frontal gyrus (pIFG) stores sound information and sequences information, making it essential for word recognition and decoding. The temporo-parietal cortex (TPC), encompassing the posterior superior temporal gyrus (pSTG), the supramarginal gyrus (SMG) and the angular gyrus (AG), is the key region for grapheme-phoneme conversion. While the pSTG contains primary and secondary auditory regions involved in phonological analyses, the SMG links phonemes onto graphemes and the AG is likely involved in word meaning processing (Kearns et al., 2019). Last, the occipito-temporal cortex (OTC) is either progressively specialized for orthographic coding during literacy acquisition (Dehaene & Cohen, 2011), or contains multimodal neurons encoding any language input (e.g., Stewart, Meyer, Frith, & Rothwell, 2001) or heterogeneous neuronal populations selectively encoding written language (Price & Devlin, 2003).

The most popular cognitive model for reading is Coltheart's dual-route cascaded model (DRC) of word recognition and overt reading (Coltheart, 2006) according to which written words are either read by graphene-to-phoneme conversion (sub-lexical pathway for unknown or very low frequency words) or by sight word reading (lexical pathway for words part of the lexicon). Researchers have tried to directly map this dual-route model on the brain (see Fig. 1; Kearns et al., 2019). According to this model, the dorsal (sub-lexical/decoding) pathway connects the left STG with the left IPL and left frontal areas, including the precentral gyrus (controlling articulation of speech) and the pIFG. Via this pathway, unknown words are read by accessing the IPL for linking letters to sounds and activating their pronunciations in the IFG. The ventral (lexical or sight word reading) pathway connects the OTC with the middle temporal gyrus (MTG) and the aIFG. As such, familiar words are directly recognized and linked to pronunciation in the IFG. The suitability of the dual-stream framework on the neural level was supported in an early meta-analysis (Jobard, Crivello, & Tzourio-Mazoyer, 2003).
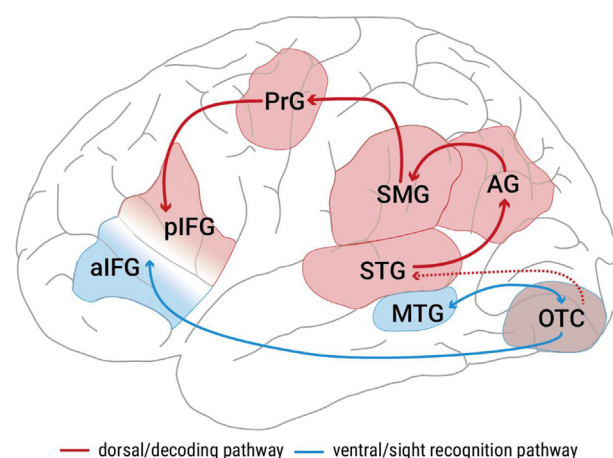

Fig. 1 − **A neurobiological dual-stream model of reading. Adapted from Kearns et al. (2019), this model is based on the dual-route model of reading (Coltheart, 2006). Decoding of unknown words is suggested to take place along the dorsal pathway, starting in the left OTC and STG, passing the inferior parietal lobe (SMG, AG, STG) and the precentral gyrus (PrG, motor cortex) on the way to the left posterior inferior frontal gyrus (IFG). Sight word reading of known words, on the other hand, is thought to happen along the ventral pathway and depends upon processing in the middle temporal gyrus (MTG), the occipito-temporal cortex (OTC) and the IFG.**

1.3. Previous NIBS research on language

NIBS has been shown to successfully modulate general learning and memory (e.g., Grafman & Wassermann, 1998), as well as semantic (Papeo et al., 2009) and overall language processing (Valero-Cabré et al., 2017). Furthermore, NIBS may alleviate aphasia symptoms (Devlin & Watkins, 2007; Hartwigsen et al., 2013), and can be used to probe short-term reorganization and adaptive plasticity in the brain (Hartwigsen, 2015). Recently, NIBS has been introduced as a potential treatment for dyslexia (Vicario & Nitsche, 2013). For instance, Van den Noort, Struys & Bush (2015) concluded that rTMS might be a valuable tool for investigating reading and dyslexia, and more recently, Cancer and Antonietti (2018) reported improvements in reading performance after tDCS to various reading-related brain regions.

The present review aims to provide the first comprehensive synthesis and discussion of studies that have applied NIBS to explore reading processing in the human brain. In particular, we focus on the contribution of NIBS studies to the functional neuroanatomy of reading-related processes to inform current models on reading. We also discuss the importance of combining NIBS with other methods and highlight the need for exploring the reading-impaired brain.

2. Methods

The search methods for the present review follow the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta Analyses) guidelines (Liberati et al., 2009). Studies exploring reading-related abilities were collected from previous reviews (Cancer & Antonietti, 2018; van den Noort et al., 2015) and three literature databases, namely PubMed, Web of Science (webofknowledge.com) and Google Scholar (see Fig. 2). Additionally, references from already included studies were screened. Searches included the key words 'reading' in combination with 'transcranial magnetic stimulation', 'transcranial direct current stimulation' and 'non-invasive brain stimulation'. The three searches yielded a total of 249 results in PubMed (59, 166 and 24 respectively for the searches) and a total of 311 results in Web of Science (59, 216 and 36 respectively for the searches). Moreover, the same search terms were used in Google Scholar and the first 1,000 search results were always screened (initially just looking at the title and then at the abstract). Overall, about 3560 studies were screened for matching the inclusion criteria, and 128 met the initial inclusion criteria and were more thoroughly and independently assessed by the two authors. Studies were then included if the following criteria were met:

(1) The study applied a NIBS protocol with either a between or within-subject design.
(2) The study applied a reading or reading-related task (e.g., silent or overt reading, lexical decision, phonological judgment, semantic judgment, syntactic judgment) of written language in the form of single words, pseudowords/pseudowords, syllables, letter strings or whole texts. Studies were generally only included if the task involved the assessment and interpretation of reading (e.g., in the form of reaction times or accuracy) for the reading processes described above. If a study included several tasks, only those in which stimulation happened during or before the reading-related task were included, i.e., the modulated process had to be the reading-related task.
(3) The participants were healthy young subjects (18—40 years).
(4) Participants' first language was an alphabetic language.

Altogether, 78 NIBS studies met the above-mentioned inclusion criteria (see Table 1). Note that differences in orthographic depth may potentially impact the neuromodulatory effects induced by NIBS. However, we did not find studies that applied the exact same stimulation parameters while targeting the same region. Consequently, the potential effect of a language's orthographic depth and its interaction with the induced NIBS effects cannot be assessed based on the included studies.

3. Results

Due to the large number of NIBS studies exploring reading processing, we divided the studies according to the targeted sub-processes, starting with the smallest reading units (i.e., letters) and progressively continuing to more abstract processes (see Table 1; different categories are marked in different colors as provided in brackets in the following
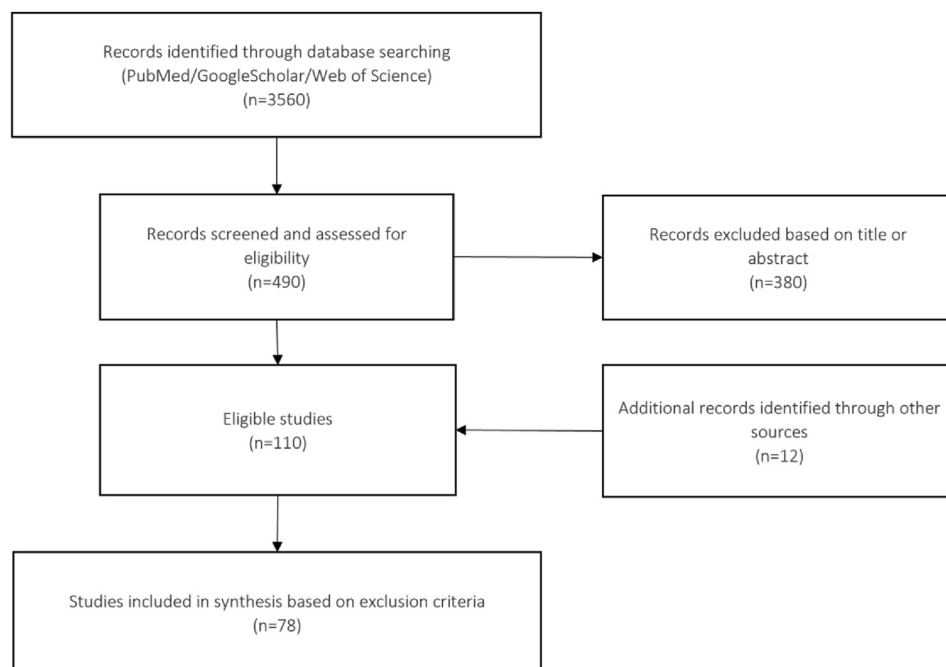

Fig. 2 — PRISMA flowchart displaying the process of literature search and screening. Cut-off date for the publication of studies was December 2020. In the third step (records excluded), studies that did not meet the inclusion criteria upon first screening and assessment were excluded. After additional records were identified, full manuscripts were then screened and after applying the exclusion criteria in the final step, 76 studies remained.

Table 1 – All included studies are sorted according to task, starting with studies applying a task of only one category, namely orthographical (green), phonological (red), and semantic tasks (blue), sentence reading (yellow) and artificial learning (grey). Then, all studies applying studies at the interface of two associated skills (e.g., phonology–semantics interface during lexical decision) or studies that use two to three tasks investigating separate skills are presented. Studies within categories are alphabetically ordered.

	Study	Subjects (L1)	Method	Site	Task	Results
🟩	Cattaneo et al. (2008) *EJN*	12 (Italian)	online spTMS (single pulse at stimulus onset)	L PPC	letter adaptation/priming	spTMS of left PPC → facilitation of detection of non-primed letters
🟩	Cattaneo, Rota, Walsh, Vecchi, and Silvanto (2009) *Cereb Cortex*	13 (Italian)	online spTMS (single pulse at stimulus onset)	L PPC R PPC	letter adaptation/priming	spTMS of right PPC → no effect spTMS of left PPC→ facilitation of detection of primed letters
🟩	Cazzoli et al. (2014) *J Cogn Neurosci*	24 (English)	rTMS (trains of 300 pulses at 50 Hz for 20s)	L/R PPC	letter migration in target words	rTMS at 50 Hz of right PPC → higher number of letter migrations lateralized to target words presented on the left
🟩	Mangano et al. (2015) *Neuropsychol*	88 (Italian)	online rTMS (1 Hz for 600 msec/10 Hz for 500 msec)	L PPC R PPC L vOTC	letter search	rTMS at 1/10 Hz of left PPC →faster and more accurate letter search
🟩	Rauschecker et al. (2011) *Neuron*	8 (English)	online ppTMS (dual-pulses 45 msec apart) + fMRI	L VWFA	lexical decision (word forms in motion-dots and luminance-dots)	ppTMS of left VWFA → disruption of reading performance for motion-dots but not luminance-dots
🟥	Aziz-Zadeh et al. (2005) *J Cogn Neurosci*	12/16 (Italian)	online rTMS (12 pulses at 5 Hz)	L pIFG L motor cortex	syllable counting	rTMS at 5 Hz of left pIFG and left motor cortex → longer latencies during overt/covert syllable counting
🟥	Hartwigsen, Price, et al. (2010) *PNAS*	28 (German)	online rTMS (4 pulse trains at 10 Hz)	L SMG R SMG	syllable judgment semantic judgment (man-made vs natural)	rTMS at 10 Hz of left/right/bilateral SMG → decreased accuracy and increased reaction times during syllable judgment
🟥	Hartwigsen et al. (2013) *PNAS*	17 (German)	rTMS (cTBS) (600 pulses at 50 Hz for 40s) + fMRI	L pIFG L aIFG	pseudoword repetition	rTMS (cTBS) at 50 Hz of left a/pIFG → no effect
🟥	Moliadze et al. (2019) *Brain Stim*	24 (German)	Offline tACS (1 mA for 20min/10 Hz) + EEG	bilateral pIFG	syllable judgment	Offline tACS at 10 Hz of bilateral pIFG → faster response speed for syllable counting task and increased theta power
🟥	Nixon et al. (2004) *J Cogn Neurosci*	6 (English)	online rTMS (10 Hz for 500 msec)	L pIFG L pars triangularis	homophone judgment	rTMS at 10 Hz of left pIFG → decreased accuracy and increased reaction times rTMS of left pars triangularis → no effect
🟥	Sliwinska et al. (2012) *Front Psychol*	40 (English)	online rTMS (double pulses at 10 Hz each 40 msec)	L SMG	homophone judgment	rTMS at 10 Hz of left SMG at 80/120, 120/160, and 160/200 msec post-stimulus onset → increased reaction times for homophone judgments
🟥	Stoeckel et al. (2009) *Cortex*	22 (English)	online rTMS (10 Hz for 300 msec) online spTMS (pulses at 120/180/240/300 msec post onset)	L SMG	homophone judgment	rTMS at 10 Hz of left SMG → disruption of homophone judgments Online spTMS at 10 Hz of left SMG → facilitation of homophone judgments at 180 msec post-stimulus onset

Table 1 — (continued)

502

	Study	Subjects (L1)	Method	Site	Task	Results
■	Wheat et al. (2013) *Brain and Language*	12 (Dutch)	online spTMS (pulse at 75/100/125/225/300/500 msec post stimulus + fMRI	L pIFG	nonword reading, word reading	spTMS of left pIFG→ slower reading times of words and pseudowords at 225−300 msec post stimulus stimulation
■	Younger et al. (2016) *Front Neurosci*	100 (English)	online atDCS (1.5 mA for 20min)	L IPL R SPL	rhyme judgment, word reading	atDCS of left IPL → worse performance during rhyme judgment atDCS of left IPL → greater improvements in sight word reading task
■	Cattaneo et al. (2010) *NeuroImage*	12 (Italian)	online spTMS (single pulse at word onset)	L premotor cortex	semantic judgment (tools *vs* animals)	spTMS of left premotor cortex → priming effect for tools eliminated
■	Davey et al. (2015) *J Neurosci*	18 (English)	offline rTMS (1 Hz for 10min)	L AG L pMTG	word-picture matching (thematic *vs* identity)	rTMS at 1 Hz of left AG → lower accuracy for strong association couples and at the subordinate level rTMS at 1 Hz of left pMTG → lower accuracy of weak associations and identity matching
■	Devlin et al. (2003) *J Cogn Neurosci*	9 (English)	online rTMS (10 Hz for 300 msec) online spTMS (single pulses at 10 Hz each 50 msec) + fMRI	L aIFG	semantic judgment (man-made *vs* natural)	r/spTMS at 10 Hz of left aIFG → increased reaction times for semantic decision
■	Hallam et al., 2016 *Neuropsychologia*	18 (English)	offline rTMS (1 Hz for 15min) + fMRI	L IFG L occipital pole	semantic association judgment	rTMS at 1 Hz of left IFG and occipital pole → no effect of stimulation on task fMRI results: task-dependent modulation in right IFG, pMTG and pre-SMA and left IFG activation reduction for easy trials
■	Harpaz et al. (2009) *Cortex*	11 (Hebrew)	online spTMS (10 Hz)	L TPJ R TPJ	semantic judgment (subordinate *vs* dominant meaning)	spTMS at 10 Hz of left TPJ → higher accuracy and higher sensitivity to dominant meaning blocks spTMS at 10 Hz of right TPJ → higher accuracy and sensitivity to subordinate meaning blocks
■	Hoffman et al. (2010) *J Neurosci*	13 (English)	offline rTMS (1 Hz for 10 min)	L VLPFC/IFG	synonym judgment (abstract *vs* concrete; context *vs* without context)	rTMS at 1 Hz of left IFG → increased reaction times only for abstract words presented out of context
■	Jackson, Lambon Ralph, & Pobric (2015) *J Cogn Neurosci*	15 (English)	online ppTMS (dual pulses 40 msec apart at 100/250/400/800 msec)	L ATL	synonym judgment	ppTMS of left ATL after 400 msec → worse performance during synonym judgment
■	Jung and Lambon Ralph (2016) *Cereb Cortex*	35 (English)	offline rTMS (5 pulses at 7 Hz for 600 msec) +fMRI	L/R ventral ATL	synonym judgment	rTMS (cTBS) at 50 Hz of left ventral ATL → slower responses during synonym judgments
■	Köhler et al. (2004) *J Cogn Neurosci Res*	12 (English)	online rTMS (5 pulses at 7 Hz for 600 msec) + fMRI	L aIFG	word encoding (abstract *vs* concrete)	rTMS at 7 Hz of left aIFG during word encoding → words recognized with higher accuracy

◼	Lambon Ralph et al. (2009) *Cereb Cortex*	10 (English)	offline rTMS (1 Hz for 10 min)	L TPC R TPC	synonym judgment	rTMS at 1 Hz of left/right TPC → increase in reaction times for synonym judgment
◼	Pobric et al. (2008) *J Cogn Neurosci*	10 (English)	online rTMS (10 Hz for 500 msec)	L IFG R STS R IFG	semantic judgment (literal *vs* metaphorical word pairs)	rTMS at 10 Hz of left/right IFG → increased reaction times and lower accuracy for literal word pairs
◼	Pobric et al., 2009 *Cortex*	12 (English)	offline rTMS (1 Hz for 600s)	L ATL R ATL	synonym judgment	OrTMS at 1 Hz of right ATL → slower semantic decisions, particularly for low imageability items
◼	Pobric et al. (2010) *Neuropsychologia*	10 (English)	offline rTMS (1 Hz for 10min)	L ATL R ATL	semantic judgment	Offline rTMS at 1 Hz of left and right ATL → slower semantic judgments
◼	Price et al. (2016) *J Neurosci*	18 (English)	offline atDCS (2 mA for 20 min)	L AG R AG	semantic judgment (meaningful *vs* not meaningful) letter string viewing	atDCS of the left AG → faster comprehension of semantically plausible word pairs
◼	Pulvermüller et al. (2005) *Eur J Neurosci*	11 (English)	online spTMS (single pulse at 150 msec post stimulus onset)	L motor cortex (arm) L motor cortex (leg)	lexical decision (action-related words for leg *vs* hand actions)	spTMS of left motor area (arm) → faster responses for arm words spTMS of left motor areas (leg) → faster lexical decisions on leg words
◼	Reilly et al., 2019 *Front Psychol*	24 (English)	online spTMS (single pulse at 150/300/450 msec post-stimulus onset	L premotor cortex	semantic plausbility judgment	spTMS of left premotor cortex 300 msec post-verb presentation → impaired comprehension of literal and metaphoric sentences
◼	Sliwinska et al. (2015) *J Cogn Neurosci*	12 (English)	online rTMS (5 pulses at 10 Hz for 500 msec)	L SMG L AG	synonym judgment	rTMS at 10 Hz of left AG → slowed responses during synonym judgment
◼	Whitney et al. (2011) *Cereb Cortex*	16 (English)	offline rTMS 1 Hz for 10min	L pars triangularis L pMTG	semantic judgment (cue-target word pair decision)	rTMS at 1 Hz of both sites → worse performance when semantic associations were weak/semantic judgments were demanding
◼	Whitney, Kirk, O'Sullivan, Ralph, and Jefferies (2012) *J Cogn Neurosci*	16 (English)	offline rTMS (1 Hz for 10min)	L pars triangularis L pMTG L IPS	semantic judgment (cue-target word pair decision)	rTMS at 1 Hz of left IFG and pMTG → worse performance during semantic judgment
◼	Willems et al. (2011) *Psychol Sci*	18 (English)	rTMS (cTBS) (3 pulses at 5 Hz in bursts for 40s; total: 600 pulses)	L premotor cortex R premotor cortex	lexical decision	rTMS (cTBS) at 5 Hz of left premotor cortex → faster responses to manual action verbs
◼	Acheson and Hagoort (2013) *J Cogn Neurosci*	43 (Dutch)	offline rTMS (cTBS) (600 pulses in trains of 3 pulses at 50 Hz) + eye tracking	L MTG L pIFG	sentence reading	rTMS (cTBS) at 50 Hz of left pIFG → increased sensitivity to ambiguity
◼	Branzi et al., 2021 *J Cogn Neurosci*	18 (English)	online rTMS (5 pulses at 10 Hz for 500 msec)	L AG	text reading	rTMS at 10 Hz of left AG → no effect on reading times

(continued on next page)

Table 1 — **(continued)**

504

	Study	Subjects (L1)	Method	Site	Task	Results
⬛	Claus et al. (1993) *J Neurol*	44 (German)	online rTMS	L TPJ/IPL R TPJ/IPL	sentence reading	rTMS of left TPJ/IPL → for those who used an integral reading strategy, stimulation led to lower accuracy; word by word reading unaffected
⬛	De Vries et al., 2009 *J Cogn Neurosci*	44 (German)	online atDCS (1 mA for 20 min)	L IFG	artificial grammar learning	atDCS of left IFG → better overall performance and better detection of syntactic violations
⬛	Fiori et al. (2011) *J Cogn Neurosci*	10 (Italian)	online atDCS (1 mA for 20 min)	L TPJ	artificial word learning	atDCS of left TPJ → shorter naming latencies during anodal stimulation
⬛	Flöel et al. (2008) *J Cogn Neurosci*	19 (German)	online a/ctDCS (1 mA for 20min)	L TPJ	artificial word learning	atDCS of left TPJ → faster and better associative learning compared to ctDCS and sham
⬛	Javadi and Walsh (2012) *Brain Stim*	32 (English)	Online a/ctDCS (1 mA)	L DLPFC L motor	word memorization/ word learning	atDCS to left DLPFC → improvement in memory during encoding ctDCS to left DLPFC → deterioration of recognition of learnt words
⬛	Liuzzi et al. (2010) *Curr Biol*	62 (German)	online a/ctDCS (1 mA for 20min)	L motor L DLPFC	artificial word learning	ctDCS of left motor cortex → reduced vocabulary learning, especially coupling action with novel verbs
⬛	Meinzer et al. (2014) *Cortex*	40 (German)	online atDCS (1 mA for 20min)	L TPJ	artificial word learning	atDCS of left TPJ → better overall learning of novel words (pseudowears) compared to sham
⬛	Younger and Booth 2018 *Front Neurosci*	79 (English)	online atDCS (1.5 mA for 20min)	L IPL	artificial alphabet learning	atDCS of left IPL → low skill readers showed better maintenance of trained material compared to high skill readers, who showed worse acquisition after stimulation
⬛⬛	Braet and Humphreys (2006) *Exp Brain Res*	10/11 (English)	online rTMS (3 pulses at 20 Hz; total: 600 pulses)	R PPC	word reading (mixed *vs* lower case)	rTMS at 20 Hz of right PPC → disruption of reading, specifically mixed case words
⬛⬛	Costanzo et al. (2012) *Neuropsychologia*	10 (Italian)	offline rTMS (10 trains of 50 stimuli at 5 Hz)	L STG L IPL	word, pseudoword and text reading	rTMS at 5 Hz of left IPL → improved pseudoword reading accuracy rTMS at 5 Hz of right STG → decreased text reading accuracy
⬛⬛	Cummine et al. (2019) *Brain Lang*	77 (English)	offline a/cTDCS (1 mA for 13min)	L AG	word reading	a/ctDCS of left AG → decreased semantic effects during word reading (subjects with greater imageability effects before stimulation showed the greatest reduction thereof after stimulation)
⬛⬛	Duncan et al. (2010) *J Cogn Neurosci*	64 (English)	online ppTMS (paired pulses at 10 Hz for 500 msec) + fMRI	L vOTC L latOC	lexical decision	ppTMS at 10 Hz of left vOTC → slowed word, but not pseudoword responses
⬛⬛	Gough et al. (2005) *J Neurosci*	11 (English)	online rTMS (3 pulses of 300 msec at 10 Hz each 100 msec)	L pIFG L aIFG	homophone judgment synonym judgment	rTMS at 10 Hz of left pIFG → increased reaction times during homophone judgment rTMS at 10 Hz of left aIFG → increased reaction times during synonym judgment

Hartwigsen, Price, et al., 2010 *Neuropsychol*	35 (German)	online rTMS (4 pulses at 10 Hz 100 msec after word onset)	L/R pIFG L/R aIFG	syllable judgment semantic judgment (man-made *vs* natural)	rTMS at 10 Hz of left/right aIFG → lower accuracy and increased reaction times during syllable judgment rTMS of left/right/bilateral pIFG → lower accuracy and increased reaction times during syllable judgment
Hauck et al. (2015a) *BMC Neurosci*	19 (German)	offline rTMS (5 Hz and 7 Hz)	various brain regions	pseudoword reading	rTMS at 5 Hz and 7 Hz → lower accuracy in pseudoword reading (3–4%)
Hauck et al. (2015b) *PLoS ONE*	19 (German)	offline rTMS (5 Hz and 7 Hz)	various brain regions	pseudoword reading (among others)	rTMS at 5 Hz and 7 Hz → highest error rates of stimulation caused for verb generation and action naming, pseudoword reading barely generated errors
Klaus and Hartwigsen (2019) *Hum Brain Mapp*	24 (German)	online rTMS (5 pulses at 10 Hz for 500 msec)	L aIFG L pIFG	production of rhyming words production of semantically related words	rTMS at 10 Hz of left pIFG → decrease in naming latencies during production of rhyming words rTMS at 10 Hz of left aIFG → increase in naming latencies during semantic task
Kuhnke et al. (2020) *NeuroImage*	26 (German)	online rTMS (10 Hz)	L IPL	lexical decision, sound judgment, action judgment	rTMS at 10 Hz of left IPL → increase in errors on action judgments; the stronger the stimulation, the worse the performance
Lavidor and Walsh (2003) *J Cogn Neurosci*	8 (English)	online rTMS (8 Hz for 500 msec)	L OTC R OTC	lexical decision	rTMS at 8 Hz of left and right OTC → increase in reaction times and error rates during the lexical decision task
Laycock et al. (2009) *Exp Brain Res*	12 (English)	online ppTMS (1 Hz 32 msec apart between 9 and 221 msec from word onset)	L V5/MT L V1/V2	word reading	ppTMS at 1 Hz of left V1/V2 (between word onset and 36 msec post word onset) → disruption of accurate word discrimination ppTMS at 1 Hz of left V5/MT (at word onset and 130 msec post word onset) → disruption of accurate word discrimination
Leff et al. (2001) *Cereb Cortex*	14 (English)	offline rTMS (15 pulses at 10 Hz for 1500 msec) + eye-tracking	L PPC R PPC	word reading	rTMS at 10 Hz of left PPC → slower reading speed for array of five words
Liederman et al. (2003) *Brain Lang*	16 (English)	offline rTMS (1 Hz for 3 blocks of 7.5 min; total: 1350 pulses)	L V5/MT	pseudoword reading (naming), phonological judgment, orthographic judgment	rTMS at 1 Hz of left visual field → lower accuracy during pseudoword naming
Malyutina et al. (2018) *Brain Lang*	72 (Russian)	online a/ctDCS (1.5 mA for 20min)	L/R IFG	lexical decision, sentence comprehension	a/ctDCS of left/right IFG → no effect of stimulation
Manenti et al. (2010) *Brain Topogr*	11 (Italian)	online rTMS (11 pulses at 10 Hz for 1000 msec) + fMRI	L/R PPC L/R DLPFC	word reading	rTMS at 10 Hz of right DLPFC and left PPC → increased reaction times for episodic retrieval of abstract but not concrete words

Table 1 — (continued)

	Study	Subjects (L1)	Method	Site	Task	Results
■ ■	Papeo et al. (2009) *PLOS one*	11/14 (Italian)	online spTMS (single pulses at 170, 350 and 500 msec)	L premotor cortex	syllable judgment semantic judgment (no physical act *vs* physical act)	spTMS of left premotor cortex → no effect of stimulation
■ ■	Pattamadilok et al. (2015) *J Cogn Neurosci*	92 (French)	online ppTMS paired pulses at 10 Hz for 400 msec	LvOT LpMTG LSMG	word reading, pseudoword reading	ppTMS at 10 Hz of left pMTG and left SMG → affecting regular and irregular word but not pseudoword reading Stimulation of vOTC → disruption affected both word and pseudoword reading
■ ■	Pattamadilok et al. (2016) *Hum Brain Mapp*	15 (French)	online ppTMS (paired pulses at stimulus onset and 40/60/100/120/160 msec post stimulus onset)	L premotor cortex	lexical decision	ppTMS of left premotor cortex in early time-windows (60 −160 msec) → increased reaction times for pseudowords
■ ■	Pattamadilok et al. (2019) *NeuroImage*	23 (French)	online ppTMS (paired pulses separated by 100 msec) + fMRI	L vOTC R vOTC	lexical decision (auditory/visual)	ppTMS of left vOTC → accelerated lexical decisions only when the adaptors and the targets shared the same modality
■ ■	Rodrigues de Almeida et al. (2019) *J Neurosci Res*	60 (English)	online a/ctDCS (1.5 mA for 20min)	L pIFG	lexical decision, word/pseudoword naming	a/ctDCS of left pIFG→ improved word naming performance
■ ■	Rodrigues de Almeida, Pope, and Hansen (2020a) *Lang Cogn Neurosci*	60 (English)	online a/ctDCS (1.5 mA for 20min)	L STG	lexical decision, word/pseudoword naming	a/ctDCS of left STG → no effect on lexical decision a/ctDCS of left STG → decrease in reaction times (more significantly cathodal) for word and pseudoword naming
■ ■	Rodrigues de Almeida, Pope, and Hansen (2020b) *Cogn Process*	20 (English)	online a/ctDCS (2 mA for 20min) + fMRI	L/R IFG	lexical decision, word/pseudoword naming	a/ctDCS of left/right IFG → no effect on word naming; post-hoc analyses of lexical decision show weak results on pseudowords
■ ■	Skarratt and Lavidor (2006) *J Cogn Neurosci*	12 (English)	online rTMS (single train at 10 Hz for 500 msec)	L OC R OC	lexical decision	rTMS at 10 Hz of left OC → impairments in word recognition with differences in word length
■ ■	Stewart et al. (2001) Neuropsychologia	8 (English)	online rTMS (10 Hz for 600 msec)	L OC R OC	word reading, pseudoword reading	rTMS at 10 Hz of left and right OC → no effect of stimulation
■ ■	Thomson et al. (2015) *Front Hum Neurosci*	39 (English)	online atDCS (2 mA for 20min)	L TPJ R TPJ	word reading	atDCS of right TPJ → faster and more accurate word reading
■ ■	Tomasino et al., 2008 *Neuropsychologia*	20 (German)	online spTMS (single pulses at 150/300/450/600/750 msec after stimulus onset)	L premotor cortex	word reading, motor imagery	spTMS of left premotor cortex → faster responses during the imagery task, but no effect on word reading

Turkeltaub et al. (2012) *Brain Stim*	25 (English)	online a/ctDCS (1.5 mA for 20min)	L TPJ/STG R TPJ/STG	word reading, pseudoword reading	a/ctDCS of left TPJ/STG → improvements in word reading efficiency in below average readers
Vignali et al. (2019) *Neurosci Lett*	40 (German)	online ctDCS (1.5 mA for 30min) + eye-tracking	L/R IPS	lexical decision	ctDCS of left/right IPS → no effect of stimulation
Weltman and Lavidor (2013) *Exp Brain Res*	32 (Hebrew)	online a/ctDCS (1.5 mA for 20min)	bilateral TPC	semantic priming, lexical decision	Online right anodal/left cathodal tDCS of both left and right TPC → decrease in word reading accuracy during lexical decision; decrease in accuracy in semantic decisions for unrelated primes and targets
Westwood et al. (2017) *Cortex*	46 (English)	online atDCS (1 mA for 15min)	L aIFG L pMTG	word reading	atDCS of left aIFG and left pMTG → no effect of stimulation
Franzmeier et al. (2012) *J Cogn Neurosci*	62 (English)	online spTMS	L STS/pMTG R STS/pMTG	sentence reading (expected *vs* unexpected *vs* incorrect endings)	spTMS of left STS/pMTG → slower responses to expected and unexpected endings
Hussey et al. (2015) PLOS one	28 (English)	Online a/ctDCS (2 mA for 30min)	L prefrontal cortex	sentence reading (non-ambiguous *vs* ambiguous)	a/ctDCS of left prefrontal cortex → overall higher accuracy on ambiguous items compared to the cathodal group
Oliveri, Romero & Papgno (2004) *J Cogn Neurosci*	15 (Italian)	offline rTMS (300 pulses at 1 Hz)	L temporal L frontal	sentence-picture matching (literal *vs* idiomatic)	rTMS at 1 Hz of left temporal cortex → lower accuracy and slower reaction times for literal and idiomatic sentences

a/pIFG — anterior/posterior inferior frontal gyrus, AG — angular gyrus, ATL — anterior temporal lobe, fMRI — functional magnetic resonance imaging, DLPFC — dorsolateral prefrontal cortex, IPL — inferior parietal lobe, L1 - first language, latOTC — lateral occipito-temporal cortex, (p)MTG — (posterior) middle temporal gyrus, OC — occipital cortex PPC — posterior parietal cortex, ppTMS — paired pulse transcranial magnetic stimulation, rTMS - repetitive transcranial magnetic stimulation, SMG -supramarginal gyrus, spTMS — single pulse transcranial magnetic stimulation, TPC — temporo-parietal cortex, TPJ — temporo-parietal junction, V1/V2 — primary and secondary visual cortex, V5/MT — middle visual field, VLPFC — ventrolateral prefrontal cortex, vOTC — ventral occipito-temporal cortex; VWFA — visual word form area.

sentence). The results are divided into (1) orthographical processing (letters; green), (2) phonological processing (red), (3) processing at the phonology—semantics interface (word and pseudoword reading, and lexical decisions) (blue/red), (4) semantic processing (blue), (5) sentence-level processing (yellow) and (6) artificial learning studies (grey). Following the presentation of the results, we approach the findings from a different perspective, namely by considering the impact of individual differences in reading performance and strategies and the potential lack of spatial focality which may affect the neuromodulatory effects of NIBS. Finally, we discuss the findings considering network effects and plasticity as accessible by the combination of NIBS with neuroimaging, electroencephalography and eye tracking.

3.1. Orthographical processing

The few studies that used orthographic tasks, such as letter priming, letter search or letter viewing, confirmed a role of the left posterior parietal cortex (PPC) for these types of tasks. Mangano et al. (2015) found that 1 Hz and 10 Hz rTMS over the left PPC facilitated a letter search task, such that letters could be faster identified with a higher accuracy. This effect was specific for the left PPC but not observed for the stimulation of control sites in the right PPC or the left vOTC, despite the latter being a classical reading region. These findings were complemented by two studies that explored the association between visual linguistic elements and the left PPC (Cattaneo et al., 2008, 2009). These studies reported that the left, but not the right PPC, was critically involved in the detection of adapted letters and single-pulse TMS facilitated the detection of non-primed letters. In other words, these results suggest that the left PPC could be highly specialized for the processing of letters, which would speak in favor of its contribution to reading (e.g., by enabling graphene-to-phoneme conversion). Moreover, Rauschecker et al. (2011) used a modified lexical decision task in which word forms were presented in motion-dots or luminance-dots and stimulated the left visual word form area (fusiform gyrus) with paired pulse TMS. Only the performance of motion-dot words was affected in the form of decreased accuracy, but not the other presentation forms, arguing for a highly selective visual contribution of that area. Finally, a 50 Hz rTMS study by Cazzoli, Müri, Kennard, and Rosenthal (2014) looked into the letter migration phenomenon. This phenomenon describes the fact that in skilled readers, short presentation of words such as "hurt" and "hint" may result in the production of "hunt" instead of either the first or second word. In that study, right PPC stimulation led to a higher number of such letter migrations for target words that were presented on the left side. The authors interpret these results in favor of a role of the right PPC for the processing of visual attributes of words. In summary, a few studies reported that the left, but not the right PPC, is critically involved in the detection of adapted letters and single-pulse TMS facilitated the detection of non-primed letters. Hence, the left PPC could be highly specialized for the processing of letters, which would support its contribution to reading, e.g., by enabling graphene-to-phoneme conversion.

3.2. Phonological processing

3.2.1. The contribution of the left inferior frontal cortex for phonological processes

All studies of the present review that combined phonological tasks with inhibitory TMS of the left pIFG report a TMS-induced disruption of phonological task performance. Inhibitory online stimulation of the left pIFG with 10 Hz rTMS led to impaired accuracy during homophone judgment tasks (Gough, Nobre, & Devlin, 2005; Nixon, Lazarova, Hodinott-Hill, Gough, & Passingham, 2004), syllable counting (Aziz-Zadeh, Cattaneo, Rochat, & Rizzolatti, 2005; Hartwigsen, Price, et al., 2010) and the reading of words and pseudowords (Wheat et al., 2013). Notably, Hartwigsen, Price, et al. (2010) targeted the left, right and bilateral pIFG with 10 Hz rTMS, and reported that stimulation of all sites resulted in a similar disruption of phonological processing, without any evidence for an additive effect when targeting both areas simultaneously. This suggests that both the left and right pIFG might contribute to phonological processes, at least when more meta-linguistic tasks such as syllable counting are used. A single language production study reported an unexpected facilitation for 10 Hz rTMS during a rhyming task (Klaus & Hartwigsen, 2019), which was explained by a priming effect of the rTMS protocol that might be time specific. Yet, the disruption of the left pIFG did not significantly affect overt pseudoword repetition in a later study by the same group (Hartwigsen et al., 2013). These authors reasoned that the disruptive effect might have been compensated by an upregulation of the homologous right-hemispheric area, as observed during task-related fMRI after TMS. Additionally, it is also conceivable that a stronger contribution of left temporo-parietal areas for decoding may have compensated for the disruption since pseudoword repetition is a very easy and automatic task that likely relies on parieto—frontal interactions (but see results of Wheat et al., 2013). Such adaptive short-term plasticity in response to inhibitory neurostimulation can be mapped by combining offline rTMS with subsequent functional MRI during different language tasks (discussed in Hartwigsen & Volz, 2021; see section 3.8. for further details).

A single tACS study provides further evidence that high-frequency offline stimulation over the bilateral pIFG leads to better phonological performance by increasing theta power in this area. Moliadze et al. (2019) combined offline 10 Hz tACS with electroencephalography (EEG) at rest and during task performance to explored the role of the bilateral pIFG for phonological processes and the underlying neurophysiology of 10 Hz stimulation. Bilateral prefrontal tACS prior to task performance decreased response speed for the phonological task (judging the number of syllables), but not for a simple decision-making task. At the neurophysiological level, the authors found a significant increase in task-related theta power after the word stimulus following active relative to sham stimulation. The individual increase in theta power was correlated with the tACS-induced facilitation of response speed, indicating that increased theta power might reflect the neurophysiological correlate of the behavioral facilitation effect. These results show that rhythmic NIBS protocols may

induce changes in task-specific oscillatory dynamics during language processing which may be related to the observed modulatory effects of a given NIBS protocol on task performance.

3.2.2. The contribution of left inferior parietal areas for phonological processes

The left SMG seems to be a critical region for the processing of phonological properties of words. Exploring the role of the SMG in single word decisions, Hartwigsen, Baumgaertner, et al. (2010) found that disruption of the left SMG with 10 Hz online rTMS delayed syllable judgments and affected task accuracy. Note that these effects were found independently of the stimulated hemisphere for either left or right SMG disruption. The functional relevance of the left SMG for phonological processing was further confirmed by two other studies that used 10 Hz online rTMS (Sliwinska, Khadilkar, Campbell-Ratcliffe, Quevenco, & Devlin, 2012; Stoeckel, Gough, Watkins, & Devlin, 2009). The latter study found slower response speed during homophone judgements after SMG stimulation, but differences in accuracy were not observed. Also, Younger, Wagner, and Booth (2016) support the role of the left IPL for phonological processing (rhyme judgments) in their tDCS study, in which they targeted the left IPL with online atDCS. Pattamadilok et al. (2015), on the other hand, reported that paired-pulse TMS of the SMG only affected word reading (regular and irregular words in their study) but not pseudoword reading, pointing towards a more semantic than phonological (decoding) contribution of that region to reading. Yet, the notion that the SMG is critically involved in phonological processing was already suggested in earlier neuroimaging and patient studies (Devlin, Matthews, & Rushworth, 2003). Recently, Oberhuber et al. (2016) reported that the posterior dorsal SMG showed highest activation for words, whereas the anterior dorsal SMG showed the highest activation for pseudowords. This suggests that the larger SMG region may be divided into several subareas that differentially contribute to reading processing. Furthermore, a key role of the left SMG for the decoding of letters into sounds has been suggested by numerous imaging studies and meta-analyses (e.g., Binder, Desai, Graves, & Conant, 2009; Vigneau et al., 2006). Hence, the findings of NIBS studies provide further evidence that the left SMG contributes to phonological processing at multiple levels, such as sublexical grapheme-phoneme relations, and phonological working memory (Oberhuber et al., 2016).

3.3. The phonology—semantics interface: implicit and explicit word and pseudoword processing

3.3.1. Time-specific contributions of brain regions for reading processes

The core reading areas are causally involved in word and pseudoword reading at different time points, as predicted by a neurobiological dual-stream model of reading. To make this more transparent, let us start with areas at the start of reading processing. In a study looking into the role of the occipital cortex (OC) for reading, disruption of the V1/V2 (visual field) and the V5/MT impaired accurate word reading during word discrimination. The disruptive effect occurred when stimulation was delivered over V1/V2 between word onset and 36 msec post word onset, and over V5/MT at word onset and 130 msec post word onset (Laycock, Crewther, Fitzgerald, & Crewther, 2009). Investigating the temporal dynamics of reading processes in temporo-parietal areas with paired-pulse online TMS, Pattamadilok, Ponz, Planton, and Bonnard (2016) found that stimulation of the left vOTC always disrupted the reading of words and pseudowords, supporting the findings of Laycock and colleagues. The authors further found that early stimulation (i.e., 60—160 msec post stimulus presentation) of the left SMG and pMTG led to an increase in reading times for pseudowords, but not for words, providing further evidence for a dual-stream route. However, 10 Hz online rTMS delivered to the right and left posterior inferior temporal cortex in close proximity to the vOTC failed to induce any modulatory effect on word and pseudoword reding in another study (Stewart et al., 2001), which stands in contrast to the aforementioned suggested time-specific contribution of that area to word processing (Laycock et al., 2009). The divergent results between both studies might indicate that different subregions within the larger vOTC may differ with respect to their specialization for distinct language functions. In another study, the authors found that perturbation of the left pIFG with single-pulse TMS led to deficits in both word and pseudoword reading 225—300 msec post-stimulus onset, suggesting that the IFG is necessary for both processes (Wheat et al., 2013). In a study by Leff, Scott, Rothwell, and Wise (2001), 10 Hz rTMS was applied over the left and right PPC in combination with eye-tracking. The results showed that left PPC stimulation slowed the scanpath across the arrays of five words, leading to a delay of 45 msec to the next saccade, and thus affecting reading. This study shows the value of mapping NIBS effects with neurophysiological measures like eye movements (quantified as gaze times or pupil dilation), which may complement behavioural measures and may be especially suited to assess reading performance, Overall, it seems that early disruption of visual areas impairs word discrimination, and an early disruption of occipito-temporal areas disrupts the processing of words and pseudowords. This supports the notion that the OTC is the starting point for both processing streams in a dual-stream model of reading. Further in accordance with the dual-stream model, early disruption of temporo-parietal areas slows pseudoword reading, whereas late pIFG inhibition impairs both word and pseudoword reading.

3.3.2. The role of the bilateral PPC and temporo-parietal areas for word reading

Word reading is very likely to rely on attentional mechanisms rooted in the bilateral PPC and temporo-parietal areas. Focussing on the reading of words in mixed and lower case letters, Braet and Humphreys (2006) found that 20 Hz rTMS over the right PPC disrupted reading performance only for words in mixed case letters, suggesting that this area is involved in visual word recognition and possibly in attentional processes related to reading, but not reading processes per se. Manenti, Tettamanti, Cotelli, Miniussi, and Cappa (2010) found that 10 Hz rTMS applied to the left PPC (relative to right PPC or DLPFC stimulation) significantly impaired the retrieval of abstract, but not concrete words in terms of reading speed. Therefore, it seems most likely that the PPC is

critical for guiding attention in the visual processing of written language. Additionally, another study found that the left TPJ is critical for word reading on a general level, with atDCS to this area resulting in faster and more accurate word reading (Thomson, Doruk, Mascio, Fregni, & Cerruti, 2015), which might be due to the relevance of the AG and pSTG for semantic processes, however. The few NIBS studies that targeted the premotor cortex before or during explicit word reading did not report any significant stimulation effects on word reading (Papeo, Vallesi, Isaja, & Rumiati, 2009; Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008).

3.3.3. The role of left inferior parietal and occipital areas for pseudoword reading

Pseudoword reading can be improved by stimulation to several areas, including the left IPL, and potentially the left OC. In a study by Costanzo, Menghini, Caltagirone, Oliveri, and Vicari (2012), pseudoword reading accuracy improved after 5 Hz offline rTMS of the left IPL but not the pSTG, while right STG stimulation decreased text reading accuracy. The authors argued that the left STG was specifically involved in reading morphologically complex words and texts, and right STG stimulation must have exerted an inhibitory influence on its homologous area, which would support the importance of considering network−level activity and compensation mechanisms at play (see 3.8.). This finding goes hand in hand with the above reported disruption of pseudoword reading through rTMS to the left TPJ (see Pattamadilok et al., 2015). A NIBS study looking into linguistic processing more generally showed that 5 Hz and 7 Hz rTMS applied to various cortical language regions such as the inferior frontal cortex, the auditory cortex, and the IPL impaired pseudoword reading accuracy, resulting in increased error rates up to 3−4%. The same group reported that higher error rates for pseudoword reading were caused by disruption of the left ventro-lateral AG, the left pSTG and left dorsal IFG with 5 Hz rTMS (Hauck et al., 2015a, 2015b). Another area that might be causally involved in pseudoword reading is the left OC, as the perturbation of this area with 1 Hz rTMS during task performance impaired accuracy during pseudoword naming, while leaving phonological and orthographic judgments unaffected (Liederman et al., 2003). However, other studies failed to find evidence for a role of the left and right occipital cortices for pseudoword, and even word reading (Stewart et al., 2001). In particular, the exact timing of disruption might be a critical factor that is currently understudied.

3.3.4. Implicit word and pseudoword reading: results from lexical decision tasks

The few studies that have addressed the role of the left vOTC for reading show a significant role of this area for the processing of written language on the word-level. For instance, Duncan, Pattamadilok, and Devlin (2010) found that paired-pulse TMS of the left vOTC selectively affected word, but not pseudoword processing in a lexical decision task. This effect was anatomically specific as disruption of the lateral OTC showed no effects on word or pseudoword processing. The authors concluded that the left vOTC is primarily involved in the processing of familiar words, which is in line with its role for sight word reading according to neurobiological models of

reading. These results were complemented by Lavidor and Walsh (2003), who applied 8 Hz rTMS over the left and right OC to test the split fovea theory of word recognition. This theory proposes that visual word recognition is mediated by the splitting of the foveal image, with letters presented to the left of a fixation point being projected to the right hemisphere and letters presented to the right of fixation being projected to the left hemisphere. First, they observed that 8 Hz rTMS to either the left or right OC significantly delayed lexical decision latencies to centrally presented words, supporting the idea that the foveal representation of words is split between the cerebral hemispheres. Regardless of TMS, words with many orthographic neighbors sharing the same initial letters (so-called lead neighbors) facilitated lexical decisions more than words with few lead neighbors in their second study. Crucially, TMS over the right but not left OC impaired lead-, but not end-neighborhood facilitation, supporting the notion that the right OC has primacy in representing lead neighbors of a written word. However, in that study, TMS was selectively applied at word but not pseudoword onsets, leaving a potential contribution of the OC to pseudoword reading (and thus phonological processes) unclear. The role of the left vOTC in reading was further confirmed by Pattamadilok, Planton, and Bonnard (2019) who found accelerated lexical decisions after paired-pulse TMS of that area. These authors argued that the left vOTC essentially contributes to reading processes by encoding written and spoken language. However, Stewart et al. (2001) did not find evidence for a role of left vOTC in reading since neither left nor right vOTC stimulation with 10 Hz rTMS affected word or pseudoword reading in this study when applied during task processing. These findings contrast with the above discussed results on the contribution of the left (or right) vOTC to word reading and might stem from methodological differences between studies. As suggested in neurobiological models on reading (see introductory paragraphs; Kearns et al., 2019), the left vOTC is central for (and highly likely the starting point of) reading processing, as confirmed in NIBS studies targeting this area before and during semantic tasks.

Overall, studies using lexical decision paradigms reveal mixed results for a contribution of specific regions to this task. Especially tDCS studies fail to provide evidence for the causal involvement of various areas. Although the left IPL is implicated in semantic processes, a recent study by Kuhnke et al. (2020) did not find any effect of 10 Hz rTMS to the left posterior IPL on a lexical decision task. Another TMS study using a lexical decision paradigm revealed a contribution of the left OC to word recognition but differences could be observed depending on word length (Skarratt & Lavidor, 2006). Using tDCS, Rodrigues de Almeida, Pope, and Hansen (2019, 2020a, 2020b) reported no significant effect of tDCS over the left pIFG, STG and left/right IFG on lexical decision tasks. Similarly, Vignali, Hawelka, Hutzler, and Richlan (2019) and Malyutina et al. (2018) did not report any effect of anodal tDCS targeted at the left and right IPS and the right and left IFG on lexical decision tasks. On the other hand, a study by Weltman and Lavidor (2013), which targeted the bilateral TPC with online tDCS, reported a decrease in accuracy for words during lexical decisions, in addition to lower accuracy in semantic decisions. The overall weak evidence for a modulation of lexical

decisions may be related to the fact that this is a very automatic and easy task that may be robust against modulatory NIBS effects. Yet, the results of tDCS studies might be due to limitations of the method per se. For instance, in the aforementioned studies by Rodrigues de Almeida et al. (2019, 2020a, 2020b), the authors reported that cathodal tDCS to the left pIFG improved word naming, and both facilitatory anodal and inhibitory cathodal tDCS led to faster reaction times for word and pseudoword reading. Note that the (unexpected) facilitatory effect was stronger for cathodal tDCS. However, in their third study, these authors failed to corroborate their earlier finding. Hence, the overall mixed results reported by tDCS studies might primarily stem from methodological limitations and the low spatial focality, which is why the results should be interpreted with caution.

3.4. Semantic processing

3.4.1. The contribution of the left inferior frontal cortex for semantic processes during reading

The left pIFG is causally involved in semantic processes accompanying the reading of words and word pairs. Disruption of the left and right pIFG with 10 Hz TMS during the processing of word pairs that are either literally or metaphorically related led to an increase in reaction times and a lower accuracy for literal word pairs only (Pobric, Mashal, Faust, & Lavidor, 2008). This could point towards an involvement of the bilateral IFG in the processing of more salient meanings, likely reflecting more general aspects of semantic processing. NIBS studies further suggest that the left pIFG might play an important role for semantic sentence processing at a general level. For instance, Acheson and Hagoort (2013) found that inhibitory stimulation of the left pIFG with cTBS contributed to the resolution of ambiguity in temporarily ambiguous sentences during reading and led to slower reading times for ambiguous relative to unambiguous sentences.

The aIFG, on the other hand seems to be essential for the semantic encoding of words (Köhler, Paus, Buckner, & Milner, 2004), semantic decisions (Devlin et al., 2003; Gough et al., 2005) and category member generation (Klaus & Hartwigsen, 2019). Almost all studies that used 5–10 Hz online rTMS (Devlin et al., 2003; Gough et al., 2005; Köhler et al., 2004) found a significant contribution of the left aIFG to the processing of semantic information in written language comprehension, as demonstrated by a decrease in task performance under aIFG stimulation. A TMS study by Hoffman, Jefferies, and Lambon Ralph (2010) further found that the very anterior portion of the left IFG was involved in the processing of abstract words only, as evident by delayed response speed after inhibitory 1 Hz rTMS over this area. This suggests very specific semantic contributions to overall concepts. Additionally, in a word production study by Klaus and Hartwigsen (2019), category member generation for written stimuli was selectively delayed under 10 Hz online rTMS of the aIFG but not the pIFG, which supports the notion of a functional-anatomical double dissociation in the IFG, with the anterior part being more engaged in semantic decisions and the posterior part being more relevant for phonological decisions, as put forward in language comprehension studies with rTMS (e.g. Devlin et al.,

2003; Gough et al., 2005). In contrast to these studies, Hartwigsen, Price, et al. (2010) did not find TMS evidence for a causal involvement of the left aIFG in semantic decisions. The negative result in their study might be explained by a relatively low stimulation intensity compared to other studies that was necessary to avoid unpleasant side effects.

Pars triangularis might especially contribute to the processing of complex semantic information during reading. Offline rTMS studies with inhibitory 1 Hz stimulation by Whitney, Kirk, O'Sullivan, Lambon Ralph, and Jefferies (2011, 2012) indicate that this region might be involved in executive semantic processing at the word level. The authors found that inhibitory stimulation led to a disruption of performance in a semantic judgment task on word pairs, but only when the cue-target word pairs shared a very weak semantic association. Additionally, they reported that rTMS over the left aIFG, the pMTG and the intraparietal sulcus (IPS) led to a disruption of semantic control. The former regions were assigned key roles in a distributed executive semantic network that supports controlled retrieval and semantic selection. The authors argued that only high semantic demands required this region, while it was not central to semantic representations per se. The task-specific role of the left aIFG was further confirmed by Nixon et al. (2004) who showed that disruption of the left pars triangularis with 10 Hz rTMS did not impair phonological processing (see also Hartwigsen, Price, et al., 2010, for a similar finding). However, no behavioral effect of 1 Hz rTMS to left IFG before a semantic association task (weak vs strong associations) was observed in the TMS-fMRI study of Hallam, Whitney, Hymers, Gouws, and Jefferies (2016).

3.4.2. The contribution of left inferior parietal and temporo-occipital areas for semantic processes during reading

The majority of the included NIBS studies point towards an essential contribution of the left AG to semantic processing during reading tasks. Price, Peelle, Bonner, Grossman, and Hamilton (2016) reported that faciliatory stimulation of the left AG with anodal tDCS only modulated semantic integration (i.e., led to faster comprehension of word pairs) but did not affect letter-string reading. Davey et al. (2015) had subjects perform semantic judgments (picture-word matching) at different semantic levels, with either thematic (strong or weak association) or identity (superordinate or specific level) relationships between the stimuli. Disruption of the left AG with 1 Hz offline rTMS significantly affected performance for strong association couples only, while disruption of the pMTG only impaired weak associations and overall identity matching. These results were taken to reflect that the pMTG contributes to the controlled retrieval of conceptual knowledge, while the AG is critical for the efficient automatic retrieval of specific semantic information. In a complementary fashion, Kuhnke et al. (2020) probed the functional relevance of the left posterior IPL (AG/SMG) for the conceptual processing of visually presented words with high or low action or sound associations with 10 Hz online rTMS. The authors found that rTMS selectively affected the retrieval of action knowledge and impaired action judgments on low sound-low action words. Based on these findings, the authors concluded that the left posterior IPL is a key region for the retrieval of action knowledge and supports conceptual processing when action

knowledge is task-relevant. Further support for the view that the left AG is central to semantic processing can be derived from two other rTMS studies (Branzi, Pobric, Jung, & Ralph, 2021; Sliwinska, James, & Devlin, 2015). In Sliwinska et al.'s study, subjects performed homophone and synonym judgments and inhibitory 10 Hz rTMS was applied to either the left AG or the left SMG. The authors reported that relative to a no-TMS baseline, inhibition of the left AG led to an increase in response times in the semantic task, while the homophone judgment task remained unaffected, arguing for a specificity of this effect. Yet, it should be noticed that two studies did not find evidence for a significant impairment of semantic performance when the left AG was disrupted with 10 Hz online rTMS (see Hartwigsen et al., 2016 for a semantic task on auditory stimuli and Hartwigsen, Baumgaertner, et al., 2010 for both auditory and visual stimulus presentation). These authors suggested that disruption of AG function may be compensated by a stronger contribution of the intact left aIFG, arguing for a strong fronto–parietal interaction during semantic processing, at least for auditory stimulus presentation (Hartwigsen, 2016). These findings highlight the need to consider network dynamics when interpreting the results of NIBS studies. Looking into a very different process and a slightly different location, Harpaz, Levkovitz, and Lavidor (2009) reported that the left and right TPJ contribute differentially to semantic processes, with single pulse TMS to the left TPJ leading to higher sensitivity and accuracy for dominant meanings of ambiguous words, and right TPJ TMS having the same effect on subordinate meanings. Overall, the included studies provide relatively strong evidence that the left AG is central for semantic processing.

3.4.3. Potential contributions of the motor cortex and the ATL for semantic processes during reading

The role of other areas such as the motor cortex and the ATL to semantic processing during reading remains to be further uncovered. Reilly, Howerton, and Desai (2019) found evidence that the left premotor cortex is functionally relevant for general sentence processing since inhibition of this area with online single-pulse TMS resulted in slower comprehension of metaphorical and literal sentences. Another study showed that early disruption of the left dorsal premotor cortex with online paired-pulse TMS delayed the response speed for pseudowords in a lexical decision task, arguing for a functional contribution of this area to early stages of sublexical processes underlying pseudoword reading (Pattamadilok et al., 2016). This contrasts with two other 1 Hz offline rTMS studies that could not find significant effects of premotor cortex stimulation on word reading, semantic and phonological judgments (Papeo et al., 2009; Tomasino et al., 2008). Other NIBS studies demonstrated that single-pulse TMS over the left premotor cortex selectively facilitated reaction times on incongruently primed trials for tool-related semantic concepts but not animal-related concepts, providing evidence for the functional contribution of this area to the processing of tool concepts (Cattaneo, Devlin, Salvini, Vecchi, & Silvanto, 2010). Moreover, manual-action and leg-action words were differentially affected by TMS depending on the exact stimulation site within the motor cortex (e.g., arm or leg motor areas; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005). The

role of the left premotor cortex for manual-action verbs was corroborated in a TMS study by Willems, Labruna, D'Esposito, Ivry, and Casasanto (2011) who found that responses to manual-action verbs were faster after cTBS of this area.

In two studies by Pobric, Lambon Ralph, and Jefferies (2009, 2010), 1 Hz offline rTMS applied to the right ATL resulted in slower semantic decisions, an effect that was most pronounced for low imageability items. However, they also reported that left ATL stimulation with 1 Hz rTMS affected judgments of semantic associations between words and pictures (Pobric, Jefferies, & Lambon Ralph, 2010). In a study by Jung and Lambon Ralph (2016), only cTBS over the left ventral ATL but not over a control site in the occipital pole resulted in slower reaction times for a synonym judgment task. These authors combined cTBS with subsequent fMRI during task performance to investigate network effects of inhibitory stimulation over the ventral ATL. Aside from the observed behavioral disruption, inhibition of the ventral ATL resulted in decreased activity at the target region and increased compensatory activity in the contralateral homologous region. This is congruent with the notion that both the left and right ATL are critical areas for semantic processing as revealed by previous lesion studies (e.g., Lambon Ralph, Ehsan, Baker, & Rogers, 2012). Jackson et al. (2015) targeted the left ATL with paired-pulse TMS at four different time points after word onset (100 msec, 250 msec, 400 msec and 800 msec) and reported a disruption of performance on a synonym judgment task only after late stimulation (400 msec and 800 msec). These authors suggested that the ATL could be a neural source of the N400 ERP component for semantic processing. Future studies should combine TMS with EEG to test this notion.

In summary, the existing NIBS literature provides evidence for the causal relevance of various regions for different aspects of semantic processing. While the left inferior frontal cortex and the left AG seem to be essentially involved in semantic processing on the word and word pair level in general, pars triangularis might only be relevant for processing complex semantic information. Moreover, the ventral OTC is essential for written language processing on the word level, as already shown in pure reading studies. Mixed evidence comes from studies with lexical decision tasks. The ATL seems to be a crucial region for semantic word processing, but its role may be confined to general aspects of semantic processing while its specific contribution to reading is less clear.

3.5. Sentence-level findings

The left AG and the prefrontal cortex are involved in lexical-syntactic retrieval and contextual integration on the sentence level. Acheson and Hagoort (2013) measured both reading performance and overall reading patterns (e.g., total reading time and fixations) via eye-tracking in their study. Inhibitory offline cTBS was applied over the left pIFG or pMTG to modulate lexical-syntactic retrieval in sentence comprehension with temporary word-class ambiguities. cTBS over the left pIFG selectively modulated the ambiguity effect in initial reading times at the disambiguating sentence region. The authors found that the IFG played a crucial role in unification operations in early and later stages of sentence comprehension. TMS over both pIFG and pMTG modulated the

ambiguity effect for total reading times in the temporarily ambiguous sentence region. However, only disruption of pIFG led to disruption of unification operations whereas no evidence for a role of the left pMTG during lexical-syntactic retrieval could be found. This may indicate that the left pMTG is relevant for the resolution of ambiguities but not for early stages of lexical-syntactic retrieval. In another recent study, inhibition of the left AG with 10 Hz rTMS significantly slowed subjects' responses during a memory task (context-related information retrieval), but text reading times per se were not affected by the stimulation (Branzi et al., 2021). These findings may indicate that the AG is critically involved in context-dependent semantic integration but does not play a role for reading processes alone.

Interesting results come from three other studies, which targeted different brain areas during sentence reading (with semantic differences) and sentence-picture matching. Franzmeier, Hutton, and Ferstl (2012), for instance, applied single pulses to the left and right STS/pMTG to modulate the reading of sentences with expected, unexpected and incorrect endings. They found that stimulation of the left STS/pMTG slowed responses to expected and unexpected endings, pointing to a semantic relevance of this region during sentence processing. Another study targeted the frontal cortex, and found that both anodal and cathodal tDCS may modulate sentence reading and improve understanding ambiguous sentences (Hussey, Ward, Christianson, & Kramer, 2015). The only study pointing out the left temporal cortex for primarily sentence, and not semantic, processing is the study by Oliveri, Romero, and Papagno (2004), who found that rTMS at 1 Hz over the left temporal cortex led to lower accuracy and slower reaction times for all sentence types. In sum, more studies are needed to confirm the potential relevance of regions for sentence processing, especially with regard to reading and not only semantic aspects of language processing.

3.6. Artificial learning studies

Few NIBS studies to date have addressed artificial word and alphabet learning, which are also relevant for reading but do not measure or assess reading per se. These studies suggest that several brain areas are significantly involved in overall learning processes and thus learning to read. A study by De Vries et al. (2010) found that anodal tDCS applied to the frontal cortex resulted in a better detection of syntactic violations and increased overall performance during artificial grammar learning. Additional evidence for a key role of the left IFG in word learning can be derived from Javadi and Walsh (2012), who showed that anodal tDCS improved memory during a word memorization task. In contrast, cathodal tDCS over the same region impaired memory performance in word recognition after training. Together, the two studies suggest that grammar or word learning strongly relies on the left IFG, most likely because subdivisions of the IFG are implicated in syntactic, semantic, and phonological processes, which interact during learning of written stimuli. Using inhibitory cathodal tDCS, Liuzzi et al. (2010) found that the acquisition of novel action words relies on intact left motor function since inhibition of this area significantly disrupted novel action word learning. This aligns with previous neurostimulation

studies demonstrating the functional relevance of the primary motor cortex in action word processing (e.g., Pulvermüller et al., 2005).

The role of the left IPL/TPJ in artificial word learning was confirmed by three other tDCS studies. Flöel, Rösser, Michka, Knecht, and Breitenstein (2008) found that anodal tDCS, but not cathodal or sham stimulation of the left IPL led to better performance in a novel pseudoword learning task. Meinzer et al. (2014) corroborated these findings using an explicit word learning paradigm. Also Fiori et al. (2011) reported shorter naming latencies, i.e., faster word access, following atDCS to the left TPJ. These studies included an acquisition and a recall phase and showed that overall learning was better after tDCS of the left IPL, and these improvements persisted up to one week post-acquisition. These two studies provide evidence that the beneficial effects of tDCS may outlast the stimulation duration, which highlights that changes in synaptic excitability bear the potential to induce lasting changes relevant for therapeutic treatment (Cirillo et al., 2017).

3.7. The impact of individual differences and methodological limitations on stimulation effects

NIBS effects may depend on individual differences in reading skills and reading strategies. One example for the impact of cognitive differences on modulatory NIBS effects is a study that reported improved word reading after anodal tDCS over left STG/TPJ in below average readers, but not in average readers (Turkeltaub et al., 2012). This might be explained through a ceiling effect in non-impaired readers, but this is only one of many interpretations. Likewise, Shaywitz et al. (2002) found that anodal tDCS over the left IPL increased the accuracy of trained alphabet letters, but the level of improvement depended on the individual reading skills. The weaker the reading skills of a subject, the better the post-training performance, indicating that tDCS had the most pronounced improvements in slow and low-accuracy readers. Similarly, anodal tDCS over the left IPL improved the retention of new graphene-phoneme relations in adults with low reading skills, but negatively impacted the learning curves of highly skilled readers in another study (Younger et al., 2016). The authors concluded that the left TPJ is important for word learning and that stimulation strengthened the phonological pathway selectively in poor readers. In contrast, in highly skilled readers, anodal stimulation may have caused the less efficient pathway to contribute more strongly, which might explain the paradoxical disruption after anodal tDCS (see also Younger & Booth, 2018). A different study showed that trains of 50 Hz applied to the left IPL selectively impaired reading performance when integral reading strategies were used but not when subjects read sentences word by word (Claus et al., 1993). This was confirmed by Acheson et al. (2011) who further showed that inhibitory offline stimulation of the left pSTG with cTBS increased error rates in a paced reading task, and also affected working memory performance. Focussing on individual differences in semantic processing, another study by Cummine and colleagues showed that stimulation of left AG with both anodal and cathodal tDCS changed imageability slopes, and individuals with high imageability effects before stimulation showed the greatest reduction after tDCS.

However, reading times per se were not disrupted across all word types, indicating that reading network pathways were only selectively modulated (Cummine, Boliek, McKibben, Jaswal, & Joanisse, 2019). Similarly, inhibition of the left ATL with 1 Hz rTMS only affected word reading performance in those subjects who showed higher semantic reliance in the pre-test in another study (Woollams, Madrid, & Lambon Ralph, 2017). Together, these results suggest that the effects of a given NIBS protocol might be more prone to individual variability than often acknowledged in language studies. For instance, individual variability in response to offline rTMS in the motor system may be influenced by differences in corticospinal excitability (Hamada, Murase, Hasan, Balaratnam, & Rothwell, 2013). Such differences are also likely to impact modulatory NIBS effects on higher cognitive functions and may interact with individual differences in cognitive strategies. Although there is first evidence that individual differences in reading skills and strategies may respond differently to modulation, more research is needed to further explore how specific protocols may be adapted and how NIBS may help to unravel individual differences more systematically.

tDCS studies may lack spatial focality to induce reliable effects. Although several studies reported behavioral effects of anodal or cathodal tDCS on reading performance, the results should be interpreted with caution, given the low spatial focality of the method and the risk that concurrent stimulation of neighboring areas may have contributed to the reported results. Consequently, some tDCS studies targeting the IFG just refer to "prefrontal stimulation" and use simulations of the current flow to assess the area(s) that may have contributed to the observed effects (e.g., Klaus & Hartwigsen, 2019). In this context, the consideration of null findings seems to be important. For instance, Westwood, Olson, Miall, Nappo, and Romani (2017) failed to find any effect of IFG and MTG stimulation with tDCS on word reading (see also Westwood & Romani, 2017). Such null findings, which contradict findings from other NIBS, in particular TMS, studies, could stem from methodological limitations of tDCS such as low spatial focality, weak stimulation intensities (see Y. Zhang et al., 2019) or limitations of a study per se (e.g., small sample size, task choice). Therefore, findings of tDCS studies should be interpreted with caution and should not directly be compared to findings of TMS studies.

3.8.   Exploring the neurophysiology of NIBS effects with neuroimaging and electrophysiological measures

Plasticity-inducing NIBS protocols induce large network effects. Notably, only a few of the above-discussed studies combined NIBS with neurophysiological or neuroimaging methods to explore modulatory effects beyond the behavioral level. For instance, the combined TMS-fMRI study by Hallam et al. (2016) provides evidence for a TMS-induced decrease in task-related activity in the stimulated left IFG, and its right-hemispheric homologue. Nonetheless, behavioral performance was unaffected, which might be explained by a "maintenance" of function via other areas of the left-hemispheric language network. In contrast, Jung and Lambon Ralph (2016) observed that the stimulation-induced decreases in left ventral ATL activity were accompanied by

an increase in activity in the right-hemispheric homologue (see also Andoh & Paus, 2011, for similar findings). The authors further reported increased intrinsic connectivity from the right to the left ventral ATL after TMS, likely compensating for the disruption of the semantic system. Likewise, Hartwigsen et al. (2013) reported decreased task-related activity in the stimulated area after disruption of left pIFG with cTBS and compensatory upregulation of the contralateral homologous region during pseudoword repetition. Overall task performance was not affected by cTBS in that study. However, effective connectivity analyses revealed an increase in the facilitatory influence from the right to the left pIFG after cTBS which correlated with the individual response speed: participants with a stronger facilitatory effect from the right to the left pIFG were faster, that is, they were less affected by the TMS-induced disruption. Together, the results by Jung and Lambon Ralph (2016) and Hartwigsen et al. (2013) speak in favor of compensatory short-term reorganization in the language network after inhibitory rTMS.

Aside from the preliminary TMS evidence for network effects of plasticity-inducing NIBS protocols, studies measuring brain oscillations with EEG provide further support for NIBS-induced modulation of network interactions and modulation of cross-frequency coupling. Moliadze et al. (2019) found a task-related increase in theta-power after alpha-tACS (10 Hz), which was correlated with tACS-induced behavioral facilitation during phonological decisions. More specifically, tACS applied to the bilateral pIFG suppressed activity in the left prefrontal cortex but increased activity in the contralateral homologous region, which may speak for a network effect.

In a complementary fashion, some studies used eye-tracking to map the modulatory effects of different TMS protocols. These studies found that rTMS to the right frontal eye field and the left PPC delayed reading processes. rTMS applied to the left PPC delayed the time to initiate the next saccade during reading an array of words by 45 msec, while rTMS over the right frontal eye field slowed the initiation of the first saccade only. Moreover, rTMS of left IFG led to longer fixation times during sentence reading, with participants needing more time disambiguate sentences at the disambiguating region (Leff et al., 2001).

In summary, relatively few studies have combined NIBS with fMRI, EEG, or other complementary electrophysiological measures to explore the neurophysiology of NIBS effects and map network-specific modulation. These studies demonstrate that inhibition of a key language area may result in distributed network effects, including increases (and decreases) in task-related activity in other areas of the language network. Increases in task-related activity after disruption may include neighboring and remote left-hemispheric areas as well as homologous regions. Such effects of short-term plasticity speak for a strong compensatory potential of the language network and highlight the value of combining NIBS with neuroimaging or neurophysiological techniques to provide insight into stimulation induced changes at the network level and their association with behavioral effects of different NIBS protocols. These compensatory mechanisms, however, need further investigation before strong conclusions on general mechanisms can be drawn. For instance, their behavioral relevance remains unclear.

3.9. Causal evidence of NIBS studies to inform current neurobiological models of reading

Synthesizing the above discussed NIBS studies, we link the presented results to an earlier discussed neurobiological dual-stream model of reading (Kearns et al., 2019; see summary of results presented in Fig. 3). Considering the results of the NIBS studies targeting the left IFG, the observed functional-anatomical double-dissociation between semantics (aIFG) and phonology (pIFG) could certainly be interpreted in favor of a classical distinction according to the involvement in sight word reading (ventral stream) and decoding (dorsal stream). However, the dissociation between aIFG and pIFG has been reported in numerous neuroimaging studies, regardless of whether written or auditory stimuli were used, making a mere reading-specific role less likely. Moreover, not all NIBS studies provide evidence for a clear double dissociation in the IFG, as some failed to find significant disruption of semantic processing when targeting the aIFG (e.g., Hartwigsen, Price, et al., 2010). It was also demonstrated that the role of the IFG is not limited to semantic and phonological processes. For instance, the left pIFG has also been found to play a role in sentence processing on a more general level, as well as artificial grammar learning and word memorization, providing further evidence that the engagement of this region is not limited to aspects of reading only. In other words, the contribution of the left IFG and its subdivisions for reading may reflect the general relevance of this area for language processing and should thus only cautiously be interpreted as an indicator that a ventral and dorsal stream for reading rely on this region and its subdivisions.

The results of the present review further suggest a double dissociation within the IPL, with phonological processing requiring the SMG, and semantic processing engaging primarily the AG. Specifically, the left SMG is identified as a critical region for the processing of phonological properties of words, pseudowords, and sentences, not entirely in concordance with what has been suggested in the dual-stream framework. Likewise, the suggested role of the left AG as a semantic key region, which is most likely not limited to decoding and novel word storage, but rather reflects its contribution to the semantic lexicon (potentially together with the left ATL), is not entirely converging with the dual-stream model of reading. Given that word processing heavily relies on the left AG, it would have to be involved in the ventral stream, which makes a clear and simple dual-stream dissociation as displayed in preliminary models unlikely.

Although very few NIBS studies have targeted the left vOTC to date, these studies suggest that both word and pseudoword processing rely on this area and that low-level visual processing could be more involved in higher-order word discrimination and recognition than often assumed. Therefore, the visual cortex and the left OTC would be associated with early reading processes, not only of sight word reading, as suggested in the current framework. We suggest that both streams − as described in the neurobiological dual-stream model − are likely to originate within this region and propose this region as the starting point of all reading processes.

Moreover, several regions that are not part of the classical reading model were associated with various reading processes, including the bilateral ATL, and the PPC. NIBS studies

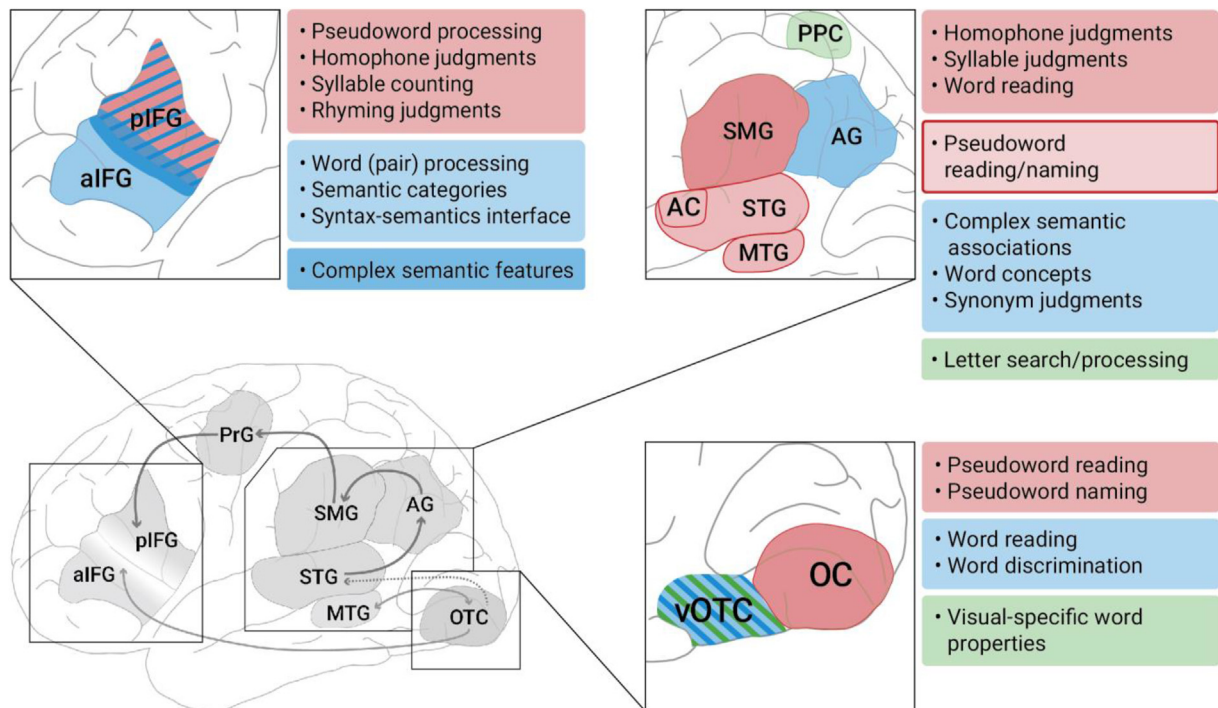**Fig. 3 − A visualization of the results of the included NIBS studies. The results suggest a functional dissociation for phonological (blue) and semantic (red) reading-related processes in the left inferior frontal cortex (top left), and the left inferior parietal lobe (top right). The results further suggest a key role for the left PPC for orthographic processes (green), which also rely on the vOTC (bottom right).**

suggest that these regions play a role in various reading-related processes, ranging from attentional mechanisms to complex semantic processing. Even if the functions of these regions might be more related to language on a general level, these studies suggest that a valid neurobiological model of reading may need to be extended to include these regions. Their specific contributions to different linguistic sub-processes need to be further investigated in future studies. We wish to emphasize that the conclusions to be drawn from the present review remain preliminary due to the small number of included studies. We therefore highly encourage future research to investigate the role of language-related regions in overall reading.

Yet, a limitation of behavioral NIBS studies is that the inferred effects might result from the modulation of structurally or functionally connected areas and could thus reflect either a network effect or a remote effect in a distant region. In such cases, the assumption of the functional relevance of the targeted area per se for a given process would not be clear. To address this issue, the combination of NIBS protocols with subsequent or simultaneous neuroimaging would be promising avenue for future studies on reading processing.

To summarize, the findings of the present review provide limited preliminary evidence that the dual stream model of reading might be applicable to the neural level. Especially, the direct mapping of the implied cognitive processes in the dual-route model to the underlying functional neuroanatomy might need to be reconsidered in the future when more neurostimulation data is available. Based on the present set of NIBS studies exploring reading-related processing, we argue that it is more likely that all reading-related regions targeted so far are to some degree required for the processing of written language, regardless of whether new or familiar stimuli are processed, and regions such as the ATL or the PPC need to be considered in future models of reading. This should be considered when exploring the neurobiology of reading and combining cognitive models with neural frameworks.

4. Conclusions and future directions

We conclude that the successful reading of words, pseudo-words or larger elements like sentences, depends on the intact functioning of a large network of areas in the left inferior frontal cortex, the TPC and the OTC. Aside from these core areas, other regions such as the bilateral PPC and the left ATL seem to be critical for overall reading performance. In general, the large number of NIBS studies conducted in the healthy brain to date suggests that reading-related tasks may be both disrupted and facilitated by targeted stimulation of a specific area, depending on specific parameters of the stimulation protocol. While the disruption of a specific region is often used to provide evidence for its functional relevance for a given task in the healthy brain, the potential enhancement of reading function is particularly interesting for intervention studies with reading-impaired individuals. While it is obvious that most areas are not purely specific to reading and further contribute to other core language functions that are crucial for comprehension or production, their contribution seems to be functionally relevant for the processing of written language.

For instance, the left AG is likely engaged in all types of semantic processes, and the left pIFG seems to contribute to a variety of tasks requiring phonology, independent of the modality of stimulus presentation. Neuroimaging and TMS studies suggest a functional specialization within larger areas, with several subareas likely contributing to different specialized processes. For instance, within the IPL, it remains to be explored whether larger regions such as the AG or TPJ can be further divided into subareas that differentially contribute to reading. It might be difficult to comprehensively identify subareas within those regions in isolation, as it is mandatory to understand the contribution of a specific area in function of a larger network. To explore such subdivisions with NIBS and their role in a larger network, a way forward is the application of multifocal TMS over several key regions with minicoils that provide a significantly increased spatial resolution relative to standard coils. Only by improving the spatial resolution of a given NIBS protocol, the functional relevance of such subdivisions can be probed, and the simultaneous or subsequent targeting of several reading nodes will provide new insight into their functional interaction.

Since the overall number of studies is scarce, it is necessary for future studies to identify the relevance of specific regions for reading processes, test larger samples and combine stimulation with different forms of behavioral interventions. Furthermore, the combination of NIBS protocols with neuroimaging will help to map stimulation-induced changes at a larger network level to increase the current understanding of the neural correlates associated with behavioral modulation. Such studies will provide a more comprehensive picture of how the reading network in impaired readers works and responds to neurostimulation.

We note that the conclusions of this review are limited due to methodological constraints. As NIBS studies are time consuming, most studies suffer from relatively small sample sizes and the effect sizes of NIBS studies are considerably small. Moreover, few studies have used the exact same design and set-up (e.g., with respect to stimulation intensity, number of pulses or current, pulse duration, montage, etc.), opening the possibility that differences in the results could have been mainly caused by methodological differences of various stimulation and design parameters. This is particularly important to consider when directly comparing the results of TMS and tDCS studies. The assumed direction of a given TMS or tDCS protocol is usually based on excitability changes observed in studies in the motor system and does not necessarily translate to behavioral effects when targeting areas for higher cognitive functions such as language.

As noted above, a promising avenue for the future will be the multimodal investigation of the induced effects at the behavioral and neural network level. Since the effects of NIBS protocols are often less focal than expected and the functional relevance of remote effects has been demonstrated in previous work (e.g., Hartwigsen et al., 2017), a network perspective will help to better understand the functional relevance and interaction of different key areas for reading. Moreover, such combinations will also provide insight into potential compensatory changes in response to disruptive NIBS protocols at a larger network level. We wish to emphasize that the above discussed results provide evidence for the functional relevance of

numerous areas for reading and reading-related processes but are limited with respect to their insight into network interactions during reading, both at the neural and neurophysiological level. The partly diverging results of the different studies may be influenced — among other factors — by the differences between online and offline NIBS protocols. Online protocols can be used to study the *immediate* consequences of a focal perturbation. The direct perturbation during a task provides the advantage that the effects are not confounded by short-term reorganization because online perturbation does not give the brain time for functional reorganization (see Walsh & Cowey, 2000). In contrast, offline protocols may be more suited for therapeutic applications because the repeated application of such protocols may induce lasting plastic after-effects at the neural network level. Such after-effects can be mapped with functional neuroimaging. Another possibility to study network interactions at the behavioral level is the use of multi-site TMS designs which apply TMS over two (or more) areas in a simultaneous or subsequent fashion (see Hartwigsen, 2015 for details). Such approaches may also help to unravel the compensatory potential of different areas in the reading network in future studies.

Methodologically, recent advances in biophysical modeling of the NIBS-induced currents in the brain may help to optimize electrode montages for tDCS interventions and coil positions for TMS application (e.g., Opitz, Fox, Craddock, Colcombe, & Milham, 2016; Weise, Numssen, Thielscher, Hartwigsen, & Knösche, 2020). Finally, the use of rhythmic TMS or tACS may offer the possibility to target and modulate specific atypical oscillatory patterns (Kraus, 2012). Identifying and modulating task-specific oscillatory patterns during different reading processes may further increase the knowledge of the neurobiology of reading and reading disorders.

CRediT authorship contribution statement

Sabrina Turker: Conceptualization, Investigation, Writing — original draft, Writing — review & editing, Visualization. **Gesa Hartwigsen:** Conceptualization, Investigation, Writing — original draft, Writing — review & editing, Visualization.

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