Posterior superior temporal sulcus supports sequence-based language processing: Evidence from low-frequency repetitive transcranial magnetic stimulation

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Abstract

Understanding the sequence (i.e. word order) of linguistic input plays an important role in sentence comprehension, particularly in languages such as English (Bornkessel-Schlesewsky et al., 2015). Neuroimaging and clinical research shows that left posterior superior temporal sulcus (pSTS) contributes towards sequence processing in both linguistic and non-linguistic contexts (Bornkessel et al., 2005; Wilson et al., 2010). To test the causal contribution of left pSTS for sequence-dependent sentence processing, we applied image-guided low-frequency repetitive transcranial magnetic stimulation (1 Hz for 15 minutes at 90% resting motor threshold) to this region in 23 healthy native English speakers. Participants undertook an auditory sentence processing task and were asked to identify the sentential actor or undergoer. Sentences were either semantically plausible or were rendered implausible by an animacy violation (e.g. “The student will write the answer” versus “The answer will write the student”). After sham-rTMS (control condition), participants predominantly selected the first noun as the actor and second noun as the undergoer, relying strongly on sequence cues (word order) for interpretation as expected in English speakers. By contrast, after real-rTMS, participants were more likely to use animacy as a cue to interpretation, with higher selections of the animate noun as the actor and inanimate noun as the undergoer regardless of word order. This effect also interacted with question focus and response time. These results indicate that sequence-based language processing is reduced after low-frequency rTMS to pSTS, suggesting a role for pSTS in processing sequential aspects of language such as word order.

Keywords: Sentence processing, sequence processing, dorsal stream, neurobiology

1. Introduction

The languages of the world show a wide diversity of features and cues that are used to derive meaning during sentence processing (MacWhinney et al., 1984; MacWhinney & Bates, 1989). As such, the architecture that underlies human language processing must be capable of supporting any one of approximately 7,000 languages (Lewis, 2009). While neuroanatomical architecture and certain functional processes are consistent across languages, recent research shows cross-linguistic differences in the electrophysiological indices of language processing (see Bornkessel-Schlesewsky et al., 2011 and Bornkessel-Schlesewsky & Schlewsky, 2020 for review). In this paper, we will test predictions put forth by a cross-linguistically motivated model of language processing in the human brain – the extended Argument Dependency Model (eADM; Bornkessel & Schlewsky, 2006; Bornkessel-Schlesewsky et al., 2015; Bornkessel-Schlesewsky & Schlewsky, 2013). We will first briefly introduce existing theoretical models, which diverge in their predictions for the role of certain cortical regions for linguistic processing. We will then describe the eADM in greater detail, focusing on the hypothesised role of the posterior superior temporal sulcus for language processing, before describing key aims and hypotheses of the paper.

1.1. Dual stream models of sentence processing

Many neurobiological models of human language support the notion that a cortical dorsal-ventral stream architecture underlies processing (Bornkessel-Schlesewsky & Schlewsky, 2013; Friederici, 2011; Hagoort, 2005; Hickok & Poeppel, 2004; Rauschecker & Scott, 2009; Rauschecker & Tian, 2000; Saur et al., 2008; Tyler & Marslen-Wilson, 2008; Ueno et al., 2011). These models share a general assumption that two discrete streams, or pathways, of processing support human language. The models generally assume a dorsal stream and ventral stream of processing which are anatomically similar to the auditory system of nonhuman primates (Rauschecker & Scott, 2009), although this is not the case for all models (e.g. Hickok & Poeppel, 2004).

From this dual-streams perspective, human language processing begins – from a cortical perspective – at the point of basic auditory comprehension¹ in the auditory cortex (AC) in the superior temporal lobe, with information then passing bi-directionally through the ventral and dorsal cortical streams to prefrontal regions (Bornkessel-Schlesewsky et al., 2015; Friederici, 2012; Hagoort, 2014). Neurobiological models such as those proposed by Tyler and Marslen-Wilson (2008), Friederici (2011, 2012), and Hagoort (2005) are similar in the assumption that traditional linguistic subdomains such as semantics, syntax, morphology and phonology can be mapped to specific functional pathways (see Bornkessel-Schlesewsky & Schlewsky, 2019 for further discussion). The role of memory for

¹ While neurobiological models of visual processing (i.e. reading) have been proposed, existing reading models are currently at the word level, as opposed to the sentence level (for discussion of reading models, see Carreiras et al., 2014; Dehaene & Cohen, 2011; Price & Devlin, 2011). The presently discussed models are relevant to auditory comprehension only.

language processing is also a foundational principle for the Memory Unification and Control (MUC) model proposed by (Hagoort, 2005) and the Declarative Procedural (DP) model proposed by (Ullman, 2001, 2004, 2016). The aforementioned models broadly agree that – amongst other functions – the ventral stream plays a role for semantic processing (Friederici, 2012; Hagoort, 2005; Tyler & Marslen-Wilson, 2008; Ullman, 2016) and the dorsal stream supports phonological (Hagoort, 2005; Tyler & Marslen-Wilson, 2008) and/or syntactic processing (Friederici, 2012; Hagoort, 2005; Ullman, 2016). Additionally, some models propose multiple dorsal and/or ventral streams (Auditory sentence comprehension model; Friederici, 2012) hypothesise that certain linguistic subdomains are supported by both streams (Bi-hemispheric model; Tyler & Marslen-Wilson, 2008) or do not make strong claims regarding separable functions between the dorsal and ventral streams (e.g. MUC; Hagoort, 2005, DP; Ullman, 2016). Thus, for some models it may be difficult to causally investigate a one-to-one mapping between a proposed (sub)stream and a linguistic subdomain.

1.2. The extended Argument Dependency Model

The extended Argument Dependency Model (eADM; Bornkessel & Schlesewsky, 2006; Bornkessel-Schlesewsky et al., 2015; Bornkessel-Schlesewsky & Schlesewsky, 2013) proposes significantly different dorsal and ventral stream functions compared to the existing literature. This model aims to be cross-linguistic by accounting for the observed differences in sentence processing across typologically diverse human languages (Bornkessel & Schlesewsky, 2006; Bornkessel-Schlesewsky et al., 2011). Moreover, the eADM posits that the computational mechanisms observed in nonhuman primate audition are qualitatively able to support human language processing, but lack the quantitative scale (Bornkessel-Schlesewsky et al., 2015). As such, the eADM is built upon the basic information-processing mechanisms of nonhuman primate auditory processing and human speech processing (Rauschecker & Scott, 2009) rather than on linguistic subdomains (Bornkessel-Schlesewsky et al., 2015; Bornkessel-Schlesewsky & Schlesewsky, 2013). The nonhuman primate auditory system exhibits functionally distinct roles for the streams, with the dorsal stream supporting spatial auditory processing and the ventral stream supporting auditory object recognition (Rauschecker, 1998; Rauschecker et al., 1995; Rauschecker & Tian, 2000).

The fundamental assumptions of the eADM are that within a cross-linguistically unified sentence processing architecture, there are differing processing strategies that may be employed: a predominantly dependency-based strategy, supported by the ventral stream, and a predominantly sequence-based strategy, supported by the dorsal stream (Bornkessel-Schlesewsky et al., 2015). The relative reliance of language processing on each of these functional streams may differ depending on linguistic differences across languages or within-language differences such as sentence structure or context (Kyriaki, Schlesewsky, & Bornkessel-Schlesewsky, 2020a). In English, sequence/word order is a prominent aspect of the linguistic subdomain of syntax, however this is not the case for other languages in which word order is not a prominent cue for sentence processing (MacWhinney et al.,

1984). In languages such as German, sequence is distinct from syntax, as syntax also includes sequence-independent cues such as case marking and gender (MacWhinney et al., 1984). This distinction also highlights the importance of cross-linguistic perspective, as for models focusing predominantly on languages such as English, the mapping between language processing architecture and linguistic subdomains may seem plausible. However, when data from other languages is considered, the functional mechanisms of the dorsal and ventral streams appear to be more general as opposed to specifically representing aspects of linguistic subdomains.

The eADM proposes an (antero)-ventral stream which recognizes successively complex auditory objects, mapping auditory input to conceptual mappings (i.e. sound to meaning) (Bornkessel-Schlesewsky et al., 2015). This is assumed to be dependency-based: rather than relying on the linear order of auditory input, non-sequential information such as case marking or animacy informs processing (Bornkessel-Schlesewsky et al., 2015; Bornkessel-Schlesewsky & Schlesewsky, 2019). Dependency-based processing is particularly relevant for languages with a flexible word order where the order of words is not the only cue to sentence interpretation (e.g. German, Mandarin Chinese, or Turkish; Bornkessel-Schlesewsky et al., 2011). Anatomically, this model follows Rauschecker & Scott (2009) in assuming that the ventral stream extends from AC to anterior superior temporal cortex and anterior/ventral regions of inferior frontal gyrus (IFG/Brodman Area 45; Bornkessel-Schlesewsky et al., 2015; see Figure 1 for schematic).

The (postero)-dorsal stream comprises a hierarchically organized predictive coding architecture underlying sequence-based processing (Bornkessel-Schlesewsky et al., 2015). The dorsal stream is proposed to perform sequence-based combinatorics, tracking the linear order of linguistic input (Bornkessel-Schlesewsky & Schlesewsky, 2019). Dorsal stream function is thus proposed to be critical for predicting upcoming events within a sequence based on previous events and/or knowledge (Bornkessel-Schlesewsky et al., 2015). As such, the dorsal stream is particularly relevant for languages that rely heavily on the sequence of words to interpret a sentence, such as English which has a strong reliance on word order (MacWhinney et al., 1984). For example, word order is the dominant cue to comprehend a sentence such as “Mary kissed Paul” and understand that it is Mary who is kissing, and Paul who is being kissed. The dorsal stream is posited to range from AC, through posterior superior temporal cortex, inferior parietal lobule and premotor cortices to posterior and dorsal regions of inferior frontal cortex (IFC/BA 44; Bornkessel-Schlesewsky et al., 2015). Here, we aim to test a specific prediction of the eADM that diverges from the alternative dual-streams language processing models discussed above: that the dorsal stream, specifically the posterior superior temporal sulcus (pSTS), is involved in the sequence-dependent processing of sentences. The role of pSTS in language processing will be expanded upon below.

Figure 3.1. The extended argument dependency model (eADM) dual-streams model of language processing in the human brain. Two functional neuroanatomical streams are proposed, homologous to the nonhuman primate auditory system. The postero-dorsal stream (shown in red) connects auditory and motor-related regions of the cerebral cortex with bidirectional perception-action loops. Integration between the dorsal and ventral stream is shown in the inferior frontal gyrus. Black broken arrows denote feedback connections while numbers denote Brodmann areas. AC = auditory cortex, CS = central sulcus, IFC = inferior frontal cortex, IPL = inferior parietal lobule, PMC = premotor cortex and supplementary motor area), STS = superior temporal sulcus. Adapted with permission from Bornkessel-Schlesewsky et al. (2015).

1.3. Posterior superior temporal sulcus for sequence processing

The eADM posits that pSTS is an “early” part of the dorsal stream, playing a role in sequence processing for language comprehension (Bornkessel-Schlesewsky et al., 2015). Left pSTS shows increased activation for syntactically complex sentences compared to simpler sentences (Wilson et al., 2010) and also for sentences with higher sequencing demands (i.e. longer compared to shorter word sequences; (Pallier et al., 2011). This region also exhibits increased activation during the interpretation and role assignment of both visually and auditorily presented sentences that involve deviations from the dominant word order of a language (Bornkessel et al., 2005; Röder et al., 2002). These findings indicate that where sequence-based demands are higher due to increased complexity, increased length, or uncommon sentence construction, pSTS has higher activation. Outside of language, this is in line with research showing a negative correlation between superior temporal gyrus activation and the predictability of non-linguistic sequences (Bischoff-Grethe et al., 2000). Recent research also proposes that left posterior temporal regions play a role in sequence predictions, showing increased activation to sentences versus lists of words (Matchin et al., 2019). Lastly, left pSTS/MTG is activated more strongly for the perception of syntax/sequences relative to production (Matchin & Wood, 2020). These findings suggest a specific contribution of left pSTS to syntactic predictions in English, indicating that this region supports the processing of linguistic sequences (Matchin et al., 2019).

Clinical investigations of aphasic patients, particularly those with primary progressive aphasia, also provide converging support for this proposed role of pSTS in language processing (Wilson, 2019). Studies of patients exhibiting the “nonfluent” variant, who experience syntactic deficits and produce agrammatic speech, show volume loss to left STS in conjunction with other regions (Wilson et al., 2010). Left pSTS activation is functionally modulated by sequence complexity (sentences deviating from typical word order and/or involving increased linguistic complexity) in healthy controls but not in primary progressive aphasia patients (Wilson et al., 2010). Lesions to left posterior temporal regions (including posterior regions of STS, superior temporal gyrus, and middle temporal gyrus) have also been implicated in poorer performance when judging the grammaticality of sentences (Wilson & Saygin, 2004). Together, functional imaging of healthy participants along with observed deficits and neural atrophy of aphasic patients implicate pSTS as a crucial region for sequence processing in language. To test the causal role of pSTS in this regard, we aim to use repetitive transcranial magnetic stimulation (rTMS) to modulate auditory sentence processing.

1.4. Low-frequency transcranial magnetic stimulation to test model predictions

Repetitive transcranial magnetic stimulation (rTMS) can be used to investigate the contribution of cortical regions to a particular function by temporarily altering activity within the targeted region (Pascual-Leone et al., 2000). This acute disruption in activity is referred to as a “virtual lesion”. Transcranial magnetic stimulation, first demonstrated by Barker et al. (1985), involves the use of a transiently changing magnetic field, generated by current flow through a coil, to induce an electric field in underlying conductive tissues. The electric field produces local ionic currents that depolarise neurons and generate action potentials (for review see Barker, 2002; Rothwell et al., 1991). Studies in primary motor cortex suggest that the threshold for stimulating intracortical inhibitory networks is lower than for excitatory networks, and thus low intensity rTMS primarily alters activity within inhibitory circuitry (Ziemann et al., 1996).

The behavioural changes that result from rTMS, such as altered reaction/response time or response errors (Krieger-Redwood et al., 2013; Whitney et al., 2011), can indicate a role of the stimulated cortical area in the motor or cognitive process of interest. However, such experiments require carefully designed control conditions for rTMS, including for example, sham stimulation (Borckardt et al., 2008). Sham stimulation is delivered with the use of a magnetically shielded ‘sham’ coil, with the participant blinded to the coil type. Sham coils deliver an auditory artefact of a similar clicking noise to that elicited by real coils, but do not emit a significant magnetic field and thus should not elicit a physiological response in the underlying tissue (Fecteau & Eldaief, 2014). The association between a cortical area and the cognitive function of interest is often explored with low-frequency rTMS (e.g. 1 Hz; Classen & Stefan, 2008). In motor cortex, 0.9-1 Hz rTMS delivered at an intensity that is at or just below the threshold for evoking an electromyographic (EMG) response (motor evoked potential or MEP) in the target muscle, has shown after effects (decreased excitability in the motor cortex) for

approximately the same length of time as stimulus duration (Chen et al., 1997; Romero et al., 2002). While the majority of rTMS research has focused on motor and sensory regions of the human cerebral cortex, rTMS can also be used to examine connections between cortical regions and language functions (for review, see Devlin & Watkins, 2007). Language processing has been investigated using rTMS over many cortical regions, including inferior frontal gyrus (Acheson & Hagoort, 2013; Berlingeri et al., 2018; Manenti et al., 2008) and parieto-temporal areas such as anterior temporal lobe, middle temporal gyrus (MTG) and posterior superior temporal gyrus/sulcus (Alba-Ferrara et al., 2012; Andoh et al., 2006; Franzmeier et al., 2012; Pobric et al., 2007; Whitney et al., 2011). Low-frequency rTMS over the left pSTS inhibits biological motion perception (Grossman et al., 2005; van Kemenade et al., 2012) and semantic processing (Alba-Ferrara et al., 2012) while high-frequency stimulation to left and right superior temporal gyri has been shown to modulate speech perception (Kennedy-Higgins et al., 2020).

1.5. The present study

The aim of the current study was to use rTMS to test the eADM prediction that the dorsal stream supports sequence-dependent language processing (Bornkessel-Schlesewsky et al., 2015). The eADM predicts that the dorsal stream plays a crucial role in English sentence processing, due to the language's reliance on the sequential ordering of words for comprehension (MacWhinney et al., 1984). Word order is much more flexible in other languages, where alternate cues such as noun animacy play more prominent roles for interpretation (Bornkessel-Schlesewsky et al., 2011; MacWhinney et al., 1984). To investigate the role of the dorsal stream, low-frequency rTMS was delivered to pSTS, a region within the dorsal stream. Sequence-dependent language processing of English speakers were examined using a common linguistic manipulation – semantic reversal anomalies (SRAs). SRAs involve the reversal of the two nouns in a plausible sentence to create an implausible sentence, allowing investigation into the relative influence of word order/sequence on sentence processing (Hoeks et al., 2004; Kim & Osterhout, 2005; Kuperberg et al., 2003; see Table 1). While an English sentence such as ‘The student will write the answer’ (1 in Table 2) is grammatical and plausible, reversing the nouns to create ‘The answer will write the student’ (2 in Table 1) leads to an implausible meaning (Bourguignon et al., 2012; MacWhinney et al., 1984). Thus, SRAs are an effective test case for sequence-dependent processing, as the linearity of word order in English is what elicits the implausibility of (2). Although general world knowledge suggests that (2) is implausible, the strength of word order as a cue overrides contrasting cues such as animacy. This is not the case for other languages where the ordering of words is not as strict and the animacy of nouns can influence sentence processing (Bornkessel-Schlesewsky & Schlewsky, 2013; MacWhinney et al., 1984). For example, in German, the cue of animacy could lead to both (1) and (2) being interpreted with the same meaning (Kyriaki, Schlewsky, & Bornkessel-Schlewsky, 2020b). Here, dependency-based processing supported by the ventral stream is proposed to play a stronger role in sentence comprehension (Bornkessel & Schlewsky, 2006; Bornkessel-Schlewsky & Schlewsky, 2013).

Table 1: Example stimuli for the present study with likely sentence interpretations in line with either a strongly sequence-dependent or sequence-independent (dependency-based) strategy. Interpretation strategies are shown in relation to a forced-choice comprehension question. Underlined words indicate the two nouns in the sentence.

Animacy	Example sentence	Sequence-dependent strategy	Sequence-independent strategy
“Who/what will write? Student / Answer”			
(1) Animate-first	“The <u>student</u> will write the <u>answer</u> ...”	“Student”	“Answer”
(2) Inanimate-first	“The <u>answer</u> will write the <u>student</u> ...”	“Answer”	“Student”

We predict that disruption of the dorsal stream via low-frequency rTMS to pSTS will decrease the prominence of sequence-based processing (i.e. word order) and increase the relative prominence of ventral stream dependency-based processing (i.e. noun animacy) of English semantic reversal anomaly (SRA) sentences. English speakers rely strongly on sequence for sentence comprehension (Bates et al., 1982; MacWhinney et al., 1984), however Inanimate-first sentences should still show a slightly higher dependency-based strategy due to the implausibility of the sentence context and the animacy reversal (Dowty, 1991; Kyriaki, et al. 2020b). Comprehension was investigated using forced-choice comprehension questions that probe for the Actor (“Who/what will compose?”), the Undergoer (“Who/what will be composed?”), or a general comprehension probe (“Was there a restaurant?”). The focus of the comprehension question can influence the behavioural response of comprehenders, with differential responses being observed for Actor versus Undergoer questions (Kyriaki, et al. 2020b). Previous research suggests that Undergoer questions lead to a more dependency-based strategy compared to Actor questions, particularly when in combination with implausible sentences such as Inanimate-first SRAs (Kyriaki, et al. 2020b). Therefore, we included a within-participants factor of question type to account for potential differences in sentence processing which may interact with rTMS.

The study employed a 2 x 2 x 2 design of factors rTMS (real- or sham-rTMS), Animacy of the first noun (Animate-first or Inanimate-first) and Question type (Actor or Undergoer probe). The dependent variable is Response Choice (which noun is selected as the Actor or Undergoer). In order to test the specificity of low-frequency rTMS for sequence processing, we will also examine Response accuracy to the general comprehension probe for both critical sentences and distractor sentences, with a 2 x 3 x 2 design of factors rTMS (real- or sham-rTMS), Sentence condition (Critical SRA sentences, Phrase structure violations or Semantic anomalies) and Grammaticality (Animate-first/grammatical or Inanimate-first/ ungrammatical).

We hypothesise that:

H1. Overall, Inanimate-first sentences and Undergoer questions will promote a more dependency-based strategy in comparison to Animate-first sentences and Actor questions.

H2. When comprehending SRAs, rTMS will significantly influence the response choice of English speakers. For sham-rTMS, participants will adopt a highly sequence-based approach, with no significant difference in Response choice between Animacy conditions. For real-rTMS, participants will show a reduction in sequence-based processing and increase in dependency-based processing compared to sham-rTMS.

H3. In response to the general yes/no comprehension probe, Response accuracy will not vary as a function of rTMS or sentence conditions. We predict that accuracy will be significantly higher for Animate-first/grammatical over Inanimate-first/ungrammatical sentences. A null effect of rTMS on the general yes/no comprehension probe will provide evidence for a specific influence of rTMS on sequence processing in relation to the critical sentences and Actor and Undergoer identification, above that of general comprehension.

2. Methods

2.1. Participants

Twenty-three TMS-naïve participants (18 female), aged between 18-40 years ($M = 22.9$, $SD = 5.9$) participated in the study. All participants were right-handed (Edinburgh Handedness Inventory; Oldfield, 1971), monolingual native English speakers, and reported normal (or corrected-to-normal) vision and normal hearing. Participants reported no history of psychiatric, neurological, cognitive or language disorders and screening showed no contraindications to MRI or TMS. Participants provided written informed consent and were offered an honorarium for participation. The experimental protocol was approved by the University of South Australia Human Research Ethics Committee. One additional participant was withdrawn from the study prior to the rTMS session due to an incidental finding in their MRI scan.

2.2. Materials

2.2.1. Stimuli. Stimuli were adapted from Kyriaki et al. (2020a) and divided between two lists, each containing sixty critical sentences (30 Animate-first, 30 Inanimate-first). These lists also contained distractor sentences, comprised of sixty phrase structure violations (30 control, 30 violation, e.g. “He started to [thank his wife/ *wife his thank]...”) and sixty semantic anomalies (30 control, 30 violation, e.g. “The bank will invest [the eggs / *the money]...”). Each list thus contained 180 sentences (60 critical, 120 distractor) and their respective comprehension questions. The two lists were pseudorandomised four times, leading to eight lists in total².

² Parameters for pseudorandomisation were: minimum distance of two between sentence condition, no more than three violations in a row, minimum distance of ten between item number, minimum number difference of

The auditory stimuli were recorded in a silent room using professional recording equipment (16-bit 44.1 kHz Wav format) by a female native English speaker. All stimuli were recorded in a natural and neutral prosody that did not give cues to the nature of the sentence. Initial recording was split over two consecutive days, with re-recording on a third day for stimuli that contained an external disturbance, poor voice quality or poor intonation. Individual sentences were extracted from the larger recording chunks manually. Intensity of individual audio files were averaged to a mean value to normalise intensity. The duration and pitch of recordings was not altered to retain the naturalness of stimuli.

2.2.3. Norming. Orthographic length and word frequency (British National Corpus version 3, 2007) were matched across Animate and Inanimate nouns (no significant differences). Pairwise cosine similarities between the first noun and verb³ were included in the statistical analysis as a covariate in line with the recommendations of Sassenhagen & Alday (2016). The mean pairwise cosine similarity for Animate-first sentences was 0.129 (SD 0.127) and for Inanimate-first was 0.241 (SD 0.166).

2.2.4. Acoustic analyses. Speech-analysis program Praat (Boersma, 2006) was used to measure the intensity, fundamental frequency (F_0)/pitch, and duration of each word (first noun, auxiliary, verb, and second noun). These measures were compared between Animate-first and Inanimate-first sentences using ANOVA (Analysis of Variance) analyses. No significant differences in intensity or pitch (mean, minimum or maximum) were observed. For duration, no significant differences were found in the first noun. Inanimate-first sentences had a significantly longer duration for the auxiliary word (always “will”, on average 23 milliseconds longer) and for the second noun (on average 52 milliseconds longer) compared to Animate-first sentences. See Appendix A for further details of the statistical comparisons using ANOVA, and descriptive statistics tables.

2.2.5. Task. The comprehension task comprised three question types: (1) probing for the Actor, (2) probing for the Undergoer, or (3) a general comprehension yes/no probe. Below the visually presented comprehension question, two possible answers were presented, either two nouns or “yes” and “no”. Table 2 has examples of the comprehension questions. Question type was pseudorandomly allocated to sentence condition and balanced within each list. For each sentence condition within a list, 10 of each question type were allocated to Animate-first/correct sentences and 10 of each to Inanimate-first/violation sentences. However, in the phrase structure violation filler condition, where the syntax violation made it difficult to create Undergoer and Actor questions, we allocated a higher ratio of yes/no probe questions.

two between item number, no more than three of the same question type in a row, no more than two of a correct answer type in a row, and no more than three repetitions of target answer location (left/right of screen) in a row.

³ Pairwise cosine similarities between the first noun and the verb (e.g. *student* – *answer*) were computed using the cbow method and 100,000 word vectors for the semantic spaces with package *LSAfun* (Günther et al., 2015) in R version 3.5.2 (R Core Team, 2018).

Table 2: Example question and response choices for the Judgement and Comprehension task conditions, including sub-conditions of the comprehension task. The positioning of the answer choice on the left or right of screen was counterbalanced.

Question type	Question presented	Answer choice presented on left / right of screen
Actor probe	Who/what will write?	Student / Answer
Undergoer probe	Who/what will be written?	Student / Answer
Yes/no probe	Was there a flower?	Yes / No

2.3. Magnetic resonance imaging (MRI)

Structural T1-weighted MRI scans of the brain were acquired (MPRAGE sequence, inversion time = 900 ms, repetition time = 23 s, echo time = 2.98 ms, flip angle = 9°, field of view = 256 mm, voxel size = 1 x 1 x 1.1 mm) on a 3T scanner (Magnetom Skyra, Siemens, Germany). The structural MRI scans were used to guide placement of the rTMS coil over the left pSTS.

2.4. Transcranial magnetic stimulation (TMS)

Single-pulse and repetitive TMS was delivered to the brain with a MagVenture MagPro X100 (MagVenture, Inc., Farum, Denmark) and figure-of-eight coil (Cool-B70, 97 mm external diameter of wings). Resting motor threshold was determined by applying single-pulse TMS to the left primary motor cortex, over the motor area of the first dorsal interosseous muscle. The evoked electromyographic response, called a motor-evoked potential (MEP), was recorded from the right first dorsal interosseous muscle using two surface electromyographic (EMG) electrodes (Ag-AgCl, 10 mm diameter, inter-electrode distance: 3 cm) positioned over the tendon and muscle belly. EMG activity was amplified at 200 μ V/div, sampled at 100 kHz and filtered (100 Hz – 5 kHz) for visual display using a data acquisition system (MagVenture Motor Evoked Potential Monitor and MagVenture MagPro X100, MagVenture, Inc., Farum, Denmark). Resting motor threshold was measured and defined as the minimal intensity of stimulation that produced a MEP amplitude of at least >50 μ V with 50% probability in 5 out of 10 consecutive stimuli delivered at ~0.2 Hz (Rossini et al., 1994).

Repetitive transcranial magnetic stimulation (rTMS) was delivered to the left pSTS at an intensity of 90% of individual resting motor threshold. One participant reported discomfort during rTMS so the intensity of stimulation was reduced to 85.7% of resting motor threshold in this individual. The frequency of stimulation was 1 Hz and the duration of each block of stimulation was 15 minutes (900 pulses in total). The rTMS protocol complied with published safety guidelines (Rossi et al., 2009; Wassermann, 1998). rTMS was delivered using a real (Cool-B70, 97 mm external diameter of wings) or sham coil figure-of-eight coil (MC-P-B70; MagVenture, Inc., Farum, Denmark). See (Wessel et al., 2019) for further technical specifications of the real-rTMS coil. ABrainsight neuronavigation system and software (Rogue Research Inc, Montreal, Canada) was used to identify the scalp position for coil placement over the left pSTS. Four anatomical landmarks were identified (left and right tragus, tip and

bridge of nose) to co-register the participants' heads to the MRI image. MRI scans were also co-registered to Montreal Neurological Institute (MNI) coordinates using the MNI registration function in Brainsight, by marking the anterior and posterior commissure on each scan. The stimulation site for the pSTS was determined by referring to two coordinates from previous fMRI studies which were marked on participant scans. Coordinates were taken from Möttönen et al. (2006) who observed stronger activity in left pSTS to modified speech sounds after training to identify the sounds compared to before training ($x = -65$, $y = -39$, $z = 0$). The second coordinates were taken from Binder et al. (2000) who observed increased activity in mid STS to speech versus nonspeech ($x = -59$, $y = -19$, $z = -5$). These sites were marked on participant scans, and were used to determine the optimal site for stimulation. In addition, identification of anatomical landmarks in individual participant neuroanatomy were used to ensure that the sulcus was stimulated rather than surrounding gyri. Across all participants, the average coordinates selected for stimulation were $x = -55.70$, $y = -22.17$, $z = -2.28$, which is in a similar region as previous functional neuroimaging activation clusters reported for pSTS (e.g. Otsuka et al., 2009; Rimol et al., 2005). The coil position was marked on an elasticated cap worn by the participant and the coil was held firmly against the scalp throughout stimulation. For both real-rTMS and sham-rTMS, the coil was positioned with the handle pointing posteriorly at approximately $35-45^\circ$ to the sagittal plane and tangentially to the skull. This orientation was established as the most comfortable for participants in pilot testing. The neuronavigation system used an infrared camera to monitor the positions of tracking devices attached to the TMS coil and to the participant's head. The relative positions of the coil and the target site on the participant's head were tracked in real time, and allowed the coil to be placed and maintained to within 2 mm of the target site during stimulation.

To record the occurrence of mild adverse effects associated with rTMS, a standardised monitoring questionnaire (Maizey et al., 2013) was administered the day following the rTMS session. This questionnaire documents incidents of seizure, fainting/collapse, dizziness, nausea/vomiting, headache, muscular ache, muscle spasm/twitch, insomnia, sensory problems, difficulties speaking or understanding speech, lack of coordination, or slowness/impairment of thought.

2.5. Sentence task

Participants were seated approximately 90 cm from a computer screen. Sentences were presented auditorily via sound-attenuating in-ear headphones worn by participants. Each trial comprised a 200 millisecond blink prompt, followed by a fixation cross presented for 500 milliseconds pre-stimulus onset. The auditory sentence was then presented, and during this time the fixation cross remained onscreen. After each sentence, a comprehension question was presented visually on-screen with two potential answers below. Participants were instructed to select the answer they deemed correct by pressing either the left or right bumper button of an Xbox controller to select the left- or right-side answer. A 5 second response window was permitted, and a participant response would end the trial.

Prior to the main experiment, participants undertook eight unrelated practice trials (two with linguistic violations).

2.6. Procedure

Each participant completed three sessions on three different days, with an optional follow-up phone call to undertake the mild adverse effects questionnaire. The first session involved eligibility screening (TMS and MRI), obtaining written informed consent, and familiarisation with TMS and the experimental room. The second session involved acquiring a structural MRI scan of the brain, usually within one week of the first session. The final session involved attending the laboratory for the experimental testing session, on average within two weeks of the brain MRI (see Figure 2A for experimental flowchart). Participants could also elect to receive a phone call from a researcher the day after the experimental session to respond to the mild adverse effects questionnaire (Maizey et al., 2013).

Upon arrival to the laboratory to undertake the experimental testing session, participants re-completed the TMS safety screen to ensure no contraindications to TMS (Rossi et al., 2009, 2011). The participant was then seated in a MagVenture treatment chair (MagVenture, Inc., Farum, Denmark) with a headrest to assist in reducing head movement. Participants were fitted with an EEG cap for planned recording of electrical activity in the brain, however due to technical issues affecting multiple recordings, EEG data was not analysed or reported. EMG electrodes were attached to the left first dorsal interosseus to monitor motor evoked potentials, and participants were asked to rest both hands on a pillow which was placed in their lap. Resting motor threshold was then determined. Next, neuronavigation was undertaken using a participant tracker attached to the EEG cap. Stimulation was split into two blocks (real-rTMS and sham-rTMS), with the order of blocks counterbalanced across participants. Participants were not shown the coils and were blinded to the TMS condition. During stimulation, participants watched a computer screen showing a nature documentary, without sound or subtitles (video only). Participants and researchers wore sound-attenuating earplugs during stimulation.

After the first 15-minute block of rTMS, a 5-minute break was undertaken, followed by the first block of sentence presentation which lasted approximately 10 minutes. Participants were then provided a 30-minute break during which they could go to the bathroom, eat snacks, drink water, read magazines, or talk to the researchers. Participants were not permitted to use phones or computers during the break. After the break, the second 15-minute block of rTMS was undertaken, followed by a 5-minute break and the second 10-minute block of sentence presentation. Participants were then asked to rest quietly for 15 minutes after the task before being debriefed. The experimental testing session lasted approximately 3.5 hours (see Figure 2B for a protocol illustration).

Figure 2. Experimental procedure. A. Schematic of overall experimental procedure. B. Schematic of rTMS protocol. Presentation of real- versus sham-rTMS in Block 1 or Block 2 was counterbalanced across participants. The x-axis indicates number of minutes from beginning to end of the rTMS protocol. Abbreviations: MRI = Magnetic Resonance Imaging, EEG = electroencephalography, rTMS = repetitive transcranial magnetic stimulation.

3. Data analysis

R version 3.5.2 (R Core Team, 2018) was used for all statistical analyses with the packages *tidyverse* version 1.2.1 (Wickham, 2017), *car* version 3.0.2 (Fox & Weisberg, 2019), *lme4* version 1.1.21 (Bates et al., 2015), and *effects* version 4.1.0 (Fox, 2003; Fox & Weisberg, 2019). *lmerOut* v0.5 (Alday, 2018) was used to produce model output tables. Plots were created in R using *ggplot2* v3.3.0 (Wickham et al., 2020). For all statistical models, categorical variables were encoded with sum encoding (ANOVA-style encoding; see Appendix B for further details) and results were summarised with Type II Wald tests. Models of response choice were fit with binomial distributions. Stimuli, raw data and analysis scripts are available via the Open Science Framework⁴. Statistical significance was assumed at $p < 0.05$.

3.1. Critical sentence interpretation

Mixed effect models (MEMs) fit by maximal likelihood were undertaken for participants' behavioural responses to the critical stimuli. The first model (binomial Response Choice, logit-link) specified participants' behavioural response (which of the two response choices were selected) as the

⁴ These stimuli and data will be available upon publication.

dependent variable. Model predictors included Animacy (Animate-first or Inanimate-first), Question Type (Actor or Undergoer probe), rTMS Condition (real- or sham-rTMS), and raw response time (RT). Pairwise cosine similarity values (between the first noun and the verb) were included as an additional covariate, and intercepts were grouped by Participant ID and Item with random slopes for the effect of Animacy constructed for Item and Participant ID. By including RT as a fixed effect in the model of Response Choice, we were able to examine the relationship between the two and determine whether the Response Choice-RT relationship (“speed-accuracy trade-off”) significantly affects the experimental factors (Davidson & Martin, 2013). Raw untransformed RT was used rather than scaled or logarithmic values, as statistically significant differences that arise from modelling transformed RT can be uninformative to significant differences in the raw data, as discussed by Lo & Andrews (2015). Although sex differences and individual motor threshold were considered for inclusion in the statistical modelling, these factors were not included due to the imbalance of sex in the current sample and convergence issues indicating overfitting of the data.

3.2. General comprehension

To examine whether there were rTMS-related differences in general comprehension (indexed by responses to the general comprehension yes/no probe), we constructed the following model. The second model (binomial Response Accuracy, logit-link) specified participants’ behavioural response to the yes/no probe as the dependent variable. Model predictors included Sentence condition (Critical sentences, semantic anomaly, or phrase structure violation) Grammaticality (Animate-first/grammatical or Inanimate-first/ungrammatical), rTMS condition and raw RT. Intercepts were grouped by Participant ID and Item with random slopes for the effect of Sentence condition constructed for Item and Participant ID.

3.3. Mild adverse effects questionnaire

Lastly, participant responses to the mild adverse effects monitoring questionnaire were collated to determine the prevalence of mild adverse effects in the participant sample.

4. Results

4.1. Participant characteristics

All participants were monolingual native English speakers, with three predominantly raised in England, one raised in England and Australia, one raised in the United States, one raised in Malaysia and Australia, and the remaining 17 raised in Australia only. Three of the female participants used the combined oral contraceptive pill. All participants were TMS-naïve. Although formal data were not collected on participant perceptions of differences between the real-TMS and sham-TMS conditions, upon debriefing participants did not report suspicion or perception that the sham-rTMS had been a control/placebo condition.

The length of time between screening and the MRI scan was 1 – 12 days ($M = 4.3$, $SD = 3.6$) and between the MRI scan and TMS session 5 – 36 days ($M = 12.8$, $SD = 8.1$). Resting motor threshold ranged from 34% to 59% of maximum stimulator output ($M = 49.2$, $SD = 5.58$, median = 49.0)⁵. Stimulation intensity for the main experiment, at 90% of resting motor threshold, thus ranged from 30% - 53% of maximum stimulator output ($M = 43.8$, $SD = 5.0$, median = 44). During the experiment, one participant reported discomfort during stimulation, and stimulation was reduced from 50% to 48% of maximum stimulator output. As the sex distribution was unbalanced in the current study (18 female, 5 male), we compared stimulator output across sex, finding that female participants on average received a higher percentage of maximum stimulator output ($M 44.5\%$, $SD 3.66\%$) compared to males ($M 41.4\%$, $SD 7.37\%$). Statistical comparisons between males and females were not conducted due to the small number of male participants ($n=5$). Order of rTMS condition was counterbalanced, with twelve participants receiving real-rTMS first and eleven receiving sham-rTMS first.

4.2. Critical sentence interpretation

We observed significant interaction effects of rTMS condition x Question type x Response Time (RT) ($\chi^2(1) = 4.08$, $p = 0.043$) and Animacy x Question type x RT ($\chi^2(1) = 5.39$, $p = 0.020$) on Response choice. As Response choice interacted with Question type, responses to the Actor and Undergoer probe will be discussed in turn. When probed for the Actor, participants predominantly selected the first noun in most trials, in line with the conception that word order is the prominent cue for English sentence interpretation. For the real-rTMS condition, Response choice was significantly modulated by RT. Where RT was fast, the first noun of Inanimate-first sentences (“the answer will write...”) had a very high selection as the Actor, in line with a sequence-based processing strategy. This selection percentage decreased as RT increased, and where RT was slow, the inanimate first noun was selected as the Actor significantly less often. In slow RT trials, the response pattern of the real-rTMS condition is in line with a dependency-based processing strategy. There were no significant differences across Animacy conditions for the sham-rTMS condition in response to the Actor question.

When probed for the Undergoer, participants predominantly selected the second noun as the Undergoer, again indicating a strong sequence-based (word order) processing strategy. The effect of Animacy is shown where Inanimate-first sentences elicited a reduced sequence-based strategy compared to Animate-first sentences. In both the real- and sham-rTMS conditions, the animate second noun of Inanimate-first sentences was selected as the Undergoer in approximately two-thirds of trials,

⁵ This average resting motor threshold is comparable to previous research using similar MagVenture coils. Van Doren et al. (2015) reported a mean resting motor threshold of the “motor hotspot” of 48.0% ($SD 5.6\%$) of maximum stimulator output. This study used an MCF-B65 (static cooling) coil and MagVenture Magpro stimulator in a sample of similar age (mean age 24.6, $SD 2.3$). See also (Hasan et al., 2016) for similar average resting motor threshold values (specific motor region not specified) using a MagVenture stimulator in a patient sample.

with one-third of trials following a dependency-based (animacy) strategy (see Figure 3 for effects plotted with raw data and Figure 4 for modelled data).

Figure 3: Raw data, aggregated by participant, plotted to show the interaction of rTMS condition, Animacy, Question type, and Response time on Response choice. In each plot, a participant has one point per Animacy condition (Animate-first or Inanimate-first). Shaded regions indicate the 95% confidence interval.

Figure 4: Modelled interaction of rTMS condition, Animacy, Question type, and Response time on Response choice. The points on each line represent the mean response time for each condition. As the statistical model was computed with a logit link, the y-axis is logit scaled. Thus, points at the upper and lower ends of the y-axis scale are further apart than points in the centre of the scale. Shaded regions indicate the 95% confidence interval. In response to the Actor probe (top row), an interaction between rTMS condition and Response Time is evident for the real-rTMS condition only. In response to the Undergoer probe, Response choice was similar across rTMS conditions, showing an animacy effect where Inanimate-first sentences prompted a dependency-based strategy more often than Animate-first sentences.

4.3. General Comprehension

Accuracy was high across all sentence conditions for both sham- and real-rTMS, indicating a ceiling effect. Average accuracy for real-rTMS was 97.74%, for sham-rTMS was 96.35%, and collapsed across rTMS conditions, accuracy was 97.04%. We observed a significant main effect of RT ($\chi^2(1) = 21.20, p < 0.001$) on Response accuracy, and accuracy showed a larger variance across conditions when RT was longer. For some sentence conditions, longer RT appeared to correspond with higher accuracy, however this difference was minimal as accuracy was extremely high across all conditions (over 90%). We also observed a significant interaction of Sentence Condition x Grammaticality ($\chi^2(2) = 6.10, p = 0.047$), where response accuracy was significantly lower for ungrammatical phrase structure violation sentences. No significant main or interaction effects including rTMS condition were observed (see Figure 5 for effects plotted with raw data and Figure 6 for modelled data).

4.4. Mild adverse effects monitoring questionnaire

Twenty-two of the 23 participants completed the mild adverse effects (MAEs) monitoring questionnaire on the day after the experimental session. The one participant who did not complete the questionnaire self-contacted the researchers and self-reported no adverse effects. Of those who completed the questionnaire, 15 (65.22%) reported no mild adverse effects. Six reported headaches; two believed that it may be due to other factors (stress and menstrual cycle, and hot weather), two reported a “small headache”, and two reported headache (one “mild”) in the evening of the session only. One participant reported slight tensing in the temple on the side of stimulation (left), subsiding after approximately 5 minutes, in the morning following the rTMS session.

Figure 5: Raw data, aggregated by participant, plotted to show the interaction of rTMS condition, Animacy, Question type, and Response time on Response accuracy in response to the yes/no general comprehension probe. In each plot, a participant has one point per sentence condition. Shaded regions indicate the 95% confidence interval.

Figure 6: Modelled interaction of rTMS condition, Sentence condition, and Sentence grammaticality on Response accuracy to the yes/no general comprehension probe. As the statistical model was computed with a logit link, the y-axis is logit scaled, thus points at the upper and lower ends of the scale are further apart than points in the centre of the scale. Shaded regions indicate the 95% confidence interval. As accuracy was very high, the full y-axis scale is not displayed. The dashed line represents the mean response time across conditions (1,176 ms). By-condition mean response times are not plotted as variance across conditions was low. Overall, accuracy was very high across rTMS conditions, sentence conditions, and sentence grammaticality, with no significant differences. At longer response times, accuracy for some sentence conditions slightly improved, indicating a speed-accuracy trade-off, but this difference was minimal.

5. Discussion

The present study aimed to test a prediction put forth by the extended Argument Dependency Model (eADM), that the dorsal stream plays a role in sequence-based sentence processing (Bornkessel-Schlesewsky et al., 2015). We applied image-guided repetitive transcranial magnetic stimulation (rTMS) to the posterior superior temporal sulcus (pSTS, a region of the dorsal stream). A low-frequency rTMS protocol was employed, with the aim of reducing the contribution of sequenced-based processing (i.e. word order cues) to English sentence comprehension. TMS-naïve participants experienced both real- and sham-rTMS (order of presentation counterbalanced across participants), before listening to auditorily presented semantic reversal anomalies (SRAs) and responding to comprehension questions. Our results support the hypothesis (H1) that, in line with previous research (Kyriaki, et al. 2020b), Inanimate-first sentences and Undergoer questions would promote a more dependency-based strategy in comparison to Animate-first and Actor questions. We further predicted (H2) a significant effect of rTMS on Response choice, where real-rTMS would lead to a reduction in sequence-based processing and increase in dependency-based processing (i.e. a higher reliance on animacy as an interpretation cue). Compared to sham-rTMS, we expected that the real-rTMS condition would show a significant behavioural difference between Animate-first and Inanimate-first sentences. We indeed observed rTMS effects on Response choice, but the pattern was more complex than expected, due to the interaction with Response time and Question type. We further hypothesized (H3) that in response to the general comprehension yes/no probe, Response accuracy would not be modulated by rTMS or sentence conditions, but accuracy would be significantly higher for Animate-first/grammatical over Inanimate-first/ungrammatical sentences. In the following paragraphs, we discuss our findings, interpret results in the context of the Response choice – Response time interaction, and apply our findings to current neurobiological models of sentence processing.

5.1. Both rTMS and task focus modulate sentence processing

Response choice was significantly modulated by rTMS condition, Animacy, Question type, and Response time (RT). When probed for the Actor (“Who/what will write?”), we observed a significant interaction of rTMS, Animacy, and RT on participants’ response choice. For the sham-rTMS condition, by contrast, response choice was similar for both Animate-first and Inanimate-first sentences, and remained similar regardless of RT latency. In the real-rTMS condition, the behavioural response across sentence types varied as a function of RT, and the predicted directionality of the effect was observed only when RT was longer than average. Here, we observed a reduced sequence-based processing strategy for Inanimate-first sentences, where selection of the inanimate first noun as the Actor was reduced. Thus, the real-rTMS condition showed the expected shift toward a dependency-based strategy in response to Inanimate-first sentences, as compared to Animate-first sentences and the sham-rTMS condition. However, where RT was short, the effect of real-rTMS on response choice was in the opposite direction than predicted: the response choice for Animate-first sentences had a lower

percentage of first noun selection compared to Inanimate-first sentences. We will return to this observation below. Thus, while the real-rTMS condition showed a reduced sequence-based processing strategy for Inanimate-first sentences, responses significantly differed from the sham-rTMS condition in the context of Actor questions and long RT latencies only.

As predicted, we observed a significantly different pattern of responses for the Undergoer probe, which promoted a more dependency-based strategy than the Actor probe. This increased prominence of animacy for sentence processing was observed in response to the Undergoer probe for both rTMS conditions. When probed for the Undergoer (“Who/what will be written?”), compared to the Actor probe, Inanimate-first sentences elicited a different response choice with participants selecting the inanimate first noun in approximately one-third of cases. This indicates a trend towards a dependency-based strategy for some trials (i.e. particular sentence stimuli), where the combination of question type and animacy cue overwhelmed the typically sequence-dependent strategy used to interpret English sentences. These results are supported by our recent findings (Kyriaki, et al. 2020b), where an Undergoer probe influenced both English and German speakers to adopt an increased dependency-based strategy when processing similar sentences.

Together, the rTMS and Question type effects and interaction show that there are multiple contexts which “push” participants towards an increased dependency-based strategy. Real-rTMS promotes a focus on interpretation cues outside of the dominant word order, such as the animacy of the sentential nouns. The same is observed for the Undergoer question type, which also draws focus to dependency-based processing via cues such as noun animacy, regardless of rTMS condition (observed for both real and sham rTMS conditions). However, when these conditions are combined (i.e. real-rTMS + Undergoer question) the effect does not appear to be additive in leading to a greater dependency-based strategy compared to real-rTMS alone or the Undergoer question alone. There are a number of potential explanations for why we did not observe an additive effect of real-rTMS and Undergoer question on an amplified dependency-based strategy. First, it could be that the Undergoer question promoted a dependency-based strategy such that participants relied on the ventral stream to a greater capacity, and thus modulation of the pSTS/dorsal stream did not have an effect. A second possibility is that there is some aspect of the Undergoer question task requirement that reduced or counteracted the influence of rTMS on processing. The Undergoer question is unusual and more difficult compared to the Actor and yes/no probes. A speed-accuracy trade-off is not observed for the Undergoer question, with little difference in response choice as a function of RT. Interestingly, previous research has reported a similar connection between rTMS effects and task difficulty. Grossman et al. (2005) reported that low-frequency rTMS to pSTS reduced accuracy in a biological motion perception task but only for the easier task type. When the stimuli were inverted (shown upside down), virtual lesion of pSTS did not reduce response accuracy (Grossman et al., 2005). The authors suggested that in comparison to recognition of upright stimuli, during recognition of the inverted stimuli, additional neural function may be recruited (Grossman et al., 2005). A similar interpretation could be applied to

the present study, where additional processing may be required for answering an Undergoer probe over an Actor probe. It is possible that the nature of the Undergoer probe may require a stronger recruitment of prefrontal regions due to increased cognitive/“executive function” demands, shifting demand from language networks to more general networks. One conception of this is the “multiple-demand” network (Duncan, 2010), where frontal regions show increased activity in response to high cognitive demand, such as when learning a novel task, suppressing a response, or perceiving and comprehending degraded stimuli (Duncan & Owen, 2000). Our data support this suggestion, where the more difficult Undergoer question may lead to increased fronto-parietal activity, and activity in these regions may compensate for the effect of rTMS on pSTS in this task context.

5.2. The response choice – response time interaction

An unexpected finding in the present study was the response choice – response time interaction for real-rTMS in response to the Actor question. These results indicate that for real-rTMS, the interaction of RT and response choice is a crucial point to consider when interpreting results. Existing rTMS research provides variable results, where the application of rTMS sometimes influences behavioural or neurophysiological responses, and in other cases, does not. While many methodological choices (e.g. intensity and frequency of stimulation, number of pulses, coil orientation) can influence the presence/absence and nature of rTMS effects on behavioural outcomes (Pell et al., 2011), one lesser-considered aspect may be the interaction with reaction or response time (RT). Reaction time (in the context of a task prompting immediate responses) and RT (in the present study) arise from the same underlying process(es) as response accuracy/choice (Davidson & Martin, 2013). Each represent the internal decision-making process of the participant, a process which is usually unknown to the researcher. In the present study, a clear speed-accuracy trade-off is evident for the sham-rTMS group in response to Actor questions. Here, increased RTs are related to a response choice that is a correct interpretation of the sentence following the standard English sequence-based processing strategy. A speed-accuracy trade-off is also observed for the real-rTMS response, albeit in a slightly different way. As RT increases, response choice is closer to the hypothesised pattern: to Animate-first sentences, responses indicate a sequence-based strategy, and to Inanimate-first sentences, responses indicate an increasingly dependency-based strategy. This suggests some aspect of decision making that is more “accurate” as RT is longer, including after real-rTMS.

Until recently, research in psychology and related fields has predominantly employed ANOVAs to analyse statistical differences, which aggregate by participant (and/or sentence item in language paradigms) thereby eliminating variance across experimental items or participants (Baayen et al., 2008; Kretzschmar & Alday, 2020). This restricts the ability to model response choice by RT, as RT is aggregated by-participant/by-item and thus does not capture the variance across the experiment. Mixed effects models (MEMs) do not aggregate, thus capturing the unique response in a trial-by-trial format while considering participant and item variability (Baayen et al., 2008; Kretzschmar & Alday,

2020). In the current study, we found that by modelling un-aggregated data with RT as a fixed effect, an interaction effect involving rTMS condition was observed. Our modelled data draw attention to two factors for consideration: (1) data aggregation may reduce the variance of data in a way such that significant interactions are not observed and (2) the interaction with RT is important for investigating the effect of rTMS on response choice or accuracy. Aggregation and/or the lack of RT as a predictor may be a possible explanation for the variability of results in the field – for example where predicted rTMS effects on language are not observed (e.g. Krocze et al., 2019 who used a language task and found no effect involving rTMS on response time or response accuracy, each analysed separately using ANOVAs). Future research should thus consider the complex relationship between response accuracy/choice and RT/reaction time – variables that some argue should not be analysed separately (Davidson & Martin, 2013) – and how they may interact as an effect of rTMS. Further, the use of MEMs to analyse data can provide a more fine-grained analysis of by-participant and by-item variation as influenced by TMS.

5.3. Posterior superior temporal sulcus (pSTS) for domain-general sequence processing

pSTS – and more broadly, STS – is proposed to be a multifunctional cortical region with bidirectional connections to frontal, premotor, parietal, and temporal regions (Hein & Knight, 2008). Activation of left pSTS has been examined in a variety of domains including motion processing (e.g. Grossman et al., 2005; Grossman & Blake, 2002), face processing (e.g. Haxby et al., 1999), audio-visual integration (e.g. van Atteveldt et al., 2004), theory of mind (e.g. Takahashi et al., 2004) and word order processing in language paradigms (e.g. Bornkessel et al., 2005; Matchin et al., 2019; Röder et al., 2002; Wilson et al., 2010). The present study indicates a causal contribution of left pSTS to sequence-dependent processing of word order for sentence comprehension. Low frequency rTMS over pSTS altered response choice in a manner indicative of an increased dependency-based strategy, increasingly so where RT was longer. This suggests that pSTS plays an important role in sequence-based processing, and thus presumed inhibition of this region leads to a more prominent dependency-based strategy. Therefore, pSTS appears to have a role in the linear processing of auditory input for comprehension – part of the hierarchical predictive coding architecture as proposed by Bornkessel-Schlesewsky et al., (2015).

Our findings fit with existing conceptions of pSTS as a multifunctional cortical region (Hein & Knight, 2008) involved in sequence and predictive processing. For example, perception of biological motion has been consistently linked to pSTS in imaging, lesion and TMS studies (Battelli et al., 2003; Grossman et al., 2005; Grossman & Blake, 2002; Herrington et al., 2011; Saygin, 2007; Vaina et al., 1990; van Kemenade et al., 2012). A key component of motion processing is matching visual input against known representations of biological motion (Herrington et al., 2011) – i.e. developing predictions about upcoming events based upon world knowledge and previous events in the sequence. As such, we can conceptualise pSTS as supporting multiple cognitive processes which have a

requirement for understanding sequencing, whether that be the order of words or the spatial ordering of movement.

5.4. General comprehension is unaffected by rTMS

As predicted, we observed no effects of rTMS condition on response accuracy to the general comprehension probe. Overall, participants exhibited extremely high levels of response accuracy across the three sentence conditions (critical sentences, phrase structure violations, and semantic anomalies). Participants were very accurate in identifying the presence/absence of a probe word in a sentence regardless of grammaticality. A significant main effect of RT was observed, where an increase in RT led to a slight increase in the already high response accuracy, indicating a speed-accuracy trade-off. Response accuracy to binary yes/no judgements are generally quite high in similar language paradigms, with comparable stimuli eliciting judgement accuracies of over 85% for both plausible and implausible English sentences (Bourguignon et al., 2012; Kuperberg et al., 2003; Kyriaki et al., 2020a). Our results show that low frequency rTMS over the posterior superior temporal sulcus (pSTS) did not modulate general comprehension related to word recall, showing a discriminant effect on the sequence-based processing of sentences.

5.6. Implications for neurobiological models of sentence comprehension

The current findings support the role of pSTS as hypothesised by the eADM (Bornkessel-Schlesewsky et al., 2015). In contrast to other prominent dual-stream models of sentence processing, the eADM proposes an architecture in line with more global cognitive functions rather than specific linguistic subdomains (Bornkessel-Schlesewsky et al., 2011, 2015; Bornkessel-Schlesewsky & Schlesewsky, 2013). As a result of real-rTMS, the reduced sequence-based processing of Inanimate-first sentences supports the prediction that the dorsal stream plays a role for hierarchically ordered sequence processing. Low-frequency rTMS over pSTS was predicted to lead to a relative increase in contribution by the ventral stream, represented by a stronger dependency-based strategy. After real-rTMS, participants showed an increase in responses indicative of a dependency-based strategy, where Inanimate-first sentences were reconceptualised to a plausible meaning and word order was a weaker cue to interpretation. Although the pattern of results was broadly consistent with the predictions of the eADM, the eADM did not predict the more complex pattern of results observed in the current study, namely the additional effect of response time and question type on response choice. A future extension to this model may thus consider the modulation of contextual and task demands on the functional neuroanatomy of sentence processing.

The current study can also contribute to alternate models assuming a dual-streams processing architecture, namely the Auditory Sentence Comprehension Model (ASCM; Friederici, 2011, 2012) and the Memory Unification and Control Model (MUC; Hagoort, 2005, 2014). The ASCM proposes two distinct dorsal streams, one of which is present from birth and supports bottom-up auditory motor

mapping (Friederici, 2012). The other is thought to develop in childhood, and supports the processing of syntactically complex sentences such as embedded clauses (e.g. “The boy that the girl saw was tall”; Friederici, 2012; Friederici et al., 2006). Syntactic information (i.e. sequence) is thus proposed to be processed by both the dorsal and ventral pathways, with the ventral pathway supporting phrase structure building. The ASCM would thus predict that low-frequency rTMS (i.e. presumed inhibition) of the dorsal stream would not affect the processing of the sentence stimuli we used, as they are syntactically simple. However, we observed a significant effect of low-frequency rTMS on comprehension of our critical sentence stimuli, shown in the differential response pattern to Actor selection for Inanimate-first sentences between rTMS conditions.

While the MUC has no strong claims about dorsal stream function, it proposes that temporal and inferior parietal regions are involved in the memory of syntactic structure, phonological word forms, and morphological information (Hagoort, 2014). The predictions of the MUC are such that low-frequency rTMS to pSTS in the current experiment may lead to reduced memory retrieval for syntactic structure (sequence), phonological word forms and/or morphological information (Hagoort, 2014). Here, real-rTMS would be expected to elicit an inhibition of memory processes, which should be evident in the responses to the general comprehension questions. The MUC would expect reduced accuracy in the real-rTMS condition, as memory is required to both understand the auditory stimuli and recall words to accurately respond to the question. This was not the case in the present study, with similar levels of performance between rTMS conditions observed. Our results thus do not support the predictions of the ASCM and MUC in relation to the specific functional role of the dorsal stream and pSTS.

5.7. Limitations and future directions

The current study has three main limitations. The first involves uncertainties about the effect of rTMS on the target brain region. The effect of rTMS on the excitability of targeted neurons in non-motor cortical areas cannot be explicitly determined. The duration of low-frequency rTMS was sufficient to induce specific functional effects in the current study but it is unknown if a longer train of rTMS would have been more efficacious. The present study applied 15 mins of rTMS at 1 Hz (900 pulses) at an intensity of 90% of resting motor threshold. Current safety guidelines state that 1,800 pulses is the maximum safe duration of stimulation for this type of rTMS protocol (Rossi et al., 2009). Thus, there is room to apply more pulses which may uncover more subtle functional effects. The duration of the aftereffects of the current rTMS protocol are also unclear and some attenuation may have occurred during the sentence comprehension task. A longer duration of rTMS (or more pulses) would mitigate this potential limitation.

The second limitation was the unbalanced design for participant sex (18 females and 5 males). While studies of sex-based differences in cortical excitability show mixed results, cortical excitability may vary as a function of the hormonal cycle in females, and stage of menstrual cycle was not measured

or controlled for in the current study (Hattemer et al., 2007; Hausmann et al., 2006; Smith et al., 1999; Smith et al., 2002). Contrastingly, other studies report no effect of the menstrual cycle (Wassermann, 2002) nor any significant sex differences (Pitcher et al., 2003) on cortical excitability as determined by the resting motor-evoked potential threshold. Further, functional MRI research of language processing suggests that females may have greater right hemisphere activation, particularly in STG (Baxter et al., 2003; Kansaku et al., 2000). In this case, greater bi-hemispheric activation in females may reduce the observed effects of rTMS applied to left pSTS, which may have reduced the modulation of rTMS in our predominantly female sample and thus the resultant effects on sentence processing. However, observed differences in activation across hemispheres have not been shown to generalise across task sets, and it has recently been suggested that previously observed differences may not be generalisable due to unaccounted variability in the data (Ihnen et al., 2009). More recently, a meta-analysis of functional MRI and positron emission tomography experiments identified no significant sex differences in activation, although females show earlier N1 and P2 event-related potentials as elicited by auditory language input (Sato, 2020). This body of work suggests that there may be sex differences in both language-related neural activation and general cortical excitability, and so future research should consider sex effects. A larger sample with equal males and females, and documentation of the menstrual stage in females, would enable exploration of potential effects of sex and sex hormone levels on studies of sentence comprehension and language circuitry.

Lastly, the current study employed a novel language processing task design, investigating the interaction of rTMS, sentence animacy, and the type of comprehension question presented. Comparing the responses to the Actor and Undergoer probe questions revealed a differential effect of real-rTMS, suggesting that the functional neuroanatomy of sentence processing is affected by such differences in task demands. This was not predicted by the eADM nor other existing models of the neurobiology of language processing. Future iterations of these models should thus consider the effect of contextual cues (such as specific task demands) on functional neuroanatomy during the processing of sentences.

6. Conclusion

The present study has shown a causal role of pSTS for linguistic sequence processing in English speakers. Our findings support current conceptions of pSTS as relevant for sequence processing (Hein & Knight, 2008), and more specifically, relevant for sequence processing in language (Bornkessel-Schlesewsky et al., 2015). We have further shown that low-frequency rTMS over pSTS effectively modulates the behavioural response to comprehension questions, and that this effect interacts with response time. Future research should assess the impact of trial aggregation and the potential influence this may have on behavioural outcome measures. The relationship between response choice/accuracy and response time should be carefully considered even where response time is not a variable of interest in the experimental design.

Data Availability

Upon publication the stimuli and datasets generated for this study and the analysis code will be found in an Open Science Framework repository.

Author contributions

LK, GT, JD, MS, and IB-S designed the research. LK conducted the research. LK and IB-S analysed the data. LK, GT, MS and IB-S wrote the paper.

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Competing interests

The authors have no competing interests to report.

List of Abbreviations

AC	Auditory cortex
ANOVA	Analysis of variance
ASCM	Auditory comprehension model
DP	Declarative procedural (model)
eADM	Extended argument dependency model
EMG	Electromyographic
IFC	Inferior frontal cortex
IFG	Inferior frontal gyrus
M	Mean
MEM	Mixed effects (regression) model
MEP	Motor evoked potential
MNI	Montreal Neurological Institute
MRI	Magnetic resonance imaging
MUC	Memory unification control (model)
pSTS	Posterior superior temporal sulcus
RT	Response time
rTMS	Repetitive transcranial magnetic stimulation
SD	Standard deviation
SRA	Semantic reversal anomaly
STS	Superior temporal sulcus
TMS	Transcranial magnetic stimulation

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Appendix A: Acoustic Analyses

Speech-analysis program Praat (Boersma, 2006) was used to measure the intensity, fundamental frequency (F_0)/pitch, and duration of each word (first noun, auxiliary, verb, and second noun). These measures were compared between Animate-first and Inanimate-first sentences using ANOVA (Analysis of Variance) analyses.

Duration. Duration analyses (ANOVA) were performed for the Subject Noun Phrase (NP), auxiliary, verb, and Object NP of critical sentences. At the Subject noun, there was no significant difference in duration between grammatical and ungrammatical conditions. For the auxiliary (always the word “will”), a significant Violation/grammaticality effect was observed ($p = 0.002$). Here, the auxiliary was on average, 23 milliseconds longer for violation compared to control sentences. There was no significant difference in duration at the verb. At the Object noun, there was a significant difference in duration, where for control sentences, the noun was on average 52 milliseconds shorter compared to violation sentences. Mean and standard deviation values are presented in Table A.1.

Intensity. ANOVAs were computed for the critical conditions to observe differences between the control and violation sentences in intensity of the Subject NP, auxiliary, verb, and Object NP. No significant effects were found for any word (all p 's < 0.05). Table A.2 shows the mean and standard deviation intensities.

Fundamental frequency/pitch (Hz). As fundamental frequency (F_0) differences between words gives rise to the perception of intonation or prosody, the minimum, maximum, and mean F_0 values were measured. These values were analysed using ANOVAs for the Subject NP, auxiliary, verb, and Object NP. No significant differences in pitch mean, minimum or maximum were observed (all p 's < 0.05). See Table A.3 for mean and standard deviations of F_0 .

Table A.1: Mean and standard deviation word duration (milliseconds) of the Subject NP, auxiliary, verb, and Object NP of critical sentences.

Grammaticality	Word Duration (ms)			
	<u>Subject NP (SD)</u>	<u>Auxiliary (SD)</u>	<u>Verb (SD)</u>	<u>Object NP (SD)</u>
Grammatical	453.33 (124.50)	153.67 (33.30)	387.00 (121.74)	451.67 (153.36)
Ungrammatical	451.33 (110.86)	176.67 (43.76)	397.00 (102.72)	503.34 (102.10)

Table A.2: Mean and standard deviation word duration intensity (dB) of the Subject NP, auxiliary, verb, and Object NP of critical sentences.

Grammaticality	Word Intensity (dB)			
	<u>Subject NP (SD)</u>	<u>Auxiliary (SD)</u>	<u>Verb (SD)</u>	<u>Object NP (SD)</u>
Grammatical	71.98 (1.29)	70.97 (1.82)	70.18 (1.67)	69.21 (1.18)
Ungrammatical	71.95 (1.28)	70.58 (1.60)	70.19 (1.48)	69.56 (1.40)

Table A.3: Mean, minimum, maximum and standard deviations of Fundamental Frequency (Hz) of the Subject NP, auxiliary, verb, and Object NP of critical sentences.

Word	Grammaticality	Word Fundamental Frequency Measure		
		<u>Mean (SD)</u>	<u>Min (SD)</u>	<u>Max (SD)</u>
Subject NP	Grammatical	167.26 (6.86)	148.28 (8.33)	181.89 (22.18)
	Ungrammatical	167.49 (8.31)	143.20 (21.34)	180.89 (10.15)
Auxiliary	Grammatical	159.80 (7.37)	151.86 (8.17)	168.42 (9.35)
	Ungrammatical	159.47 (16.13)	146.38 (22.87)	172.59 (25.52)
Verb	Grammatical	156.19 (7.60)	145.78 (14.92)	169.02 (8.74)
	Ungrammatical	154.76 (6.97)	141.40 (18.57)	169.74 (12.07)
Object NP	Grammatical	149.17 (5.35)	134.42 (16.89)	168.03 (26.41)
	Ungrammatical	147.76 (5.04)	135.52 (12.02)	160.64 (12.22)

Appendix B: Model outputs

Table B.1: Model summary for the mixed effects model analysis of critical sentence interpretation.

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)					
Family: binomial Link:logit					
	AIC	BIC	logLik	deviance	
	1033	1144	-494	987	
Scaled residuals:					
	Min	1Q	Median	3Q	Max
	-3.82	-0.65	0.43	0.58	1.25
Random effects:					
	Groups	Name	Std.Dev.	Corr	
	item	(Intercept)	0.41136		
		cond[Animate-Inanimate]	0.17385	1.000	
	subj	(Intercept)	0.62684		
		cond[Animate-Inanimate]	0.27375	0.468	
Number of obs: 931, groups: item, 54; subj, 23.					
Fixed effects:					
		Estimate	Std. Error	z value	Pr(> z)
	(Intercept)	1.5	0.34	4.5	5.8e-06 ***
	cond[Animate-Inanimate]	0.22	0.27	0.82	0.41
	tms[Real]	-0.12	0.24	-0.52	0.6
	question[Actor Probe]	-0.4	0.24	-1.7	0.093 .
	rt	-0.00011	0.00012	-0.92	0.36
	en _s im	0.012	0.65	0.019	0.98
	cond[Animate-Inanimate]:tms[Real]	-0.39	0.24	-1.6	0.099 .
	cond[Animate-Inanimate]:question[Actor Probe]	-0.83	0.24	-3.4	0.00058 ***
	tms[Real]:question[Actor Probe]	0.37	0.24	1.6	0.11
	cond[Animate-Inanimate]:rt	5.4e-06	0.00011	0.048	0.96
	tms[Real]:rt	5.8e-05	0.00011	0.54	0.59
	question[Actor Probe]:rt	0.0002	0.00011	1.9	0.056 .
	cond[Animate-Inanimate]:tms[Real]:question[Actor Probe]	-0.14	0.24	-0.58	0.56
	cond[Animate-Inanimate]:tms[Real]:rt	0.00016	0.00011	1.5	0.13
	cond[Animate-Inanimate]:question[Actor Probe]:rt	0.00026	0.00011	2.4	0.014 *
	tms[Real]:question[Actor Probe]:rt	-0.00021	0.00011	-2	0.048 *
	cond[Animate-Inanimate]:tms[Real]:question[Actor Probe]:rt	3.4e-05	0.00011	0.32	0.75

Note. Categorical variables were encoded with sum encoding (ANOVA-style coding) where the model coefficient represents the size of the contrast from a given predictor level to the grand mean. For a two-level predictor, this is half the distance between the two levels, as the mean is an equal distance from both points.

Table B.2: Model summary for the mixed effects model analysis of general comprehension.

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation)
Family: binomial Link:logit

	AIC	BIC	logLik	deviance	
	395	591	-162	323	
Scaled residuals:					
	Min	1Q	Median	3Q	Max
	-22.03	0.06	0.09	0.13	0.87
Random effects:					
	Groups	Name	Std.Dev.	Corr	
	item	(Intercept)	0.84005		
		cond[ASV]	1.67573	-0.058	
		cond[PSV]	0.56630	-0.961	-0.221
	subj	(Intercept)	0.74841		
		cond[ASV]	0.22964	-1.000	
		cond[PSV]	0.26845	1.000	-1.000
Number of obs: 1697, groups: item, 59; subj, 23.					
Fixed effects:					
	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	4.4	0.95	4.6	3.6e-06	***
cond[ASV]	-2.4	1.5	-1.6	0.12	
cond[PSV]	2.4	0.98	2.4	0.016	*
gram[C]	0.79	0.88	0.89	0.37	
tms[R]	-0.33	0.87	-0.38	0.71	
rt	0.0009	0.00098	0.92	0.36	
cond[ASV]:gram[C]	2.3	1.5	1.5	0.13	
cond[PSV]:gram[C]	0.012	0.96	0.013	0.99	
cond[ASV]:tms[R]	-3.1	1.5	-2.1	0.032	*
cond[PSV]:tms[R]	0.021	0.95	0.022	0.98	
gram[C]:tms[R]	0.37	0.86	0.43	0.67	
cond[ASV]:rt	0.0024	0.0018	1.4	0.16	
cond[PSV]:rt	-0.0029	0.00099	-2.9	0.0034	**
gram[C]:rt	-0.0015	0.00097	-1.5	0.13	
tms[R]:rt	0.00068	0.00095	0.72	0.47	
cond[ASV]:gram[C]:tms[R]	2.5	1.5	1.7	0.094	.
cond[PSV]:gram[C]:tms[R]	-0.65	0.94	-0.69	0.49	
cond[ASV]:gram[C]:rt	-0.0024	0.0018	-1.4	0.17	
cond[PSV]:gram[C]:rt	0.0009	0.00099	0.91	0.36	
cond[ASV]:tms[R]:rt	0.0032	0.0017	1.9	0.063	.
cond[PSV]:tms[R]:rt	-0.00033	0.00098	-0.34	0.73	
gram[C]:tms[R]:rt	-0.00072	0.00095	-0.76	0.45	
cond[ASV]:gram[C]:tms[R]:rt	-0.0027	0.0017	-1.6	0.11	
cond[PSV]:gram[C]:tms[R]:rt	0.00085	0.00097	0.87	0.38	

Note. Categorical variables were encoded with sum encoding (ANOVA-style coding) where the model coefficient represents the size of the contrast from a given predictor level to the grand mean. For a two-level predictor, this is half the distance between the two levels, as the mean is an equal distance from both points.