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The P600, but not the N400, is modulated by sustained attention

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Abstract

The functional significance of the two prominent language-related ERP components N400 and P600 is still under debate. It has recently been suggested that one important dimension along which the two vary, is in terms of automaticity versus attentional control, with N400 amplitudes reflecting more automatic and P600 amplitudes reflecting more controlled aspects of sentence comprehension. The availability of executive resources necessary for controlled processes depends on sustained attention, which fluctuates over time. Here, we thus tested whether P600 and N400 amplitudes depend on the level of sustained attention. We re-analyzed EEG and behavioral data from a sentence processing task by Sassenhagen & Bornkessel-Schlesewsky (2015, *Cortex*), which included sentences with morphosyntactic and semantic violations. Participants read sentences phrase by phrase and indicated whether a sentence contained any type of anomaly as soon as they had the relevant information. To quantify periods of high versus low sustained attention, we extracted a moving reaction time coefficient of variation over the entire course of the task. We found that the P600 amplitude was significantly larger during periods of low reaction time variability (high sustained attention) than in periods of high reaction time variability (low sustained attention). In contrast, the amplitude of the N400 was not affected by reaction time variability. These results thus suggest that the P600 component is sensitive to sustained attention while the N400 component is not, which provides independent evidence for accounts suggesting that P600 amplitudes reflect more controlled and N400 amplitudes more automatic aspects of sentence comprehension.

Keywords P600, N400, sustained attention, automaticity vs control, reaction time variability

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Event-related potential (ERP) components observed during sentence processing play an important role for neurocognitive models of language comprehension (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2013; Brouwer et al., 2017; Friederici, 2011; Kuperberg, 2007, 2021; Rabovsky et al., 2018). The N400 is mostly sensitive to the semantic fit of a word within a given context, with more negative amplitudes the less predictable the word (Kutas & Hillyard, 1980). The later P600 is triggered by a wide range of syntactic violations, semantic incongruencies, syntactic ambiguities and even pragmatic factors and spelling errors (e.g., Hagoort et al., 1993; Kim & Osterhout, 2005; Osterhout & Holcomb, 1992; Regel et al., 2014; Van de Meerendonk et al., 2011). However, even after four decades of empirical studies, their functional significance is still actively debated (see, e.g., discussions in Kutas & Federmeier, 2011; Leckey & Federmeier, 2019).

Recently, it has been suggested that the two components differ along the automaticity vs control dimension (e.g., Kolk & Chwilla, 2007; Kuperberg, 2007; Rabovsky & McClelland, 2020; van Gaal et al., 2014). This distinction and related dichotomies, such as between conscious vs unconscious processes, are ubiquitous across domains in cognitive (neuro)science (Posner & Snyder, 1975; Schneider & Shiffrin, 1977). Language comprehension often seems like a fast and effortless process and indeed, N400 amplitude might reflect a more automatic brain response, for instance signaling the change in a probabilistic representation of sentence meaning corresponding to an implicit semantic prediction error (Rabovsky & McClelland, 2020). Sometimes however, this automatic process might not result in a coherent interpretation and an additional, more controlled process might be needed for successful comprehension. This process could be reflected in the P600 as a controlled revision process when automatic update fails, resulting in an initial state of uncertainty or conflict (Rabovsky & McClelland, 2020). Relatedly, the positivity might act as an error monitoring signal, where the language system interacts with the domain-general executive system (Kolk et al., 2003; Kolk & Chwilla, 2007; Van De Meerendonk et al., 2010).

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There are several lines of evidence supporting the automaticity vs control distinction regarding the N400 and P600. For example, the P600 – but not the N400 – is modulated by task relevance, with a reduced or absent P600 when the instructions do not require the participant to process the anomaly (Gunter & Friederici, 1999; Hahne & Friederici, 1999; Molinaro et al., 2011; Schacht et al., 2014; Vissers et al., 2007) or participants do not notice the anomaly (Batterink & Neville, 2013; Osterhout & Mobley, 1995; Xu et al., 2019). The two components are also differentially affected by error probability, with increasing number of violations within an experimental stimulus set diminishing the P600, but not affecting the N400 (Coulson et al., 1998; Hahne & Friederici, 1999; Yano et al., 2021). Relatedly, the P600, but not N400, is sensitive to the attentional blink and other manipulations testing conscious vs unconscious processing of linguistics stimuli (Batterink & Neville, 2013; Kiefer, 2002; Luck et al., 1996; Rohaut & Naccache, 2017; Service et al., 2007; van Gaal et al., 2014). The P600 further correlates with indices of executive control (Brothers et al., 2021), exhibits sequential adaptation effects (Xu et al., 2021), and relates to eye movement regressions during natural reading (Dimigen et al., 2007; Metzner et al., 2017). Lastly, the P600 has also been linked to the more domain-general P3 component (Coulson et al., 1998; Sassenhagen et al., 2014; Sassenhagen & Bornkessel-Schlesewsky, 2015; Sassenhagen & Fiebach, 2019), which has been related to, for instance, stimulus saliency, surprise, and context updating (Donchin, 1981; Nieuwenhuis et al., 2005; Polich, 2007). Despite this previous evidence, the proposed distinction between the P600 and N400 is still debated. Some argue that the process underlying the P600 might also reflect a default process, for instance sentence meaning integration (Brouwer et al., 2017). Conversely, the N400 might also involve controlled aspects of sentence comprehension (Lau et al., 2008) or it might not be possible to clearly categorize the component within this dichotomy (Kutas & Federmeier, 2011).

Generally, the availability of executive resources necessary for controlled processes - but less required for automatic processes - depends on the level of sustained attention.

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Sustained attention, the focus on a task over a period of time which is also known as "vigilance", is enabled by arousal (possibly via a noradrenergic route) and in turn, modulates the amount of cognitive resources and resulting performance (Esterman & Rothlein, 2019; Oken et al., 2006). When arousal is in an optimal, medium range during task engagement, sustained attention is high, so more cognitive resources are available, which leads to high performance (e.g., fast reaction times and low error rates). During very low or very high arousal, sustained attention to the current task is reduced (e.g., during mind wandering), resources for the task at hand are limited, and performance suffers. Indeed, the actual level of sustained attention correlates with, for instance, response inhibition (Bellgrove et al., 2004; Connolly et al., 2005; Esterman et al., 2013), set shifting (MacDonald et al., 2009), and selective attention (Weissman et al., 2006). Under current view, sustained attention is by no means an all-or-nothing phenomenon but fluctuates over time (e.g., over the course of a task; Esterman et al., 2013; Fortenbaugh et al., 2018; Johnson et al., 2015; Van Den Brink et al., 2016).

That attention enables executive resources has important implications for the processes underlying the P600 and N400. If the P600 indeed reflects a controlled process, it should be reduced when sustained attention is low, and thus, less of the necessary executive resources are available. Conversely, if the N400 reflects an automatic process, its amplitude should not depend on sustained attention. To date, direct evidence on the role of attention on the P600 and N400 besides the manipulation of task relevance (see above) is still scarce.

To further investigate whether the P600 and N400 might be dissociated on the automaticity versus control dimension, we thus tested their susceptibility to sustained attention in a sentence processing paradigm using reaction time variability as an index of sustained attention. We re-analyzed EEG and behavioral data from a visual sentence processing task by Sassenhagen & Bornkessel-Schlesewsky (2015, henceforth SBS). SBS investigated the relationship between reaction time measures and language-related ERPs and

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found that the P600 latency is aligned with the RT rather than stimulus onset. Sentences in their task were either correct, contained a morphosyntactic, or semantic violation. Instead of a typical grammaticality judgment prompt *following* each complete sentence, participants were instructed to respond whether a sentence contained any type of anomaly as soon as they had the relevant information. To continuously measure fluctuations in sustained attention, we focused on reaction time variability within participants. The underlying idea is that in periods when sustained attention is high, there is less variability in reaction times than when sustained attention is low. We quantified sustained attention with a moving reaction time coefficient of variation over the entire course of the task for each participant (see e.g., Esterman et al., 2013; Van Den Brink et al., 2016). We expect P600 amplitudes, but not N400 amplitudes, to be larger in periods of low RT variance (high sustained attention) than high RT variance (low sustained attention).

Method

Participants

Participants were right-handed, native speakers of German, with normal or corrected-to-normal vision, no history of neurological disorders, between the ages of 18 and 40, of either sex. For our analyses, we analyzed the data from the 20 participants that were also analyzed and made publicly available by SBS.

Data Acquisition

Participants' electroencephalogram (EEG) was recorded using a BrainProducts actiCHamp system (Brain Products GmbH, Gilching, Germany) at 1000 Hz, using 64 electrodes spaced according to the international 10-20 system. Impedances were reduced below 35 kOhm if possible. A forehead ground and a reference-free recording were used. Each subject took part in both a face detection experiment designed to elicit a P3 (not reported

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here), and a sentence processing experiment designed to elicit a P600 and N400. For more details on the data collection procedure, see SBS (p. A6).

Sentence Processing Task

Participants read German sentences on screen phrase by phrase. Half of the sentences were control sentences which introduced a category word (hypernym) and three category members (hyponyms), for instance, "Zur Kategorie | Obst | gehören | der Apfel, | die Birne | und | die Mango" (lit: *To the category* | *fruit* | *belong* | *the apple,*| *the pear,*| *and* | *the mango*). In deviant sentences with a morphosyntactic violation, one of the hyponyms was preceded by a mismatching determiner regarding its grammatical gender (e.g., "das Birne", *the*$_{\text{neut}}$ *pear*$_{\text{fem}}$). In semantically deviant sentences, one of the hyponyms was exchanged for a hyponym from another experimental sentence, and hence, another semantic category (e.g., "der Vogel", *the bird*, instead of *the pear* in the example above). Single violations appeared equally often in position one, two, or three. A portion of the violation sentences contained a double violation, i.e., a morphosyntactic violation on one hyponym and a semantic violation on another (e.g., "Zur Kategorie | Obst | gehören | der Vogel, | das Birne | und | die Mango", lit: *To the category* | *fruit* | *belong* | *the bird*$_{\textit{(semantic violation)}}$, | *the*$_{\text{neut}}$ *pear*$_{\text{fem}}$ $_{\textit{(morphosyntactic violation)}}$, | *and* | *the mango*).

Stimulus presentation for each participant was randomized and comprised 150 correct control sentences, 75 sentences with a morphosyntactic as the only or first violation, and 75 sentences with a semantic violation as the only or first violation. Sentences appeared phrase by phrase, for 350 ms per phrase with a 350 ms blank screen between phrases (indicated by vertical lines in the example above). Importantly, participants were instructed to respond as quickly as possible whether a sentence was anomalous or not as soon as they had the relevant information. Specifically, they were instructed to "[…] press a pre-assigned button once they know the sentence to be either correct, or (structurally or semantically) incorrect." (SBS, p. A7). Participants were encouraged to respond as quickly and accurately as possible by a) a

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specific feedback tone following correct and incorrect (or timeout) responses and b) displaying their average RT and accuracy in between trials. The negative feedback tone was also played following time-outs (responses > 2000 ms after last word). If accuracy dropped below 80% or mean RT rose above 1000 ms, they were additionally urged to respond more rapidly and accurately by the experimenter. For additional details on stimulus construction and the experimental procedure, see SBS (p. A6f.).

Reaction Time Coefficient of Variation

For each participant, we extracted RTs from every trial, that is, including both control and violation trials and irrespective of accuracy of the response. For violation trials, RT was time-locked to the onset of the respective violation phrase (in either position 1, 2 or 3). If the sentence contained a double violation, RT was time-locked to the onset of the first one. For control trials, RT was time-locked to the onset of the last phrase of the sentence. We then log-transformed RTs and calculated the moving RT coefficient of variation (RT CV) adjusted to log-normal data. Specifically, for each trial, we calculated the RT CV as the square root of e^{s^2}, where s equals the standard deviation of a time period surrounding that trial (window size = 10 trials, ~ 60 s). For trials in which participants responded before the onset of the respective phrase, the resulting negative values were replaced with NA before log-transformation, ignored for the calculation of the RT CV and interpolated during the smoothing process.

We then smoothed over the resulting RT CV line (see Fig. 1) using a Gaussian kernel of two trials. Since RTs on control trials were systematically faster than on violation trials ($t(19) = -16.46$, $p < .001$) and these two trial types appeared in random order, different degrees of trial type variability alone could lead to variance in the RT CV. To rule out that any potential effect of RT variance on ERP amplitudes might simply reflect an effect of trial type variability (i.e., more mixed vs homogenous trial types within a given time period), we regressed out trial type variability from the RT CV line vector. We did so by coding violation

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and control conditions as – 1 and +1, respectively, and then calculating a moving average with the same window size as the moving RT coefficient of variation (10 trials). The resulting absolute value thus indicated the degree of trial type variability in the window around each trial. We linearly regressed the RT CV against this trial type variability and took the residual variance as the final "RT CV" line.

We calculated a median split of the final RT CV line for each participant. To get a more reliable measure of periods of low versus high sustained attention over the entire task, the RT CV and median split was calculated over both control and violation trials. However, for subsequent ERP analyses, we were primarily interested in violation trials (basic comparisons between ERPs for violation versus control trials are reported in SBS). Therefore, using the median split, we binned only violation trials as having occurred during a high RT variance period (low sustained attention) versus low RT variance period (high sustained attention).

Figure 1

Example reaction time coefficient of variation (RT CV) of one representative participant over the course of the experiment (300 trials), indicating the variance of the 10 (log-transformed) RTs around each trial. High RT CV values indicate periods of low sustained attention.

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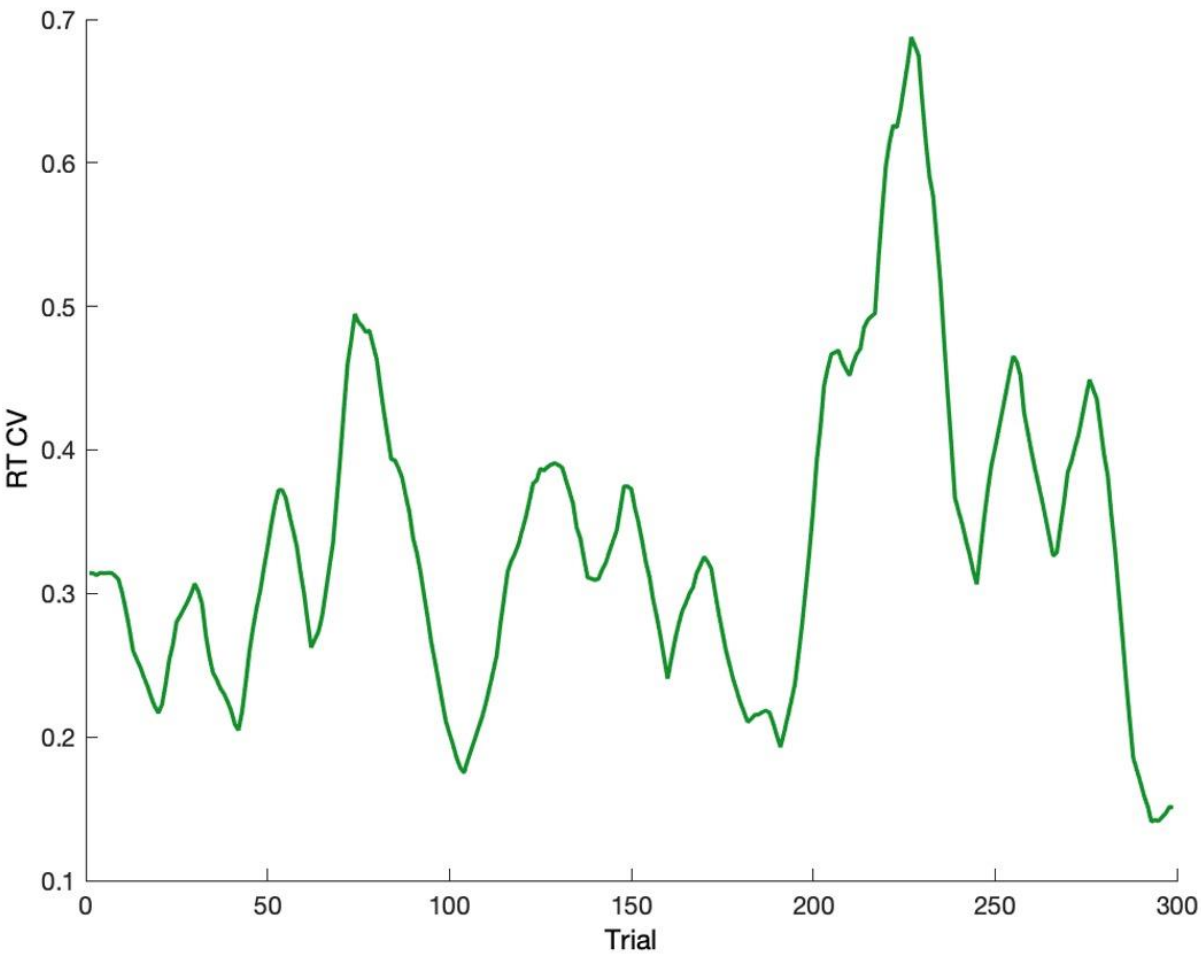

EEG Data Preprocessing

EEG data were preprocessed in Matlab R2020a using the EEGLAB (Delorme & Makeig, 2004) toolbox. Data were downsampled to 100 Hz and re-referenced to the average of the left and right mastoids. Ocular artifacts were removed using independent component analysis (Infomax ICA; Jung et al., 2001; Makeig et al., 1997) on segments spanning -500 ms pre- and 2000 ms post stimulus onset, which were extracted from continuous data filtered with a 1-30 Hz Butterworth filter. Independent components (IC) were removed which the IClabel plug-in (Pion-Tonachini et al., 2019) identified to be eye related with a probability greater than 30%. Upon visual inspection, we additionally identified and removed one channel noise IC in seven participants (see also SBS).

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The corrected, continuous data were high-pass filtered (0.1 Hz, two-pass Butterworth with a 12 dB/oct roll-off) and low-pass filtered (30 Hz, two-pass Butterworth with a 24 dB/oct roll-off). Data were then epoched from -200 to 3000 ms time-locked to the critical phrase onset and baseline-corrected relative to a 200ms interval preceding the onset. Epochs with absolute values exceeding 75 μV within the seven channels of interest (see below) were removed.

For analyses, we extracted epochs from trials with either semantic or morphosyntactic violations. Conservatively, only data from trials in which participants responded correctly and with RT values > 0 remained for analyses. Trial ERP data were then categorized as having occurred during a high RT versus low RT variance period, according to their RT CV value calculated above. On average, there were 63 (range: 46-74) trials in each of the two RT variance conditions per participant. Data for both components were analyzed for a parietal region of interest (ROI: CP1, CP2, P3, Pz, P4, PO3, PO4). The ROI was selected to capture both the somewhat more central distribution of the N400 (e.g., Hodapp & Rabovsky, 2021) and the somewhat more posterior distribution of the P600 (e.g., Kuperberg et al., 2020; Münte et al., 1998; Tanner et al., 2017) and is an area where both effects in SBS were maximal (p. A14). The components were analyzed within a 300-500 ms (N400) and 600-900 ms (P600) time window.

Statistical analyses

We performed linear mixed-effects model (LMM) analyses using the package lme4 as implemented in R (R core Team, 2018) to investigate the effect of RT variance separately on the amplitude of the N400 and P600 component. For both analyses, we controlled for (log-transformed) trial RT and violation type (semantic vs morphosyntactic) by adding them as additional fixed effects to the models. Following the recommendations by Barr et al. (2013), we tried to fit the maximal random effect structure as justified by the design but reduced its complexity successively until the model converged. For both components, models including

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random slopes for RT variance by participant could not be fit and thus only included random intercepts by participant. The final models were thus: *ERP amplitude ~ RT variance + RT + violation type + (1 | participant)*. Sum coding (Schad et al., 2018) was used as contrasts for the two categorical predictors (High RT variance: -0.5, low RT variance: 0.5; syntactic violation: -0.5, semantic violation: 0.5). The significance of fixed effects was determined via likelihood ratio tests to compare the fit of the model to that of a reduced model lacking the respective fixed effect but including all remaining fixed effects as well as the same random effect structure.

Results

ERP condition means on morphosyntactic and semantic violations for high vs. low RT variance trials are shown in Figure 2 and 3, respectively. As to be expected from previous literature and the results by SBS, both semantic and morphosyntactic violations generally elicited a large positive deflection approximately 600-1000 ms after phrase onset, in comparison to correct control phrases. In contrast, only semantic violations exhibited an increase in N400 amplitudes. Still, in order to increase power and be able to compare results between components, we included data from both violation types in the models testing the effect of RT variance on both P600 and N400 amplitudes.

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Figure 2

Grand average waveforms of trials with morphosyntactic violations at parietal ROI in high vs. low RT variance periods, time-locked to the onset of the violation phrase. The additional control phrase mean includes data from all non-violation targets (on average 652 phrases per participant, range = 577-695). Control phrase means are for visualization only, that is, they were not part of our statistical analysis. Error bands indicate the SEM. The topography of the RT variance effect within the N400 and P600 time window is plotted below the waveforms. Note that trial outliers (values exceeding +/- 75 µV) in channels outside the ROI (green squares) were additionally excluded here for illustration only.

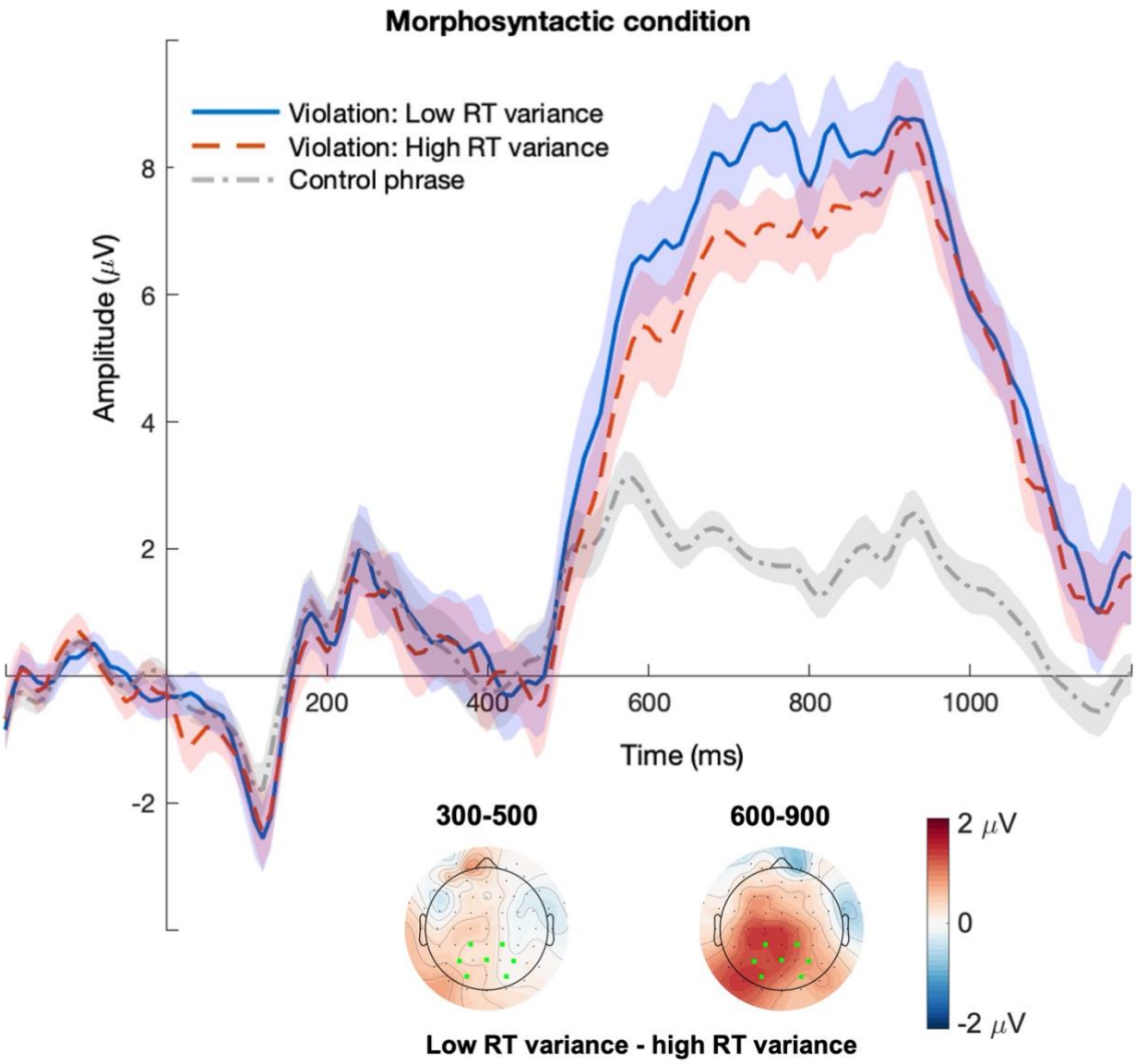

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Figure 3

Grand average waveforms of trials with semantic violations at parietal ROI in high vs. low RT variance periods, time-locked to the onset of the violation phrase. The additional control phrase mean includes data from all non-violation targets. Control phrase means are for visualization only, that is, they were not part of our statistical analysis. Error bands indicate the SEM. The topography of the RT variance effect within the N400 and P600 time window is plotted below the waveforms. Trial outliers (values exceeding +/- 75 µV) in channels outside the ROI (green squares) were additionally excluded here for illustration only. Note the unexpected finding that during periods high RT variance (low sustained attention), there seem to be larger amplitudes at more frontal areas in the N400 time window compared to periods of low RT variance, which we did not predict. Note that the polarity, topographical distribution and time course (see Fig. A1 in the appendix) differs from the N400. We discuss this observation in the discussion section.

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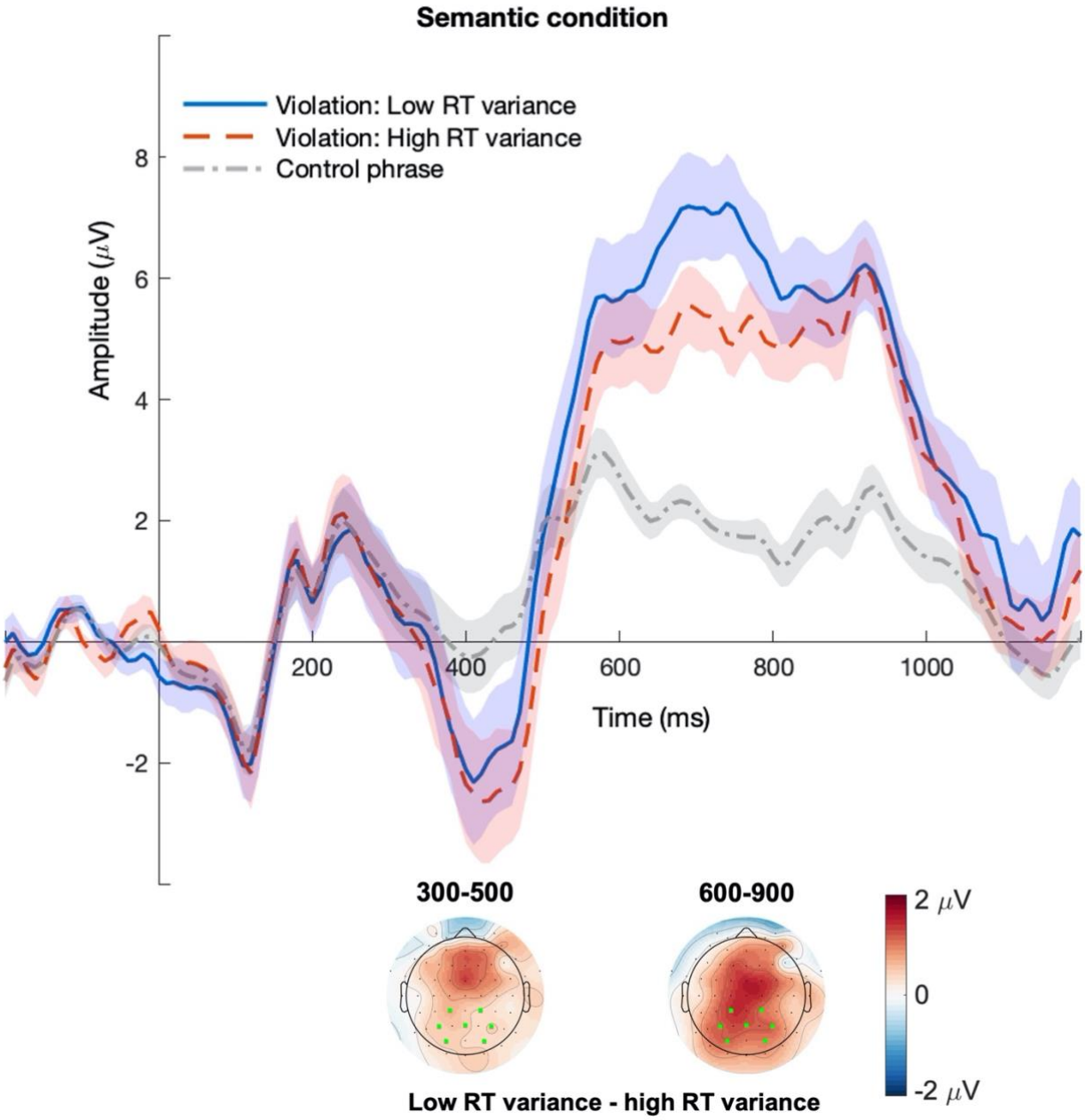

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P600

P600 amplitudes were significantly larger in trials with morphosyntactic than semantic violations (β = -2.08, *SE* = 0.32, *t* =-6.51, $\chi 2$ = 42.06, *p* < .001), in line with previous evidence that P600 amplitudes are primarily (though not exclusively) sensitive to syntactic violations (e.g., Osterhout & Mobley, 1995). Further, there was a negative effect of RT on the P600, thus amplitudes were smaller on trials with longer RTs (β = -4.7, *SE* = 0.46, *t* = -10.26, $\chi 2$ = 102.64, *p* < .001). Crucially, the model revealed a significant effect of RT variance on the amplitude of the P600. Specifically, amplitudes were smaller in trials that had occurred during periods of high RT variance (indexing low sustained attention) compared to trials that had occurred during periods of low RT variance (indexing high sustained attention) (β = 0.77, *SE* = 0.32, *t* = 2.38, $\chi 2$ = 5.64, *p* = .017).

Note that the two RT predictors - RT of the respective trial and RT variance condition - might be related and thus, might also share variance in explaining the P600 amplitude. However, the variance inflation factors of the model did not indicate any collinearity problem (Violation type: 1.02, RT: 1.05, RT variance: 1.03).

N400

N400 amplitudes were more negative on semantic than syntactic violations (β = -2.54, *SE* = 1.00, *t* = -2.55, $\chi 2$ = 6.49, *p* = .011) consistent with previous evidence that N400 amplitudes are sensitive to semantic but not syntactic violations (e.g., Kutas & Federmeier, 2011). However, N400 amplitudes were neither affected by RT (β = -0.52, *SE* = 0.40, *t* = -1.30, $\chi 2$ = 1.67, *p* = .2), nor RT variance (β = 0.38, *SE* = 0.28, *t* = 1.36, $\chi 2$ = 1.85, *p* = .17).

In order to better compare the results regarding the two components, the N400 model included data from both semantic and morphosyntactic violations. However, the N400 is primarily modulated by semantic factors and indeed, Figure 2 also indicates that there was no N400 effect for morphosyntactic violations to begin with. To take this into account and make sure not to miss any potential effect of RT variance on N400 amplitudes, we fit an additional

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N400 model including only data from semantic violations (and thus also excluding the fixed factor of violation type). However, the pattern remained the same: There was no effect of RT on the N400 amplitude (β = -0.22, *SE* = 0.55, *t* = -0.4, $\chi 2$ = 0.16, *p* = .69). Similarly, N400 amplitudes were not modulated by RT variance (β = 0.49, *SE* = 0.38, *t* = 1.26, $\chi 2$ = 1.6, *p* = .21).

Discussion

To investigate whether the P600 and N400 might be dissociated on the automaticity vs control dimension, we tested whether they are differentially modulated by sustained attention as indexed by high versus low RT variability. Indeed, P600 amplitudes were significantly larger during periods of low RT variability (i.e., periods of high sustained attention) than in periods of high RT variability (i.e., periods of low sustained attention), even when controlling for individual trial RT. In contrast, the amplitude of the N400 was not affected by RT variability. These results suggest that the P600 component is sensitive to the current level of sustained attention while the N400 component is not. Since sustained attention is needed to enable executive resources needed for controlled processes, these findings thus provide further evidence that P600 amplitudes reflect more controlled and N400 amplitudes more automatic aspects of sentence comprehension (Rabovsky & McClelland, 2020).

Our findings also align well with previous evidence on differential effects of task relevance on the two components (e.g., Schacht et al., 2014), together fostering the idea that the P600, but not N400, is modulated by attention. In contrast to previous studies, the current study did not manipulate the relevance of the stimuli, or the instruction given to participants, but rather measured sustained attention more directly, across the experiment, using reaction time variability as an index. This measure also takes into account that sustained attention naturally fluctuates over time. To our knowledge, this was the first attempt to adopt this method from fMRI research on inhibition and attention (e.g., Esterman et al., 2013;

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Fortenbaugh et al., 2018) in the context of (language-related) ERPs. Evidently, the task demands in the commonly used continuous performance paradigms – execution or inhibition of quick consecutive responses to simple perceptual differences – differ from a linguistic judgement task as used here. Our results indicate that RT variability might have further potential as a measure for continuous monitoring of fluctuations in sustained attention in language processing, complementing recent related indices such as the shape of RT distributions in self-paced reading (e.g., Payne & Federmeier, 2017).

We additionally found that P600 - but not N400 - amplitudes exhibit a negative relationship to RT, which is also in line with the assumption that the P600 is more tightly linked to performance and executive control than the N400. Note though, that we quantified P600 amplitude as the mean amplitude in a pre-defined time window and SBS's study suggests that the P600 latency is RT- rather than stimulus onset-aligned. Thus, our negative relationship might be an inevitable consequence: The longer the RT, the more the P600 "moves away" from the pre-defined window, decreasing the mean amplitude in this window. However, SBS also found such a negative correlation between P600 and RT when quantifying the P600 amplitude as the 60ms around the component's peak (see their supplementary material). Though pending more direct investigation, the observed relationship between RT and ERP amplitude might indicate that the amplitude of the positivity on a given sentence reflects how much executive resources (such as reorientation of attention) are recruited upon detecting the violation and in turn, how fast the reader can respond to it.

The topography of the RT variance effect in the early (300-500 ms) time window on semantic violations additionally suggested more positive amplitudes in frontal regions in periods of low compared to high RT variance. This more frontal distribution and the time course (see Figure A1 in the appendix) indicate that this descriptive difference between conditions is clearly separate from the N400. Note, if this would nonetheless be interpreted as an effect of sustained attention on the N400, it would go into the opposite direction than the

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P600 effects, namely larger amplitudes in the N400 time window in periods of lower sustained attention (high RT variability). For these reasons, we interpret a positive effect at the observed latency around 450 ms in frontocentral areas not as an N400 but rather as resembling the anterior positivity sometimes observed for semantic mismatches in highly constraining sentences (e.g., DeLong et al., 2014) or the Go/Nogo P3 (e.g., Smith et al., 2008). Interestingly, both of these components have been associated with inhibitory processes, either in the form of suppressing the lexical prediction (DeLong & Kutas, 2020) or the response (Albert et al., 2013), respectively. A potential effect of RT variance on one of these earlier components would thus be in line with previous evidence that sustained attention affects executive control processes such as inhibition (Connolly et al., 2005). Here, we did not predict such an early, frontal effect of RT variance but our observation might motivate further investigation on the influence of sustained attention on processes involved in language comprehension that occur prior to the posterior P600.

Our main finding that sustained attention modulated P600 amplitudes also has interesting implications for a current hypothesis on the neural generator of the P600. Sustained attention is assumed to be enabled by arousal, possibly via tonic norepinephrine (NE) levels (Esterman & Rothlein, 2019; Van Den Brink et al., 2016). Under medium tonic NE levels and an optimal state of arousal, sustained attention on the current task is high. When tonic NE levels and arousal are very low or too high, participants are either drowsy or highly alert and sustained attention on the current task is compromised. Interestingly, phasic noradrenaline activity also exhibits such a non-linear relationship with tonic NE levels: Strong responses under medium tonic levels, small or absent responses under very low or high tonic levels (Aston-Jones & Cohen, 2005). Crucially, the P600, just like the P3, has been proposed to reflect such phasic NE release (Nieuwenhuis et al., 2005; Sassenhagen et al., 2014; Sassenhagen & Bornkessel-Schlesewsky, 2015; Sassenhagen & Fiebach, 2019). Taken together, our data might contribute to the assumption that under optimal arousal (medium NE

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tonic levels), sustained attention on the task is high, and participants have executive resources available to detect and/or "act upon" violations, which leads to good performance and a large P600. Conversely, under very low or very high arousal and tonic NE levels, sustained attention suffers, so participants are disengaged, are less likely to detect violations, diminishing the P600 and leading to poor performance. Indeed, in periods of high RT variance, accuracy in violation trials was significantly lower than in periods of low RT variance ($t(19) = 6.15$, $p < .001$). This might imply that low sustained attention reduces the ability to detect linguistic violations in the first place. Importantly however, we found the effect of RT variance on the P600 even though we considered only correct violation trials in our analysis. This might suggest that sustained attention affects processing aspects underlying the component over and above error detection, possibly involving controlled revision and behavioral adaptation, akin to the proposed "network reset" induced by phasic norepinephrine (Bouret & Sara, 2005).

In conclusion, the current study suggests that the P600 is sensitive to sustained attention, providing further evidence that the underlying process might require cognitive control. In turn, the N400 seems to depend less on sustained attention, further indicating that it reflects more automatic aspects during sentence comprehension. Our adopted measure of reaction time variability could be a promising method to monitor the impact of ongoing fluctuations in sustained attention on higher level cognitive processing such as language comprehension.

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References

Albert, J., López-Martín, S., Hinojosa, J. A., & Carretié, L. (2013). Spatiotemporal characterization of response inhibition. *NeuroImage*, *76*, 272–281. https://doi.org/10.1016/j.neuroimage.2013.03.011

Aston-Jones, G., & Cohen, J. D. (2005). An Integrative Theory of Locus Coeruleus-Norepinephrine Function: Adaptive Gain and Optimal Performance. *Annual Review of Neuroscience*, *28*(1), 403–450. https://doi.org/10.1146/annurev.neuro.28.061604.135709

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Batterink, L., & Neville, H. J. (2013). The human brain processes syntax in the absence of conscious awareness. *Journal of Neuroscience*, *33*(19), 8528–8533. https://doi.org/10.1523/JNEUROSCI.0618-13.2013

Bellgrove, M. A., Hester, R., & Garavan, H. (2004). The functional neuroanatomical correlates of response variability: evidence from a response inhibition task. *Neuropsychologia*, *42*(14), 1910–1916. https://doi.org/10.1016/j.neuropsychologia.2004.05.007

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2013). Reconciling time, space and function: A new dorsal-ventral stream model of sentence comprehension. *Brain and Language*, *125*(1), 60–76. https://doi.org/10.1016/j.bandl.2013.01.010

Bouret, S., & Sara, S. J. (2005). Network reset: A simplified overarching theory of locus coeruleus noradrenaline function. *Trends in Neurosciences*, *28*(11), 574–582. https://doi.org/10.1016/j.tins.2005.09.002

Brothers, T., Zeitlin, M., Choi Perrachione, A., Choi, C., & Kuperberg, G. R. (2021). Domain-general conflict monitoring predicts neural and behavioral indices of linguistic error processing during reading comprehension. *Preprint on Biorxiv*.

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.18.469143; this version posted November 20, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

https://doi.org/10.1101/2021.01.06.425590

Brouwer, H., Crocker, M. W., Venhuizen, N. J., & Hoeks, J. C. J. (2017). A Neurocomputational Model of the N400 and the P600 in Language Processing. *Cognitive Science*, *41*, 1318–1352. https://doi.org/10.1111/cogs.12461

Connolly, J. D., Goodale, M. A., Goltz, H. C., & Munoz, D. P. (2005). fMRI activation in the human frontal eye field is correlated with saccadic reaction time. *Journal of Neurophysiology*, *94*(1), 605–611. https://doi.org/10.1152/jn.00830.2004

Coulson, S., King, J. W., & Kutas, M. (1998). Expect the Unexpected: Event-related Brain Response to Morphosyntactic Violations. *Language and Cognitive Processes*, *41*(1), 21–58. https://doi.org/10.1080/016909698386582

DeLong, K. A., & Kutas, M. (2020). Comprehending surprising sentences: sensitivity of post-N400 positivities to contextual congruity and semantic relatedness. *Language, Cognition and Neuroscience*, *35*(8), 1044–1063. https://doi.org/10.1080/23273798.2019.1708960

DeLong, K. A., Quante, L., & Kutas, M. (2014). Predictability, plausibility, and two late ERP positivities during written sentence comprehension. *Neuropsychologia*, *61*(1), 150–162. https://doi.org/10.1016/j.neuropsychologia.2014.06.016

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Dimigen, O., Sommer, W., & Kliegl, R. (2007). Long reading regressions are accompanied by a P600-like brain potential: Evidence from Simultaneous Recording of Eye Movements and ERPs. *Proceedings of the 14th European Conference on Eye Movements (ECEM) (p. 63)*.

Donchin, E. (1981). Surprise!? Surprise? *Psychophysiology*, *18*(5), 493–513. https://doi.org/10.1111/j.1469-8986.1981.tb01815.x

Esterman, M., Noonan, S. K., Rosenberg, M., & Degutis, J. (2013). In the zone or zoning out?

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.18.469143; this version posted November 20, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Tracking behavioral and neural fluctuations during sustained attention. *Cerebral Cortex*, *23*(11), 2712–2723. https://doi.org/10.1093/cercor/bhs261

Esterman, M., & Rothlein, D. (2019). Models of sustained attention. *Current Opinion in Psychology*, *29*, 174–180. https://doi.org/10.1016/j.copsyc.2019.03.005

Fortenbaugh, F. C., Rothlein, D., McGlinchey, R., DeGutis, J., & Esterman, M. (2018). Tracking behavioral and neural fluctuations during sustained attention: A robust replication and extension. *NeuroImage*, *171*(December 2017), 148–164. https://doi.org/10.1016/j.neuroimage.2018.01.002

Friederici, A. D. (2011). The brain basis of language processing: From structure to function. *Physiological Reviews*, *91*(4), 1357–1392. https://doi.org/10.1152/physrev.00006.2011

Gunter, T. C., & Friederici, A. D. (1999). Concerning the automaticity of syntactic processing. *Psychophysiology*, *36*(1), 126–137. https://doi.org/10.1017/S004857729997155X

Hagoort, P., Brown, C., & Groothusen, J. (1993). The syntactic positive shift (sps) as an erp measure of syntactic processing. *Language and Cognitive Processes*, *8*(4), 439–483. https://doi.org/10.1080/01690969308407585

Hahne, A., & Friederici, A. D. (1999). Electrophysiological evidence for two steps in syntactic analysis: Early automatic and late controlled processes. *Journal of Cognitive Neuroscience*, *11*(2), 194–205. https://doi.org/10.1162/089892999563328

Hodapp, A., & Rabovsky, M. (2021). The N400 ERP component reflects an error-based implicit learning signal during language comprehension. *European Journal of Neuroscience*, *September*, 1–16. https://doi.org/10.1111/ejn.15462

Johnson, B. P., Pinar, A., Fornito, A., Nandam, L. S., Hester, R., & Bellgrove, M. A. (2015). Left anterior cingulate activity predicts intra-individual reaction time variability in healthy adults. *Neuropsychologia*, *72*, 22–26. https://doi.org/10.1016/j.neuropsychologia.2015.03.015

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.18.469143; this version posted November 20, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Jung, T.-P., Makeig, S., McKeown, M. J., Bell, A. J., Lee, T.-W., & Sejnowski, T. J. (2001). Imaging brain dynamics using independent component analysis. *Proceedings of the IEEE*, *89*(7), 1107–1122. https://doi.org/10.1109/5.939827

Kiefer, M. (2002). The N400 is modulated by unconsciously perceived masked words: further evidence for an automatic spreading activation account of N400 priming effects. *Cognitive Brain Research*, *13*(1), 27–39. https://doi.org/10.1016/S0926-6410(01)00085-4

Kim, A., & Osterhout, L. (2005). The independence of combinatory semantic processing: Evidence from event-related potentials. *Journal of Memory and Language*, *52*(2), 205–225. https://doi.org/10.1016/j.jml.2004.10.002

Kolk, H. H. J., & Chwilla, D. (2007). Late positivities in unusual situations. *Brain and Language*, *100*(3), 257–261. https://doi.org/10.1016/j.bandl.2006.07.006

Kolk, H. H. J., Chwilla, D. J., Van Herten, M., & Oor, P. J. W. (2003). Structure and limited capacity in verbal working memory: A study with event-related potentials. *Brain and Language*, *85*(1), 1–36. https://doi.org/10.1016/S0093-934X(02)00548-5

Kuperberg, G. R. (2007). Neural mechanisms of language comprehension: Challenges to syntax. *Brain Research*, *1146*(1), 23–49. https://doi.org/10.1016/j.brainres.2006.12.063

Kuperberg, G. R. (2021). Tea With Milk? A Hierarchical Generative Framework of Sequential Event Comprehension. *Topics in Cognitive Science*, *13*(1), 256–298. https://doi.org/10.1111/tops.12518

Kuperberg, G. R., Brothers, T., & Wlotko, E. (2020). A Tale of Two Positivities and the N400: Distinct neural signatures are evoked by confirmed and violated predictions at different levels of representation. *Journal of Cognitive Neuroscience*, *32*(1), 12–35. https://doi.org/10.1101/404780

Kutas, M., & Federmeier, K. D. (2011). Thirty Years and Counting: Finding Meaning in the N400 Component of the Event-Related Brain Potential (ERP). *Annual Review of*

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Psychology, *62*(1), 621–647. https://doi.org/10.1146/annurev.psych.093008.131123

Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: brain potentials reflect semantic incongruity. *Science*, *207*(4427), 203–205. https://doi.org/10.1126/science.7350657

Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (De)constructing the N400. *Nature Reviews Neuroscience*, *9*(12), 920–933. https://doi.org/10.1038/nrn2532

Leckey, M., & Federmeier, K. D. (2019). The P3b and P600(s): Positive contributions to language comprehension. *Psychophysiology*, *August 2018*, 1–15. https://doi.org/10.1111/psyp.13351

Luck, S. J., Vogel, E. K., & Shapiro, K. L. (1996). Word meanings can be accessed but not reported during the attentional blink. *Nature*, *383*(6601), 616–618. https://doi.org/10.1038/383616a0

MacDonald, S. W. S., Cervenka, S., Farde, L., Nyberg, L., & Bäckman, L. (2009). Extrastriatal dopamine D2 receptor binding modulates intraindividual variability in episodic recognition and executive functioning. *Neuropsychologia*, *47*(11), 2299–2304. https://doi.org/10.1016/j.neuropsychologia.2009.01.016

Makeig, S., Jung, T.-P., Bell, A. J., Ghahremani, D., & Sejnowski, T. J. (1997). Blind separation of auditory event-related brain responses into independent components. *Proceedings of the National Academy of Sciences*, *94*(20), 10979–10984. https://doi.org/10.1073/pnas.94.20.10979

Metzner, P., von der Malsburg, T., Vasishth, S., & Rösler, F. (2017). The Importance of Reading Naturally: Evidence From Combined Recordings of Eye Movements and Electric Brain Potentials. *Cognitive Science*, *41*, 1232–1263. https://doi.org/10.1111/cogs.12384

Molinaro, N., Barber, H. A., & Carreiras, M. (2011). Grammatical agreement processing in

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.18.469143; this version posted November 20, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

reading: ERP findings and future directions. *Cortex*, *47*(8), 908–930. https://doi.org/10.1016/j.cortex.2011.02.019

Münte, T. F., Heinze, H. J., Matzke, M., Wieringa, B. M., & Johannes, S. (1998). Brain potentials and syntactic violations revisited: No evidence for specificity of the syntactic positive shift. *Neuropsychologia*, *36*(3), 217–226. https://doi.org/10.1016/S0028-3932(97)00119-X

Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3, and the locus coeruleus-norepinephrine system. *Psychological Bulletin*, *131*(4), 510–532. https://doi.org/10.1037/0033-2909.131.4.510

Oken, B. S., Salinsky, M. C., & Elsas, S. M. (2006). Vigilance, alertness, or sustained attention: physiological basis and measurement. *Clinical Neurophysiology*, *117*(9), 1885–1901. https://doi.org/10.1016/j.clinph.2006.01.017

Osterhout, L., & Holcomb, P. J. (1992). Event-related brain potentials elicited by syntactic anomaly. *Journal of Memory and Language*, *31*(6), 785–806. https://doi.org/10.1016/0749-596X(92)90039-Z

Osterhout, L., & Mobley, L. A. (1995). Event-Related Brain Potentials Elicited by Failure to Agree. *Journal of Memory and Language*, *34*(6), 739–773. https://doi.org/10.1006/jmla.1995.1033

Payne, B. R., & Federmeier, K. D. (2017). Pace Yourself: Intraindividual Variability in Context Use Revealed by Self-paced Event-related Brain Potentials. *Journal of Cognitive Neuroscience*, *29*(5), 837–854. https://doi.org/10.1162/jocn_a_01090

Pion-Tonachini, L., Kreutz-Delgado, K., & Makeig, S. (2019). ICLabel: An automated electroencephalographic independent component classifier, dataset, and website. *NeuroImage*, *198*(3), 181–197. https://doi.org/10.1016/j.neuroimage.2019.05.026

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*(10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.18.469143; this version posted November 20, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Posner, M. I., & Snyder, C. R. R. (1975). Attention and cognitive control. In R. L. Solso (Ed.), *Information Processing and Cognition: The Loyola Symposium* (pp. 55–85). Lawrence Erlbaum Associates.

Rabovsky, M., Hansen, S. S., & McClelland, J. L. (2018). Modelling the N400 brain potential as change in a probabilistic representation of meaning. *Nature Human Behaviour*, *2*(9), 693–705. https://doi.org/10.1038/s41562-018-0406-4

Rabovsky, M., & McClelland, J. L. (2020). Quasi-compositional mapping from form to meaning: A neural network-based approach to capturing neural responses during human language comprehension. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1791). https://doi.org/10.1098/rstb.2019.0313

Regel, S., Meyer, L., & Gunter, T. C. (2014). Distinguishing neurocognitive processes reflected by P600 effects: Evidence from ERPs and neural oscillations. *PLoS ONE*, *9*(5), 1–11. https://doi.org/10.1371/journal.pone.0096840

Rohaut, B., & Naccache, L. (2017). Disentangling conscious from unconscious cognitive processing with event-related EEG potentials. *Revue Neurologique*, *173*(7–8), 521–528. https://doi.org/10.1016/j.neurol.2017.08.001

Sassenhagen, J., & Bornkessel-Schlesewsky, I. (2015). The P600 as a correlate of ventral attention network reorientation. *Cortex*, *66*, A3–A20. https://doi.org/10.1016/j.cortex.2014.12.019

Sassenhagen, J., & Fiebach, C. J. (2019). Finding the P3 in the P600: Decoding shared neural mechanisms of responses to syntactic violations and oddball targets. *NeuroImage*, *200*, 425–436. https://doi.org/10.1016/j.neuroimage.2019.06.048

Sassenhagen, J., Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2014). The P600-as-P3 hypothesis revisited: Single-trial analyses reveal that the late EEG positivity following linguistically deviant material is reaction time aligned. *Brain and Language*, *137*, 29–39. https://doi.org/10.1016/j.bandl.2014.07.010

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.18.469143; this version posted November 20, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Schacht, A., Sommer, W., Shmuilovich, O., Martíenz, P. C., & Martín-Loeches, M. (2014). Differential task effects on N400 and P600 elicited by semantic and syntactic violations. *PLoS ONE*, *9*(3), 1–7. https://doi.org/10.1371/journal.pone.0091226

Schad, D. J., Vasishth, S., Hohenstein, S., & Kliegl, R. (2018). How to capitalize on a priori contrasts in linear (mixed) models: A tutorial. *Journal of Memory and Language*, *110*(November 2018), 104038. https://doi.org/10.1016/j.jml.2019.104038

Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information processing: I. Detection, search, and attention. *Psychological Review*, *84*(1), 1–66. https://doi.org/10.1037/0033-295X.84.1.1

Service, E., Helenius, P., Maury, S., & Salmelin, R. (2007). Localization of syntactic and semantic brain responses using magnetoencephalography. *Journal of Cognitive Neuroscience*, *19*(7), 1193–1205. https://doi.org/10.1162/jocn.2007.19.7.1193

Smith, J. L., Johnstone, S. J., & Barry, R. J. (2008). Movement-related potentials in the Go/NoGo task: The P3 reflects both cognitive and motor inhibition. *Clinical Neurophysiology*, *119*(3), 704–714. https://doi.org/10.1016/j.clinph.2007.11.042

Tanner, D., Grey, S., & van Hell, J. G. (2017). Dissociating retrieval interference and reanalysis in the P600 during sentence comprehension. *Psychophysiology*, *54*(2), 248–259. https://doi.org/10.1111/psyp.12788

Van de Meerendonk, N., Indefrey, P., Chwilla, D. J., & Kolk, H. H. J. (2011). Monitoring in language perception: Electrophysiological and hemodynamic responses to spelling violations. *NeuroImage*, *54*(3), 2350–2363. https://doi.org/10.1016/j.neuroimage.2010.10.022

Van De Meerendonk, N., Kolk, H. H. J., Vissers, C. T. W. M., & Chwilla, D. J. (2010). Monitoring in language perception: Mild and strong conflicts elicit different ERP patterns. *Journal of Cognitive Neuroscience*, *22*(1), 67–82. https://doi.org/10.1162/jocn.2008.21170

bioRxiv preprint doi: https://doi.org/10.1101/2021.11.18.469143; this version posted November 20, 2021. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-ND 4.0 International license.

Van Den Brink, R. L., Murphy, P. R., & Nieuwenhuis, S. (2016). Pupil diameter tracks lapses of attention. *PLoS ONE*, *11*(10), 1–16. https://doi.org/10.1371/journal.pone.0165274

van Gaal, S., Naccache, L., Meuwese, J. D. I., van Loon, A. M., Leighton, A. H., Cohen, L., & Dehaene, S. (2014). Can the meaning of multiple words be integrated unconsciously? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1641). https://doi.org/10.1098/rstb.2013.0212

Vissers, C. T. W. M., Chwilla, D. J., & Kolk, H. H. J. (2007). The interplay of heuristics and parsing routines in sentence comprehension: Evidence from ERPs and reaction times. *Biological Psychology*, *75*(1), 8–18. https://doi.org/10.1016/j.biopsycho.2006.10.004

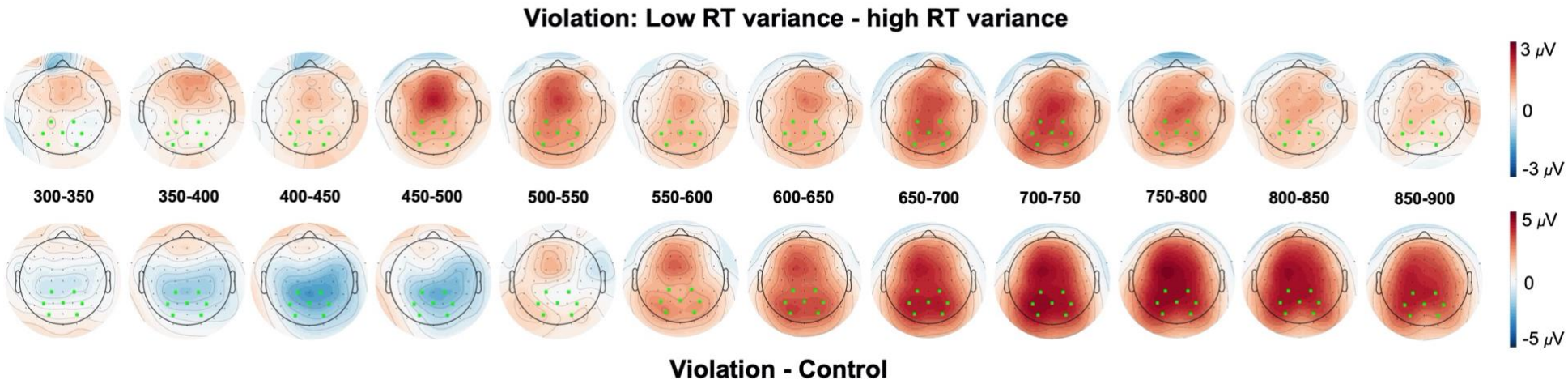
Weissman, D. H., Roberts, K. C., Visscher, K. M., & Woldorff, M. G. (2006). The neural bases of momentary lapses in attention. *Nature Neuroscience*, *9*(7), 971–978. https://doi.org/10.1038/nn1727

Xu, J., Abdel Rahman, R., & Sommer, W. (2019). Perceived language competence modulates criteria for speech error processing: evidence from event-related potentials. *Language, Cognition and Neuroscience*, *0*(0), 1–14. https://doi.org/10.1080/23273798.2018.1562558

Xu, J., Abdel Rahman, R., & Sommer, W. (2021). Sequential adaptation effects reveal proactive control in processing spoken sentences: Evidence from event-related potentials. *Brain and Language*, *214*, 104904. https://doi.org/10.1016/j.bandl.2020.104904

Yano, M., Suwazono, S., Arao, H., Yasunaga, D., & Oishi, H. (2021). Selective adaptation in sentence comprehension: Evidence from event-related brain potentials. *Quarterly Journal of Experimental Psychology*, 174702182098462. https://doi.org/10.1177/1747021820984623

Appendix

Figure A1.

Topography of RT variance effect (top) and semantic violation effect (bottom) over time (middle row, in ms). Green squares mark our parietal ROI for the N400 and P600.