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Perturbation of left posterior prefrontal cortex modulates top-down processing in sentence comprehension

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ABSTRACT

Communication is an inferential process. In particular, language comprehension constantly requires top-down efforts, as often multiple interpretations are compatible with a given sentence. To assess top-down processing in the language domain, our experiment employed ambiguous sentences that allow for multiple interpretations (e.g., *The client sued the murderer with the corrupt lawyer.*, where *the corrupt lawyer* could either belong to *The client* or *the murderer*). Interpretation thus depended on whether participants chunk the words of the sentence into short or long syntactic phrases. In principle, bottom-up acoustic information (i.e., the presence or absence of an intonational phrase boundary at the offset of *the murderer*) indicates one of the two possible interpretations. Yet, acoustic information often indicates interpretations that require words to be chunked into overly long phrases that would overburden working memory. Processing is biased against these demands, reflected in a top-down preference to chunk words into short rather than long phrases. It is often proposed, but also hotly debated, that the ability to chunk words into short phrases is subserved by the left inferior frontal gyrus (IFG). Here, we employed focal repetitive transcranial magnetic stimulation to perturb the left IFG, which resulted in a further decrease of the aptitude to tolerate long phrases, indicating the inability of the left IFG to assist the chunking of words into phrases. In contrast, the processing of auditory information was not affected. Our findings support a causal top-down role of the left inferior frontal gyrus in the chunking of words into phrases.

1. Introduction

Communication is an inferential process. In particular, the comprehension of spoken language constantly requires cognitive efforts, as often more than a single interpretation is compatible with a given utterance (January et al., 2009; Novick et al. 2010, 2013; Meyer et al., 2016). For example, the sentence *The client sued the murderer with the corrupt lawyer.* is ambiguous—because *the corrupt lawyer* can have been hired by either *the murderer* or *the client*. In the written sentence, there is no information to decide whether *the client* or *the murderer* has hired *the corrupt lawyer*. In the spoken sentence, speech prosody contains acoustic modulations that indicate the intended interpretation (Price et al., 1991; Clifton et al., 2002; Snedeker and Casserly, 2010): An intonational phrase boundary (IPB) at the offset of *the murderer*, consisting of pitch modulations, vowel lengthening, and a pause, would indicate that *the corrupt lawyer* is not to be chunked with *the murderer*. In contrast, the absence of an IPB would indicate the alternative interpretation. In reality, however, participants show a bias to ignore these modulations (Meyer et al., 2016) and instead choose the interpretation that minimizes processing demands. In the given example, participants prefer not to chunk *the corrupt lawyer* with *the murderer*—but link it to *the client* instead. This bias to terminate the syntactic phrase at the offset of *the murderer* avoids an overly long syntactic phrase that would overburden working memory (Swets et al., 2007; Webman-Shafran and Fodor, 2015).

Participants' bias to terminate the syntactic phrase provides a subtle window into the projection of internally generated representations onto the incoming speech stimulus. In general, the chunking of words into syntactic phrases is independent from the processing of auditory information, as chunking also occurs without any prosodic modulations (Steinhauer et al., 1999; Ding et al., 2015). The independent internal process of syntactic chunking even can influence auditory processing (Fodor and Bever, 1965; Garrett et al., 1966; Buxó-Lugo and Watson, 2016). In particular, internally generated syntactic phrases can dissolve the perception of conflicting prosodic modulations, such that participants would perceive an IPB as less pronounced when not corresponding to a syntactic boundary (Meyer et al., 2016; Dinctopal Deniz and Fodor, 2017). Indeed, even the positioning of prosodic modulations during speech production is determined by the bias to generate syntactic phrases that keep

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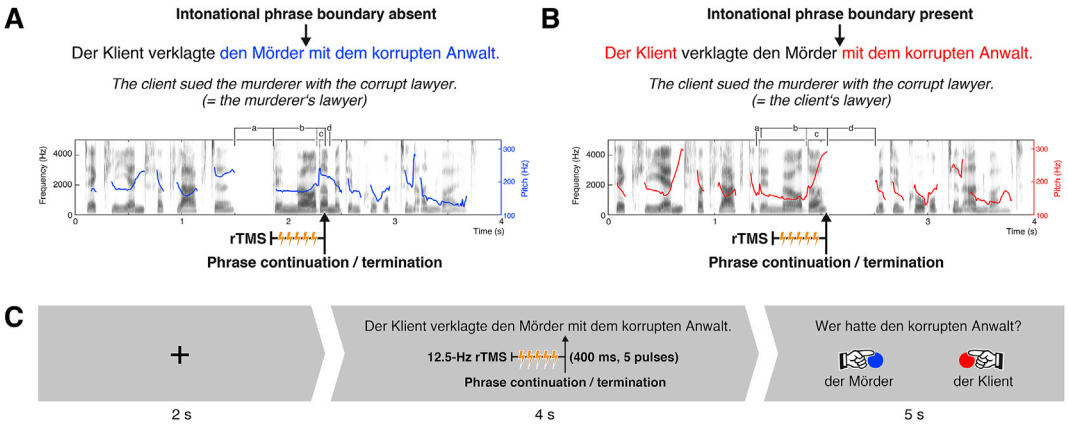

Fig. 1. Overview of stimuli and experimental procedure. (A) In IPB-absent sentences, *mit dem korrupten Anwalt* (*with the corrupt lawyer*) and the preceding *den Mörder* (*the murderer*) form a single long syntactic phrase. The spectrogram shows that *den Mörder* (b) is preceded by a long pause (a) and neither accompanied by a lengthened final syllable (c) or pause (d); pitch is flat (c). The cues indicate that the syntactic phrase should be continued after *den Mörder*. (B) In IPB-present sentences, *mit dem korrupten Anwalt* (*with the corrupt lawyer*) forms a second phrase, interpreted as linking to *Der Klient* (*the client*) instead. The spectrogram shows that *den Mörder* (b) is not preceded by a long pause (a), accompanied by a pitch rise (b) and a lengthened final syllable (c), and followed by a long pause (d). The cues indicate that the phrase should be terminated at the offset of *den Mörder*. A five-pulse burst of 12.5-Hz rTMS was applied from 400 to 0 ms prior to the offset of *den Mörder* until offset. (C) Experimental procedure (example trial). After auditory stimulus presentation, participants indicated via button press which of the two alternatives of chunking the words into syntactic phrases they had chosen; for the example sentence, the comprehension question would have been *Wer hatte den korrupten Anwalt? (Who had the corrupt lawyer?)*.

processing demands within limits (Webman-Shafran and Fodor, 2015).

The ability to chunk words into syntactic phrases is a critical benefit for language comprehension (Baddeley et al., 2009; Bonhage et al., 2014), because working memory is too limited to encode sentences as lists of single words (Miller, 1962; Levelt, 1970). The neural substrate of this ability is still debated. Current neuroanatomical models of language comprehension localize the ability to chunk words into syntactic phrases in the left inferior frontal gyrus (IFG; e.g., Friederici, 2011; Dehaene et al., 2015; Hagoort, 2017), but the supporting literature is still equivocal. Functional neuroimaging experiments show neural activity in the left IFG during the chunking of words into syntactic phrases, but various other regions in the left temporal cortex were found active as well (e.g., Brennan et al., 2012; Pallier et al., 2011). Recent work shows that this activity does focalize to the left IFG when carefully controlling for confounding factors such as semantics and working memory demands (Zaccarella et al., 2015). Still, in any case, functional neuroimaging cannot provide a causal link. The available causal evidence from patients with brain lesions or cortical atrophy and from neurostimulation work in healthy participants merely associates the left IFG with sentence comprehension in general (Grodzinsky et al., 1999; Zurif and Piñango, 1999; Kinno et al., 2009; Wilson et al., 2010, 2016; Kuhnke et al., 2017). However, much of this work focused on more complex functions beyond the simple notion of syntactic phrase formation. Moreover, some of the lesion evidence is controversial: While behavioral problems in language production are a canonical symptom of stroke-induced lesions of the left IFG, stroke lesions to the left IFG do not entail behavioral problems in sentence comprehension (Berndt and Caramazza, 1999; Bastiaanse and van Zonneveld, 2006).

Here, we employed focal repetitive transcranial magnetic stimulation (rTMS) to study the causal role of the left IFG in the chunking of words into syntactic phrases. Our experimental design dissociated the projection of internally generated syntactic phrases onto speech (i.e., top-down processing, indexed by the termination bias) from the processing of auditory information (i.e., bottom-up processing, indexed by prosody discrimination). We hypothesized that stimulation of the left IFG affects termination bias, but not the sensitivity to auditory information.

2. Materials and methods

2.1. Participants

Forty-eight healthy native German speakers (24 females; mean age = 26.06 years, standard deviation (SD) = 3.78 years) participated in the study. Participants were recruited via the database of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany (MPI CBS). All subjects were right-handed (Oldfield, 1971; mean laterality quotient = 92.96, SD = 9.78). Written informed consent was obtained prior to the experiment. Exclusion criteria included neurological or psychiatric disorders, and alcohol or drug abuse. Participation in the study was reimbursed with 10 € per hour. 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. Materials

Stimuli were auditory German sentences that allowed for two alternative chunking patterns (e.g., *Der Klient verklagte den Mörder mit dem korrupten Anwalt./The client sued the murderer with the corrupt lawyer.*; Fig. 1), indicated by either the presence or absence of an IPB at the offset of *den Mörder* (*the murderer*). The IPB-absent condition (Fig. 1 A) indicated a continuation of the syntactic phrase, resulting in the long phrase *den Mörder mit dem korrupten Anwalt* (*the murderer with the corrupt lawyer.*). This indicates the interpretation that *the murderer* hired *the lawyer*. In contrast, in the IPB-present condition (Fig. 1 B), the syntactic phrase *den Mörder* (*the murderer*) should be terminated and a new syntactic phrase *mit dem korrupten Anwalt* (*with the corrupt lawyer*) should be started, which refers back to *Der Klient* (*the client*). This corresponds to the interpretation that *the client* hired *the lawyer*. Critically, these stimuli enable us to dissociate the processing of bottom-up prosodic cues from the top-down projection of syntactic phrases: Bottom-up sensitivity is indexed by participants' consistent behavioral choice for chunking patterns that obey prosodic cues (i.e., a one-phrase chunking pattern in the IPB-absent condition and a two-phrases chunking pattern in the IPB-present condition); orthogonally, top-down bias would be indexed by participants' arrival at a single, preferred chunking pattern (i.e., a two-phrases chunking pattern in both the IPB-absent and IPB-present conditions).

We extended the stimulus set from a previous study (Meyer et al., 2016) to 48 items. Stimuli were matched for word length and frequency within sentential positions across experimental items (Biemann et al., 2004). To avoid confounding the experimental manipulation with a semantic association between the subject or object noun (i.e., *Klient/client* versus *Mörder/murderer*, respectively) and the sentence-final noun (i.e., *Anwalt/lawyer*), we matched their length and frequency and counterbalanced the subject and object nouns within item (Taraban and