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Left posterior inferior frontal gyrus is causally involved in reordering during sentence processing

Philipp Kuhnke*, Lars Meyer, Angela D. Friederici, Gesa Hartwigsen

Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

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ABSTRACT

Storage and reordering of incoming information are two core processes required for successful sentence comprehension. Storage is necessary whenever the verb and its arguments (i.e., subject and object) are separated over a long distance, while reordering is necessary whenever the argument order is atypical (e.g., object-first order in German, where subject-first order is typical). Previous neuroimaging work has associated storage with the left planum temporale (PT), and reordering with the left posterior inferior frontal gyrus (pIFG). Here, we tested the causal role of the PT and pIFG in storage and reordering using repetitive transcranial magnetic stimulation (rTMS). We applied either effective rTMS over PT or pIFG, or sham rTMS, while subjects listened to sentences that independently varied storage demands (short vs. long argument–verb distance) and reordering demands (subject– vs. object-first argument order). We found that rTMS over pIFG, but not PT, selectively affected reordering during the processing of sentences with a long argument–verb distance. Specifically, relative to sham rTMS, rTMS over pIFG significantly increased the performance difference between object– and subject-first long-distance sentences. These results demonstrate a causal involvement of left pIFG in reordering during sentence comprehension and thus contribute to a better understanding of the role of the pIFG in language processing.

1. Introduction

During language comprehension, the core meaning of a sentence—who is doing what to whom—is established by linking the main verb to its arguments, consisting of the subject and object(s) (Frege, 1879; Heim and Kratzer, 1998). The linking of arguments and verb can be impeded by an increased argument–verb distance (Babyonyshev and Gibson, 1999; Cowper, 1976; Gibson, 2000; Grodner and Gibson, 2005), and an atypical argument order (e.g., object-first order in German or English; Friederici et al., 2006; King and Just, 1991). Thus, both long argument–verb distances and atypical argument orders can substantially increase processing demands. On the one hand, long argument–verb distances require the storage of arguments in working memory until their verb is encountered, so that arguments and verb can be linked (Fiebach et al., 2001; Kluender and Kutas, 1993; Meyer et al., 2013). On the other hand, atypical argument orders are associated with the reordering of arguments into the typical order (e.g. subject-first order in German or English), the order in which arguments are linked to their verb (Just and Carpenter, 1992; Kintsch and van Dijk, 1978; Meyer and Friederici, 2015).

For instance, the German sentence “Darum hat *den Autor der Leser* nach der Präsentation auf der Buchmesse *eingeladen*” (“Therefore has *the author [object] the reader [subject]* after the presentation at the book fair *invited [main verb]*”) requires both storage and reordering. The sentence's subject “der Leser” and object “den Autor” are separated from their verb “eingeladen” by a prepositional phrase (“nach der Präsentation auf der Buchmesse”). Consequently, they are stored in working memory across the argument–verb distance. Additionally, because the argument order differs from the typical order, the arguments need to be reordered before they are finally linked with their verb.

A number of previous neuroimaging studies investigated the neural correlates of storage and reordering. Across these studies, the posterior inferior frontal gyrus (pIFG; Brodmann area 44) was consistently activated for atypical versus typical argument orders (Ben-Shachar et al., 2003; Friederici et al., 2006; Kim et al., 2009; Meyer and Friederici, 2015). In contrast, the left temporo-parietal cortex was engaged in the short-term storage of verbal material (Kim et al., 2002; Novais-Santos et al., 2007; Owen et al., 2005; Smith and Jonides, 1998). In a previous neuroimaging study that independently manipulated both reordering and storage demands, Meyer et al. (2012a) found reordering demands (atypical, as compared to typical, argument order)

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* Corresponding author.
E-mail address: kuhnke@cbs.mpg.de (P. Kuhnke).

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to activate the left pIFG, whereas storage demands (long, as compared to short, argument–verb distance) increased activity of left temporo-parietal regions, with the activation peak located in the planum temporale (PT).

While these results provide evidence for a functional neuroanatomical dissociation of reordering and storage, correlative neuroimaging methods cannot determine whether a region is necessary for a particular cognitive function (Price and Friston, 2002). It is thus unknown whether the left pIFG and PT are indeed causally relevant for reordering and storage, respectively—or whether they are involved in activation that is incidental to task performance (i.e., redundant processing, cf. Price and Friston, 2002).

The causal relevance of a given cortical region for a certain function can be determined by repetitive transcranial magnetic stimulation (rTMS) applied during the task of interest (“online”) (Hartwigsen et al., 2015a; Pascual-Leone et al., 2000; Siebner et al., 2009; Walsh and Cowey, 2000). Although the precise physiological mechanisms underlying a TMS-induced disruption of a specific function are unclear, it is likely that online rTMS induces “neural noise” in the stimulated area that interferes with ongoing task-relevant activity and thereby impairs performance (Miniussi et al., 2010; Ruzzoli et al., 2010).

Here, we used online rTMS to probe the functional relevance of the left pIFG and PT for reordering and storage. rTMS was applied either over left pIFG or PT, or as ineffective sham-stimulation, while subjects listened to German sentences that systematically varied both the argument order (taxing reordering, presumably subserved by the pIFG) and argument–verb distance (taxing storage, presumably subserved by the PT). We expected online rTMS to disrupt language processing in our study because a number of previous studies reported impairments in language comprehension with this protocol (e.g., Devlin et al., 2003; Gough et al., 2005; Hartwigsen et al., 2016, 2010a, 2010c).

In addition to determining causality in the functional-anatomical dimension, we aimed to extend Meyer et al.’s (2012a) findings by timing information as their methodology did not allow to pinpoint the critical times where pIFG and PT become involved in reordering and storage, respectively. This information can be provided by TMS applied at different time points during the task. It was previously argued that storage becomes crucial when the arguments are encoded in working memory (Meyer et al., 2013). Reordering, on the other hand, seems to take place at the verb (Meyer et al., 2012b; Nicol and Swinney, 1989). Therefore, rTMS was applied either early—during argument encoding in long-distance sentences (presumably disrupting storage), or late—on the verb (presumably disrupting reordering).

rTMS-induced disruption of sentence comprehension was assessed with a drift diffusion model (Ratcliff, 1978), which represents a powerful statistical tool to analyze data from binary decision tasks, and has already been successfully applied to model the behavioral effects of TMS (cf. Hartwigsen et al., 2015a; e.g. Georgiev et al., 2016; Philiastides et al., 2011; Soto et al., 2012).

Based on the results of Meyer et al. (2012a), we hypothesized to find a functional-anatomical double dissociation. Hence, rTMS over pIFG should selectively disrupt reordering, but not storage. That is, comprehension performance should selectively decrease for object–, as compared to subject-first, sentences. rTMS over PT, on the other hand, should selectively disrupt storage, and not reordering. Here, performance should selectively decrease for long–, as compared to short-distance, sentences. These effects should critically depend on the timing of the TMS pulses: Early TMS (applied during argument encoding in long-distance sentences) should selectively interfere with the storage of incoming information, while late TMS (applied with verb onset) should only affect reordering.

2. Materials and methods

2.1. Subjects

Data from 24 native German speakers (13 females, mean age=26.96 years, standard deviation (SD)=3.34) were analyzed. Initially, 31 participants had been recruited, but 7 subjects were excluded from further analyses because they experienced discomfort with the stimulation procedure. All subjects were recruited via the subject database of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. All subjects were right-handed (Oldfield, 1971; mean laterality quotient=94.41, SD=7.13) and had no history of psychiatric, neurological, or hearing disorders. Each participant was paid 8 € per hour of participation. Written informed consent was obtained before the experiment. The study was performed according to the guidelines of the Declaration of Helsinki and approved by the local ethics committee of the University of Leipzig, Germany.

2.2. Experimental procedures

The study used a 3×2×2×2 within-subjects factorial design with the factors TMS-SITE (pIFG, PT, sham), TMS-TIME (early, late), argument ORDER (subject-first, object-first), and argument–verb DISTANCE (short, long).

The experiment consisted of three TMS sessions (one for each TMS-SITE level), separated by at least 7 days (mean inter-session interval=7.83 days, SD=4.04 days) to prevent carry-over effects of TMS and minimize learning effects. Session order was counterbalanced across participants (to the degree possible due to exclusion of some participants).

Fig. 1A shows the timeline of one experimental session. All sessions comprised two runs of 128 trials each. Breaks between runs were used for coil cooling and adjustment, if necessary. Each run was split into two blocks of 64 trials. Prior to the first run, subjects practiced with 10 demo-trials (5 without and 5 with TMS), which were not included in the actual experiment. Total duration of each experimental session including preparation and neuronavigation (see below) was approximately 110 min.

Stimuli were presented using the software program *Presentation* (Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com). Questions were visually presented on an *EIZO* 19” LCD monitor positioned ~1–1.5 m in front of the participant. Auditory stimuli were played via *Shure* SE215 sound isolating earphones, which simultaneously shielded the subject against the TMS-induced noise. Sound volume was individually adjusted during the demo trials.

Fig. 1B depicts the timeline of a single trial of the experiment. Each trial began with a fixation cross shown on the screen, followed by the presentation of an auditory German sentence. Four types of sentences were created, which systematically and independently manipulated the argument order and argument–verb distance (Fig. 2A; see Stimuli): (1) subject-first short-distance; (2) subject-first long-distance; (3) object-first short-distance; (4) object-first long-distance. During sentence presentation, 5 pulses of 10 Hz repetitive TMS (rTMS) were applied either (1) early (i.e., on the first word following the auxiliary verb) or (2) late (i.e., on the main verb). After stimulus presentation, a visual comprehension question was presented on the screen (Fig. 2B; white letters, font: Verdana, font size: 16 px; gray background), which subjects had to answer within 4 s by pressing a button on a response-box. Response button assignment was counterbalanced across subjects. Finally, participants received visual feedback with a happy or sad emoticon for a correct or false answer, respectively. Subsequently, the next trial was presented. Average trial duration ranged from 9.2 to 15.8 s. Response times (measured from question onset) and accuracy were measured for each trial.