



ERP signatures of conscious and unconscious word and letter perception in an inattentional blindness paradigm



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ABSTRACT

A three-phase inattentional blindness paradigm was combined with ERPs. While participants performed a distracter task, line segments in the background formed words or consonant-strings. Nearly half of the participants failed to notice these word-forms and were deemed inattentively blind. All participants noticed the word-forms in phase 2 of the experiment while they performed the same distracter task. In the final phase, participants performed a task on the word-forms. In all phases, including during inattentional blindness, word-forms elicited distinct ERPs during early latencies (~200–280 ms) suggesting unconscious orthographic processing. A subsequent ERP (~320–380 ms) similar to the visual awareness negativity appeared only when subjects were aware of the word-forms, regardless of the task. Finally, word-forms elicited a P3b (~400–550 ms) only when these stimuli were task-relevant. These results are consistent with previous inattentional blindness studies and help distinguish brain activity associated with pre- and post-perceptual processing from correlates of conscious perception.

1. Introduction

How consciousness could arise from biological states has been a longstanding mystery in both neuroscience and philosophy. Current research has focused on identifying neural correlates of consciousness (NCCs), the minimal neural mechanisms that are sufficient for conscious experience (Crick & Koch, 2003). It is hoped that once NCCs are identified, research into the causal relationship between the relevant neural mechanisms and conscious experience will be more tractable.

One popular method for identifying potential NCCs (the topic of this special issue) is to record the scalp electroencephalogram (EEG), derive event-related potentials (ERPs) time-locked to stimulus onset, and compare ERPs for “seen” versus “unseen” stimuli. Over the years, a number of EEG/ERP correlates of perceptual awareness have been proposed, including pre-stimulus alpha power/phase (8–12 Hz) (Busch, Dubois, & VanRullen, 2009; Hanslmayr et al., 2007; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Romei, Gross, & Thut, 2010; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008), the P1 component (Pins & Ffytche, 2003), the mid-latency visual awareness negativity (VAN, 200–400 ms) (Koivisto & Revonsuo, 2010; Koivisto et al., 2008; Pitts, Martínez, & Hillyard, 2012; Railo, Koivisto, & Revonsuo, 2011), the P3b component (Dehaene, 2014; Dehaene & Changeux, 2011), and enhanced gamma oscillations (30–80 Hz) (Batterink, Karns, & Neville, 2012; Melloni et al., 2007). However, separating putative NCCs from other processes preceding and following conscious experience is notoriously difficult (Aru, Bachmann, Singer, & Melloni, 2012). In particular, it has recently been argued that “no report” paradigms are necessary to separate NCCs from neural correlates of post-perceptual activity involved in generating perceptual reports (Tsuchiya, Wilke, Frässle, & Lamme, 2015).

In an attempt to isolate potential ERP correlates of consciousness from markers of other brain activity preceding or following

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consciousness, a no-report paradigm that utilizes inattention blindness (Mack & Rock, 1998) was recently developed (Pitts et al., 2012; Shafto & Pitts, 2015). Inattention blindness has been described as a failure to consciously perceive otherwise easily visible stimuli because attention is occupied elsewhere (Mack, 2003). Inattention blindness differs from other manipulations of visual awareness such as backward masking, interocular suppression, and degraded stimuli (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). In these other manipulations, unawareness is due to insufficient sensory input or artificial interference with perceptual processing, which rarely occurs outside of the laboratory. Inattention blindness, however, occurs frequently in everyday life and leads to unawareness despite adequate sensory input without perceptual interference (Castel, Vendetti, & Holyoak, 2012; Drew, Vö, & Wolfe, 2013; Hyman, Boss, Wise, McKenzie, & Caggiano, 2009; Most, Scholl, Clifford, & Simons, 2005; Simons & Chabris, 1999; Simons & Levin, 1998; Strayer, Drews, & Johnston, 2003; Cohen, Alvarez, & Nakayama, 2011; Mack & Clarke, 2012). Manipulating visual awareness via inattention blindness (as well as the attentional blink) may bring us closer to discovering the critical difference between conscious and unconscious perception (Dehaene, 2014; Prinz, 2012; but see Lamme, 2015).

The inattention blindness/no-report paradigm used in the current study included three experimental phases. In the first phase, participants were repeatedly exposed to a critical stimulus (and a corresponding control stimulus) while performing an unrelated distracter task. After this phase, participants completed an awareness assessment to determine whether they noticed the critical stimulus. As in our previous studies (Pitts et al., 2012; Shafto & Pitts, 2015), between 40 and 50% of participants failed to notice the critical stimulus, despite this stimulus being well above perceptual threshold (high contrast), for fairly long durations (300 ms), and repeated across many trials (> 200 trials). During the second phase, participants resumed the same distracter task, but because the intervening questions had alerted them to the presence of the critical stimulus, all participants noticed the critical stimulus in this phase. In the third and final phase, participants were tasked with reporting a subset of the critical stimuli on a trial-by-trial basis. In essence, the first two phases allowed measurements of brain activity during conditions in which subjects were unaware (phase 1) versus aware (phase 2) of the critical stimulus, but without trial-by-trial perceptual reports (i.e., a no-report paradigm). The third phase served to isolate and measure additional brain activity necessary for generating perceptual reports.

Two previous studies using this paradigm presented simple geometric shapes (Pitts et al., 2012) and line drawings of faces (Shafto & Pitts, 2015) as the critical stimuli. For subjects who were inattentionally blind to these stimuli in phase 1, evidence was found for unconscious shape processing (~200 ms), but not for unconscious face processing (N170 was absent). In both studies, the so-called visual awareness negativity (VAN) was observed (~200–400 ms) when participants were aware of the critical stimuli, regardless of whether or not the stimuli were task-relevant (i.e., VAN was present in phases 2 and 3 for participants who were inattentionally blind in phase 1, and in all three phases for participants who spontaneously noticed the critical stimuli in phase 1). Interestingly, gamma oscillations and the P3b component were evident only when the critical stimuli were task-relevant, in phase 3 (Pitts, Padwal, Fennelly, Martínez, & Hillyard, 2014). The current study utilized this same inattention blindness paradigm, but instead of shapes or faces, the critical stimuli were words and consonant strings.

It is generally accepted that many linguistic processes, such as those used during reading, are highly efficient and carried-out automatically (Dehaene et al., 2001; Holcomb & Grainger, 2006; Liotti, Woldorff, Perez, & Mayberg, 2000; Luck, Vogel, & Shapiro, 1996; Ruz, Worden, Tudela, & McCandliss, 2005; Sergent, Baillet, & Dehaene, 2005). The current study focused on two basic aspects of reading: orthographic and lexical processing. Orthographic processing refers to the operations utilized by the visual system to form, store, and recall representations of printed letters and words. In previous studies, orthographic processing has been linked with differential ERP amplitudes within the 150–300 ms time frame (Carreiras, Armstrong, Perea, & Frost, 2014; Carreiras, Duñabeitia, & Molinaro, 2009; Holcomb & Grainger, 2007; Nobre, Allison, & McCarthy, 1994). More specifically, orthographic stimuli such as words, pseudowords, and consonant strings lead to more negative ERP amplitudes over the posterior scalp during the interval 150–300 ms after stimulus onset compared to non-orthographic stimuli, such as symbols, false fonts, and strings of geometric forms (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Nobre et al., 1994). Left-hemisphere brain areas associated with language processing seem to differentiate between word and non-word stimuli, even if subjects are not aware of the word forms (Axelrod, Bar, Rees, & Yovel, 2015; Diaz & McCarthy, 2007). However, no previous studies have used inattention blindness to suppress word-form stimuli from awareness, and it remains possible that attention is required for such processing while awareness is not.

Lexical processing refers to the activation of stored semantic associations triggered by incoming visual (or auditory) input. Lexical processing has been associated with differential ERPs at slightly later time frames than orthographic processing, from approximately 250 to 350 ms (Bentin et al., 1999; Proverbio, Vecchi, & Zani, 2004; Ruz et al., 2005; Sergent et al., 2005). In this case, increased ERP negativities to words compared to non-pronounceable consonant strings have been observed in left-lateralized posterior areas (Bentin et al., 1999; Proverbio et al., 2004). When describing lexical processing, Laszlo and Federmeier (2007, 2008, 2009) propose that instead of a filter on incoming written input dictating which inputs can be processed for semantics and which cannot, all letter strings may automatically initiate attempts at semantic access (even if not always successful). Interestingly, both the orthographic and lexical ERP indices appear to persist even when words and letter-strings are unattended, e.g. when participants perform a non-linguistic task (Appelbaum et al., 2009; Ruz et al., 2005), but in such paradigms it is likely that attention to these stimuli was not completely absent in the unattended conditions. The current study examined this type of processing during inattention blindness, which more closely approximates a complete lack of attention to the stimuli of interest.

By including both words and random consonant strings as critical stimuli, the current study investigated whether orthographic and lexical processing persist during inattention blindness. To test for orthographic processing, ERPs elicited by word forms (words and consonant strings) were compared to ERPs elicited by control stimuli made of scrambled line segments. To test for lexical processing, ERPs were compared between word and consonant string stimuli. In addition, the three-phase paradigm allowed us to test

for NCCs that uniquely track subjective awareness of visual word-forms under no-report conditions (phases 1 and 2). Finally, by including a linguistic task in phase 3, ERPs associated with post-perceptual task performance could be isolated from ERPs linked with sensory and perceptual processing. We predicted that ERPs reflecting orthographic and lexical processing would be present in all phases (even during inattentive blindness), that the VAN would uniquely index conscious perception of word forms (being absent during inattentive blindness), and that the P3b would not correlate with awareness but rather with task-relevance of the word-form stimuli (being present only in phase 3).

2. Materials and methods

2.1. Participants

Fifty-three healthy college-student volunteers (31 female, 22 male) participated in the study and received \$25 compensation. All participants were between the ages of 18 and 24 (mean = 20.02 SD = 2.04), and 2 were left-handed (as assessed by the Edinburgh handedness inventory). After excluding six participants for excessive EEG artifacts and one subject for reporting having seen the foil stimuli (see below), the final data set included 46 participants (26 female, 20 male). All participants had normal or corrected to normal vision. All procedures were approved by the Reed College Institutional Review Board.

2.2. Stimuli

The stimulus set consisted of 180 words of similar frequency (KFRQ range = 11–30, M = 18.27, SD = 5.01), 180 consonant strings, 360 scrambled line controls, and 80 animal words (these served as targets in phase 3). Thus, word forms (all words and consonant strings) appeared on 55% of trials and scrambled control stimuli on 45% of all trials. All word-form stimuli were five letters long, and the scrambled line controls consisted of five “non-letter” regions (see below). KFRQ values were taken from the UWA MRC Psycholinguistic database (Coltheart, 1981).

The consonant strings were generated using Javascript's native random method (www.textmechanic.com). All 21 consonants were equally likely to be chosen and were selected with replacement. Analysis of the resulting strings confirmed that the letter frequency did not violate the expectation of randomness, χ^2 (20, N = 900) = 15.97, *n.s.*

A custom true type font was used to present all the words and consonant strings. Glyphs for all the letters of the English alphabet were manually created in Adobe Illustrator CS5 out of 31 basic lines and curves of different sizes and orientations. The glyphs were then imported into Fontforge (<https://fontforge.github.io/en-US/>) compiled for Windows by Matthew Petroff (<http://www.mpetroff.net/software/fontforge-windows>, 2012), to generate the custom font. Once the linguistic stimuli were created using this font, the number of times each of the 31 segments appeared was counted to generate the scrambled line controls.

The scrambled line controls contained five “non-letter” regions, each comprised of three line segments (the average number of segments in each letter for the linguistic stimuli in this study). The segments were randomly chosen in proportion to the number of times each appeared in the linguistic stimuli throughout the experiment. Each line segment was randomly oriented in intervals of 45°. Fig. 1 provides examples of the three stimulus categories.

The word forms and scrambled line controls were centered inside of a larger 13 × 13 array of line segments (dimensions: 16.0° × 16.0°) randomly chosen from the 31 lines used to generate the glyphs. The center of the line segment array (height = 2.1°; width = 7.9°) was left blank so that the key stimuli (words, consonant strings, and scrambled lines) could be presented there. Each line segment appeared roughly an equal number of times in the surrounding array within each trial. The position of each line segment was varied by a random translation jitter up to 10 pixels in either direction, and the orientation of each line segment was varied by a random rotational jitter up to 360° in 1° increments. The images for the stimulus arrays were generated using Processing 2.2.1.

The distracter stimuli, which were task-relevant in the first two phases of the experiment, consisted of three concentric green ellipses overlaid on top of the line array (height = 1.6°, 3.3°, 5.0°; width = 4.0°, 5.6°, 7.4°, respectively), each containing four evenly spaced green (RGB: 0, 100, 0) disks. The disks were smallest on the innermost ellipse (0.32°), larger on the middle ellipse (0.41°), and largest on the outermost ellipse (0.52°). Participants fixated on a black cross in the center of the screen and were trained to track the moving disks with their covert attention rather than with eye movements. All stimuli were presented on a white background on a 1920 × 1200 pixel display screen, Planar SA2311w23“ - LCD monitor (refresh rate = 60 Hz), and were viewed from a distance of 72 cm. Stimuli were controlled by Presentation software (Neurobehavioral Systems, Albany, CA).

On each trial, the configuration of the line segment array alternated between a baseline random configuration (duration = 600–800 ms) and three other possible configurations: word, consonant string, or scrambled lines (duration = 300 ms). The trials were presented in 1-min blocks, each followed by a self-paced break, for a total of 12 blocks per phase. The ring of green disks rotated continuously at a rate of 52°/s as the line segments changed configurations. The direction that the green disks rotated alternated between clockwise and counterclockwise after each 1-min block of trials, but did not change within blocks.

For the first two phases of the experiment, target stimuli consisted of slightly brighter green disks (RGB: 0, 140, 0) that were randomly presented on 10% of trials during the critical 300 ms time window when the words, consonant strings, or scrambled lines were presented (equally likely to appear during each stimulus type). In the third and final phase, the targets were animal words, which appeared in 10% of the trials. Importantly, all aspects of the physical stimuli (including the bright disk targets and animal words) were identical in all three phases of the experiment, except that the order of presentation (of words, consonant strings, and scrambled lines) was randomized within each phase. Therefore, participants viewed the same stimulus set in each phase, for a total of 800 trials per phase (180 words, 180 consonant strings, 80 animal word targets, and 360 scrambled controls). To avoid

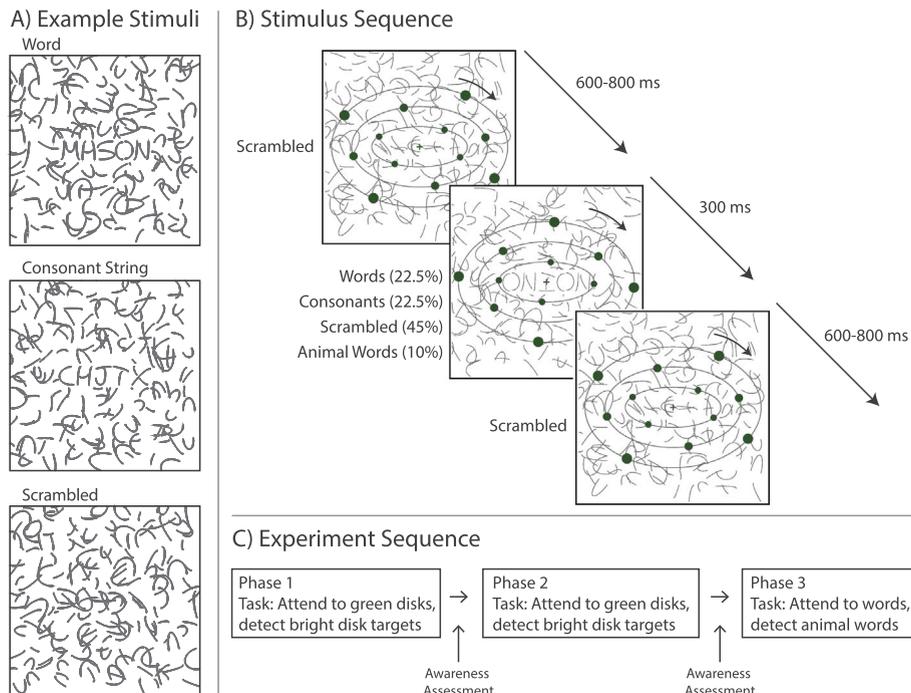


Fig. 1. Stimuli and procedure. (A) Example stimuli for words, consonant strings, and scrambled lines. (B) On each trial, a scrambled line configuration was presented for a variable interval (600–800 ms) followed by either a word, consonant string, or another scrambled line configuration. This sequence was then repeated (the screen was never blank). ERPs were time-locked to the onset of the 300 ms configurations (words, consonant strings, scrambled). Twelve green disks continuously rotated around the three concentric ovals. On 10% of trials one of the green disks became brighter during the 300 ms configuration. (C) Overview of the three phase design. During phases 1 and 2, participants attended to the green disks and pressed a button whenever they noticed a brighter disk. During phase 3, participants attended to the words and pressed a button whenever they detected an animal word. Awareness assessments were conducted after phases 1 and 2 to determine if participants noticed the word form stimuli (words and consonant strings) during the previous phase. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

contamination from motor-related brain activity, trials including target stimuli (brighter disks and animal words) were excluded from ERP analyses for all phases of the experiment.

2.3. Procedure

The experiment was divided into three phases, with practice trials preceding phase 1 and phase 3. Initially, participants were told that the experiment was a test of peripheral attention under high visual load. For phases 1 and 2, participants were instructed to maintain fixation on a central cross while paying attention to the orbiting disks to detect the bright disk targets. Participants pressed a response button with their right index finger whenever they detected a brighter disk. During the practice trials (five 1-min blocks), only scrambled lines (no words or consonant strings) were presented. The word form stimuli first appeared in phase 1 of the experiment. After phase 1, participants answered a series of questions designed to assess whether they noticed the word form stimuli (Supplemental Fig. 1). In brief, participants were first asked if they had noticed any patterns within the grid of line segments, and if they did, to describe or draw what they saw. Regardless of their answer, they were then presented with five example stimuli (words, consonant strings, and 3 foils). Participants rated their confidence in having seen each type of stimulus during phase 1 on a 5-point scale (confidence ratings), and then estimated how frequently they saw each stimulus on a separate 5-point scale (frequency ratings). Participants were considered “inattentionally blind” to the word forms if they failed to report seeing any word forms on the initial open-ended question *and* rated their confidence as a 3 or less after seeing the example words and consonant strings. Participants who mentioned seeing letters or words on the initial question *or* rated their confidence as a 4 or 5 after seeing the examples were considered “noticers” of the word forms. Noticer subjects were then asked to approximate when they first noticed the words. Participants who ranked their confidence in having seen any of the foil stimuli as a 4 or 5 were excluded from analysis (1 subject was excluded for this reason). Three participants reported noticing the word forms only during the last few blocks of phase 1, and were thus considered to be inattentionally blind (but their ERP data from the last few blocks of phase 1 were excluded from analysis). One of these three participants was later excluded due to not having enough trials after artifact rejection.

After completing the awareness assessment, participants were not explicitly informed about the presence of word forms but were simply instructed to continue performing the bright-disk detection task in phase 2. After phase 2, the same awareness assessment was repeated. Prior to phase 3, participants were instructed to perform a different task in which they were to ignore the green disks and instead pay attention to the words. Their task was to detect (and respond with a button press to) animal words (e.g. lions, tiger, etc.). Participants practiced this new linguistic task immediately prior to phase 3 (for the same amount of time they practiced the bright

disk detection task prior to phase 1).

2.4. EEG recording and ERP pre-processing

Brain electrical activity was recorded non-invasively from the scalp using a custom 96 channel Herrsching DE-8211 “Easycap” with 96 equidistant electrode placements. Electrode impedances were kept below 5 k Ω . Electrode signals were sampled at a 500 Hz digitization rate and amplified by BrainVision “Professional BrainAmp” amplifiers, with a high cutoff filter at 150 Hz (data was later low-pass filtered offline at 25 Hz with a 24 dB/Oct roll-off). During task performance, eye movements were monitored by vertical and horizontal EOG recordings. A vertex electrode served as the reference for all scalp channels during recording, and data were subsequently re-referenced to the average of the two mastoids offline. Each session lasted 150–180 min, including electrode cap preparation and recording time.

ERPs were time-locked to the onset of words, consonant strings, and scrambled line stimuli, and baseline corrected from –200 to 0 ms. The left and right horizontal EOG channels were re-referenced as a bipolar pair. Trials were discarded if they contained eye movements, blinks, or other muscle artifacts in a –600 to +600 ms interval surrounding stimulus-onset. Artifact detection was accomplished semi-automatically via per-subject adjustment of the following peak-to-peak thresholds: eye movements (50 μ V, 50 ms steps, in bipolar HEOG), blinks (100 μ V, 200 ms steps, in VEOG and FP1), and muscle noise (150 μ V, 200 ms steps, all remaining channels). On average, 18.8% of trials were rejected due to a combination of these artifacts. Any participant with greater than 40% of trials rejected per stimulus type per phase was excluded from analysis due to an insufficient number of trials to obtain reliable ERPs (six subjects were excluded). Individual electrodes showing extended periods of noise in the raw EEG were removed and replaced by interpolated signals from surrounding channels using topographic spherical splines. The average number of channels interpolated per participant was 5.37. The interpolated channels were typically located in the outermost rings of the EEG cap, such as on the back of the neck or sides of the face.

3. Results

3.1. Awareness assessment

Participants were split into two groups (inattentionally blind, noticers) based on their responses to the awareness assessment administered after phase 1. Based on the criteria outlined above, 20 out of 52 participants (38%) were deemed inattentionally blind to the word forms in phase 1, while 32 participants spontaneously noticed the word forms. The same awareness assessment was conducted again after phase 2 to ensure participants became aware of the word forms. In this case, 100% of the participants reported seeing the word forms. After excluding several participants due not having enough trials after artifact rejection, the final dataset included 46 participants, with 18 participants in the inattentionally blind group (39%) and 28 in the noticer group.

3.2. Task performance

To determine whether noticing the word forms disrupted participants on the bright-disk detection task, group (inattentionally blind, noticers) \times phase (1, 2) ANOVAs were run on d' (a measure of sensitivity that takes into account both accuracy and false alarm rate) and reaction times. For d' , a main effect of phase was found ($F_{(1,44)} = 28.53, p < 0.001, \eta_G^2 = 0.089$), with larger d' scores in phase 2 for both groups [inattentionally blind group, d' in phase 1: $M = 3.04$ ($SD = 0.75$); phase 2: $M = 3.76$ ($SD = 1.19$); noticer group: d' in phase 1: $M = 3.23$ ($SD = 0.90$); phase 2: $M = 3.76$ ($SD = 1.03$)]. A main effect of phase was also found for reaction time ($F_{(1,44)} = 27.15, p < 0.001, \eta_G^2 = 0.072$), with faster reaction times in phase 2 for both groups [inattentionally blind group: RTs in phase 1, $M = 612.80$ ms ($SD = 50.71$); phase 2, $M = 570.75$ ms ($SD = 50.06$); noticer group: RTs in phase 1, $M = 608.72$ ms ($SD = 58.39$); phase 2, $M = 585.26$ ms ($SD = 54.01$)]. No main effects of group or interactions between group and phase were evident. Together, these results suggest that noticing the words did not impair participants' abilities to perform the distracter task.

To test whether the word task differed in difficulty from the bright-disk detection task, an ANOVA with all three phases was conducted. A main effect of phase was evident when testing both d' ($F_{(2,88)} = 25.84, p < 0.001, \eta_G^2 = 0.46$) and reaction time ($F_{(2,88)} = 134.24, p < 0.001, \eta_G^2 = 0.21$). No main effect of group or any interactions were found in either test. Follow-up paired t -test comparisons revealed that d' for the word task (phase 3: $M = 2.69, SD = 0.51$) was lower than for the disk task (phase 1: $M = 3.16, SD = 0.85$; phase 2: $M = 3.76, SD = 1.08$) in phase 1 ($t_{(45)} = 5.89, p < 0.001, d = 0.67$) and phase 2 ($t_{(45)} = 5.89, p < 0.001, d = 0.61$). Reaction times were slower for the word task (phase 3: $M = 695.83$ ms, $SD = 52.79$) than for the disk task (phase 1: $M = 610.14$ ms, s.d. = 55.31; phase 2: $M = 580.21$ ms, $SD = 53.88$) in both phase 1 ($t_{(45)} = -10.45, p < 0.001, d = -1.58$) and phase 2 ($t_{(45)} = -14.23, p < 0.001, d = -2.17$). Accuracy rates (SD) for phases 1, 2, and 3 were 77% (12%), 80% (11%) and 68% (13%). Together, these results suggest that the word task was slightly more difficult than the disk task.

3.3. ERP analysis

Difference amplitudes obtained by subtracting trials with word forms (words and consonant strings combined) minus trials with scrambled lines, and separately, trials with words minus trials with consonant strings, were subjected to repeated measures, two-tailed t -tests for each phase and each group of subjects separately, using the false discovery rate (FDR) correction for multiple comparisons at the 5% level (Benjamini & Yekutieli, 2001). The ERP data was down-sampled to 100 Hz before these mass univariate

analyses. All time points between 100 and 600 ms for all 94 scalp electrodes (excluding HEOG and VEOG) were included in the analyses (4900 total comparisons). These analyses were carried out using the mass univariate ERP Toolbox (Groppe, Urbach, & Kutas, 2011). While the mass univariate tests indicated the presence or absence of the hypothesized ERP differences, subsequent ANOVAs were employed to test for magnitude differences of the ERP effects across groups and phases (and in some cases laterality). Time-windows and electrodes for the ANOVAs were selected based on the mass univariate analyses.

3.4. Orthographic effect

Word forms elicited more negative ERPs than scrambled lines over occipital scalp sites from approximately 200–280 ms in all phases of the experiment (including during inattentional blindness). The timing and scalp distribution of these differential ERPs resembled those reported previously in the literature (Carreiras et al., 2009; Holcomb & Grainger, 2007). Grand-averaged ERPs from a representative set of electrodes are shown in Fig. 2. This orthographic effect (OE) was most clearly visible at electrode Oz, but was also apparent at neighboring sites. Mass univariate results are provided in Fig. 3. The mass univariate tests established the presence of this ERP difference in all phases, but to compare the magnitude of this effect across phases and groups, a $2 \times 3 \times 3$ ANOVA with the factors group (inattentionally blind, noticers), phase (1, 2, 3), and laterality (left, right, center) was conducted using mean difference amplitudes from 200–280 ms at a posterior cluster of electrodes informed by the FDR results. This ANOVA revealed significant main effects of phase ($F_{(2,88)} = 6.81, p < 0.01, \eta_G^2 = 0.068$) and laterality ($F_{(2,88)} = 25.17, p < 0.001, \eta_G^2 = 0.063$), with an interaction between phase and laterality ($F_{(4,176)} = 32.77, p < 0.001, \eta_G^2 = 0.054$). The amplitude of the orthographic effect in phase 3 was larger than in phase 1 ($t_{(45)} = 3.09, p < 0.01, d = 0.68$) and phase 2 ($t_{(45)} = 2.54, p < 0.05, d = 0.45$), which did not significantly differ from each other ($t_{(45)} = 1.38, n.s., d = 0.25$). The amplitude of the effect was larger in the left hemisphere than in the right hemisphere ($t_{(45)} = 2.44, p < 0.05, d = 0.39$) and center ($t_{(45)} = 7.99, p < 0.001, d = 0.89$). The amplitude of the effect in the right hemisphere was also larger than in the center ($t_{(45)} = 4.62, p < 0.001, d = 0.57$). To interpret the phase by laterality interaction, we also ran series of pairwise comparisons between left and right hemisphere for each phase. In phase 1, the left and right hemispheres did not differ from each other ($t_{(45)} = 0.33, n.s., d = 0.038$). The amplitude in the left hemisphere was marginally larger than the right in phase 2 ($t_{(45)} = -1.71, p < 0.1, d = -0.23$), and this left-hemisphere lateralization effect reached significance in phase 3 ($t_{(45)} = -3.19, p < 0.01, d = -0.46$). A summary of the mean amplitude differences are provided in Table 1.

3.5. Lexical effect

ERPs elicited by words and consonant strings did not differ at any time for any electrode during inattentional blindness. Differences were evident in the ERPs from ~280 to 350 ms during all phases in which participants were aware of the word form stimuli (see “LE” in Fig. 2). This lexical effect occurred primarily in the left hemisphere scalp channels. However, mass univariate analyses (Fig. 4) found that these differences were statistically reliable in only 3 out of 5 of these conditions (phase 3 for both groups and phase 2 for the noticer group). While visually apparent in the ERP data, lexical differences were not statistically significant (according to the conservative FDR-corrected mass univariate analysis) in phase 2 for the inattentionally blind group nor in phase 1 for the noticer group. In phase 1 for the inattentionally blind group, the lexical effect was clearly absent. To further explore the lexical effect, especially in the conditions in which differences were apparent in the ERPs but did not statistically differ in our conservative mass univariate analyses, we ran a series of one-tailed *t*-tests over a cluster of left posterior electrodes during the 280–350 ms time window. In the aware group, the lexical effect was significant in phase 1 ($t_{(27)} = -2.49, p < 0.05, d = -0.47$) and phase 2 ($t_{(27)} = -5.23, p < 0.001, d = -0.99$). The inattentionally blind group did not show a lexical effect when unaware of the stimuli in phase 1 ($t_{(17)} = -0.79, n.s., d = -0.19$), and showed a trending effect once they attended and became aware of the stimuli in phase 2 ($t_{(17)} = -1.30, p = 0.11, d = -0.31$). The magnitude of the lexical effect did not differ between phases 1 and 2 for either the inattentionally blind ($t_{(17)} = 0.31, n.s., d = 0.12$) or the aware group ($t_{(27)} = 1.19, n.s., d = 0.29$). Mean amplitudes for the lexical effect (LE) are included in Table 1.

3.6. VAN

A negative-going ERP difference over bilateral occipital-parietal sites from approximately 320–380 ms was evident for word forms versus scrambled lines in all groups and phases except for the inattentionally blind group in phase 1 (see Figs. 2 and 3). In other words, an ERP difference resembling the visual awareness negativity (VAN) was only evident in conditions in which subjects reported awareness of the word forms, regardless of the task. Although the scalp distribution and timing of the VAN partially overlapped the orthographic effect, the VAN appeared to be slightly more ventral-lateral, slightly later in time, and most importantly, absent during inattentional blindness. To explore potential magnitude differences in VAN across phases and groups, we conducted follow-up *t*-tests. First, we were interested in whether the VAN differed across groups in the phase in which they first noticed the word form stimuli (phase 2 for the inattentionally blind group versus phase 1 for the noticer group). VAN amplitude did not differ in this comparison ($t_{(44)} = 0.32, n.s., d = 0.093$). Next, we tested whether the VAN was larger when the word form stimuli were task-relevant. Here, VAN amplitudes were significantly larger in phase 3 versus phase 2 for the inattentionally blind group ($t_{(17)} = 2.84, p < 0.05, d = 0.85$), but not for the noticer group ($t_{(27)} = 1.28, n.s., d = 0.34$). Because the noticer group was aware of the word-form stimuli prior to phase 2 (but the inattentionally blind group was not), we decided to also test whether the VAN in the noticer group differed in phase 3 from when they first noticed the word form stimuli (phase 1). In this comparison, we did find a significant increase in VAN amplitude ($t_{(27)} = 2.28, p < 0.05, d = 0.63$). See Table 1 for a summary of VAN amplitudes in each phase for each group. Because

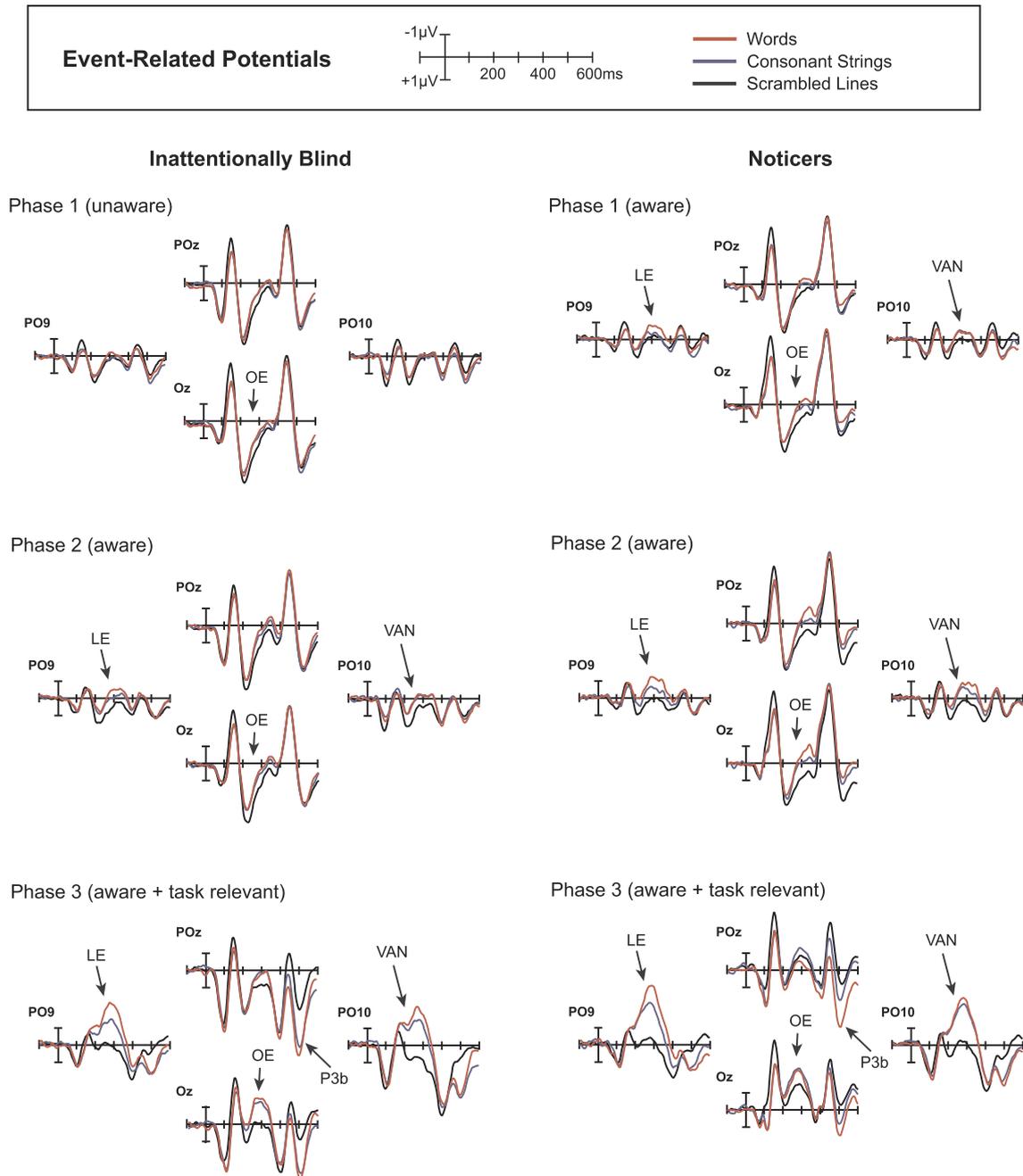


Fig. 2. Grand-averaged ERPs elicited by words (red), consonant strings (blue), and scrambled lines (black) at representative parietal and occipital electrodes for the inattentively blind group of subjects (left) and the noticer group of subjects (right) across the three experimental phases (top to bottom). ERP differences between word forms and scrambled: OE = orthographic effect; VAN = visual awareness negativity; P3b. ERP differences between words and consonant strings: LE = lexical effect. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the inattentively blind group had fewer participants than the aware group, one concern may be that the VAN was present in the inattentively blind group during phase 1, but that there was not enough statistical power to detect it. However, because this same pattern of results was observed in previous studies using similar paradigms (Pitts et al., 2012; Shafto & Pitts, 2015), it is unlikely that the VAN was present but undetected in this study.

3.7. P3b and other task-related differences

In phase 3, when the word forms were task-relevant, several additional ERP effects were apparent. From approximately

Mass Univariate Analysis:
Word forms vs. Scrambled lines

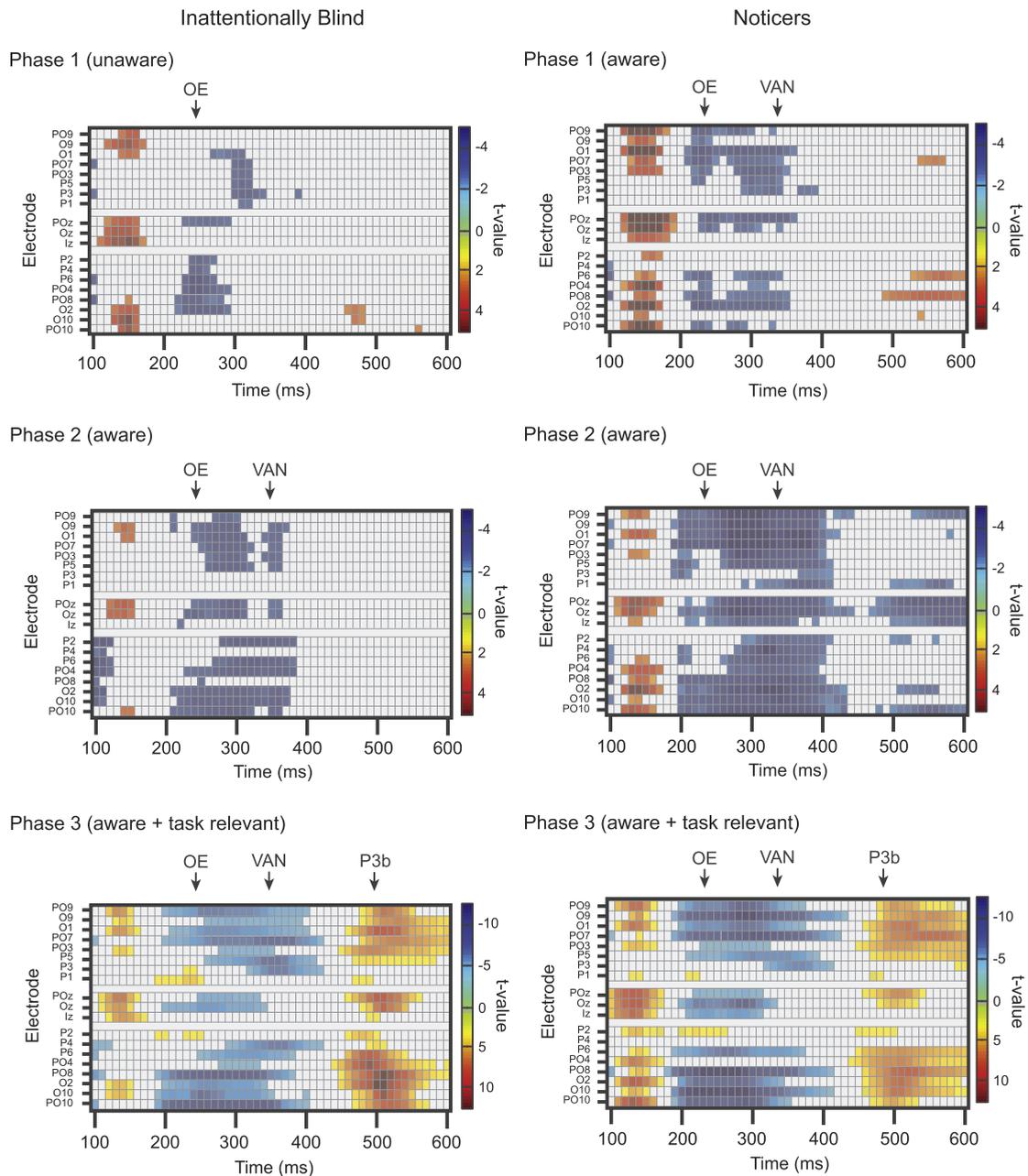


Fig. 3. Mass univariate results at posterior electrode sites for the difference of word forms versus scrambled lines, for the inattentively blind group (left) and the aware group (right) across the three experimental phases (top to bottom). Within each panel, electrodes are plotted in rows with those on the top and bottom being most lateral, and those in the center being most medial. The top section of electrodes is from the left hemisphere, the bottom from the right hemisphere, and the middle from the midline. Colors reflect t-values that passed the statistical threshold after false discovery rate (FDR) correction for multiple comparisons. OE = orthographic effect; VAN = visual awareness negativity. Note that early positive differences in all phases (~120–160 ms) were due to physical stimulus attributes which were controlled for in a follow-up experiment (see Supplemental Figs. 2c and 3). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

200–350 ms, ERPs elicited by words and consonant strings were more positive than scrambled lines over anterior scalp regions. This effect was present in both groups of subjects, and resembles the anterior P2 (P2a) or “selection positivity” (SP) described previously as reflecting the evaluation of stimuli for task-relevance (Harter & Aine, 1984; Hillyard & Anllo-Vento, 1998; Potts, 2004). A selection

Table 1

Mean ERP difference amplitudes (μV) along with *SD* for the 4 components of interest (each column) in each phase for each group of subjects [Noticers and Inattentionally Blind (IB)]. Time windows and electrodes for extracting these mean amplitudes were based on the results of the FDR-corrected mass univariate analyses. OE = orthographic effect; LE = lexical effect; VAN = visual awareness negativity. Asterisks indicate statistically significant ERP differences ($p < 0.01$).

	OE	LE	VAN	P3b
<i>Phase 1</i>				
Noticers	−0.54 (0.73)*	−0.47 (0.92)	−0.60 (1.12)*	0.15 (0.94)
IB	−0.57 (0.81)*	−0.35 (0.79)	−0.34 (0.77)	0.16 (0.63)
<i>Phase 2</i>				
Noticers	−0.74 (0.90)*	−0.89 (0.75)*	−1.03 (0.97)*	−0.33 (0.92)
IB	−0.81 (1.00)*	−0.65 (0.91)	−0.69 (0.79)*	0.00 (0.77)
<i>Phase 3</i>				
Noticers	−1.29 (1.28)*	−2.25 (1.18)*	−1.48 (1.62)*	0.81 (1.21)*
IB	−1.27 (1.39)*	−2.25 (1.48)*	−1.57 (1.23)*	0.98 (0.81)*

negativity (SN) was also most likely present for words (and less so for consonant strings), but this component overlapped with the orthographic, lexical, and VAN components in space and time over the posterior scalp and was thus difficult to separately visualize or analyze (see Pitts et al., 2012 and Shafto & Pitts, 2015 for similar SN results). The SP and SN were followed by a significantly greater P3b for words compared to consonant strings and for word forms compared to scrambled lines in centro-parietal sites from approximately 400 to 550 ms. In the mass univariate analyses (Figs. 3 and 4) for both the inattentionally blind group and the noticer group the P3b was clearly absent in phases 1 and 2 and present in phase 3. Difference maps showing the scalp topographies of the main ERP effects of interest [orthographic effect (OE), lexical effect (LE), visual awareness negativity (VAN), and P3b], are provided in Fig. 5.

3.8. Early sensory differences

The mass univariate analyses, as well as visual inspection of the ERPs suggested unexpected amplitude differences early in time (~120–160 ms) that were characterized by more positive-going ERPs for word forms compared to scrambled lines (e.g. see channel Oz in Fig. 2, all phases, both groups, and positive clusters in the MUA in Fig. 3). While this ERP effect could potentially index an early stage of visual word-form processing, we suspected that low-level stimulus differences were likely responsible for these differential amplitudes. In particular, these differences might reflect a larger N1 peak for the scrambled line stimuli compared to the word-form stimuli because there were more intersections in the scramble line glyphs relative to the letter glyphs (see Supplemental Fig. 2a versus b).

To further explore these early ERP differences, we ran a follow-up control experiment that eliminated the line segment intersections in the scrambled line stimuli to make them more similar to the letter stimuli (see Supplemental Fig. 2c). This control experiment consisted of two phases that were direct replications of phases 2 and 3 of the original experiment. Participants ($N = 14$) were informed of the presence of the word forms from the outset, effectively eliminating phase 1. The stimuli and tasks were identical to the original experiment, except for the change in how the scrambled line segments were designed. Controlling for line intersections in the scrambled line stimuli completely abolished this N1 (~120–160 ms) difference in the control experiment (Supplemental Fig. 3). Importantly, the other effects found in phase 2 and 3 of the original experiment (OE, LE, VAN, P3b) were clearly evident in this control experiment.

4. Discussion

A three-phase inattentional blindness paradigm was employed to study neural signatures of conscious and unconscious orthographic and lexical processing. The ERP results were consistent with our hypotheses, except for lexical processing. A stage of unconscious orthographic processing was suggested by a negative ERP difference for word forms versus scrambled lines from 200–280 ms, over posterior scalp regions, that was present in all phases of the experiment including during inattentional blindness. The visual awareness negativity (VAN), measured here from 320–380 ms at bilateral occipital-parietal electrodes, was absent during inattentional blindness and present in all other phases of the experiment, including conditions in which immediate perceptual reports were not required. This finding supports the view of the VAN as a prime candidate for an ERP signature of visual awareness (Railo et al., 2011; but see alternative interpretations below). The P3b (400–550 ms) was present only in phase 3 when the word stimuli were task-relevant. This result further supports the claim that late wide-spread cortical activity, indexed by the P3b, is more closely associated with carrying-out the task rather than generating visual awareness per se (Pitts, Padwal, et al., 2014). Contrary to our predictions, ERP signatures of lexical processing, measured here by comparing ERPs elicited by words versus consonant strings (280–350 ms), were absent during inattentional blindness. Further studies will be necessary to confirm this pattern of results for orthographic and lexical processing, but it may be the case that the visual system can differentiate between letters and non-letters without attention or awareness, while at least a minimal amount of attention is necessary for lexical processing.

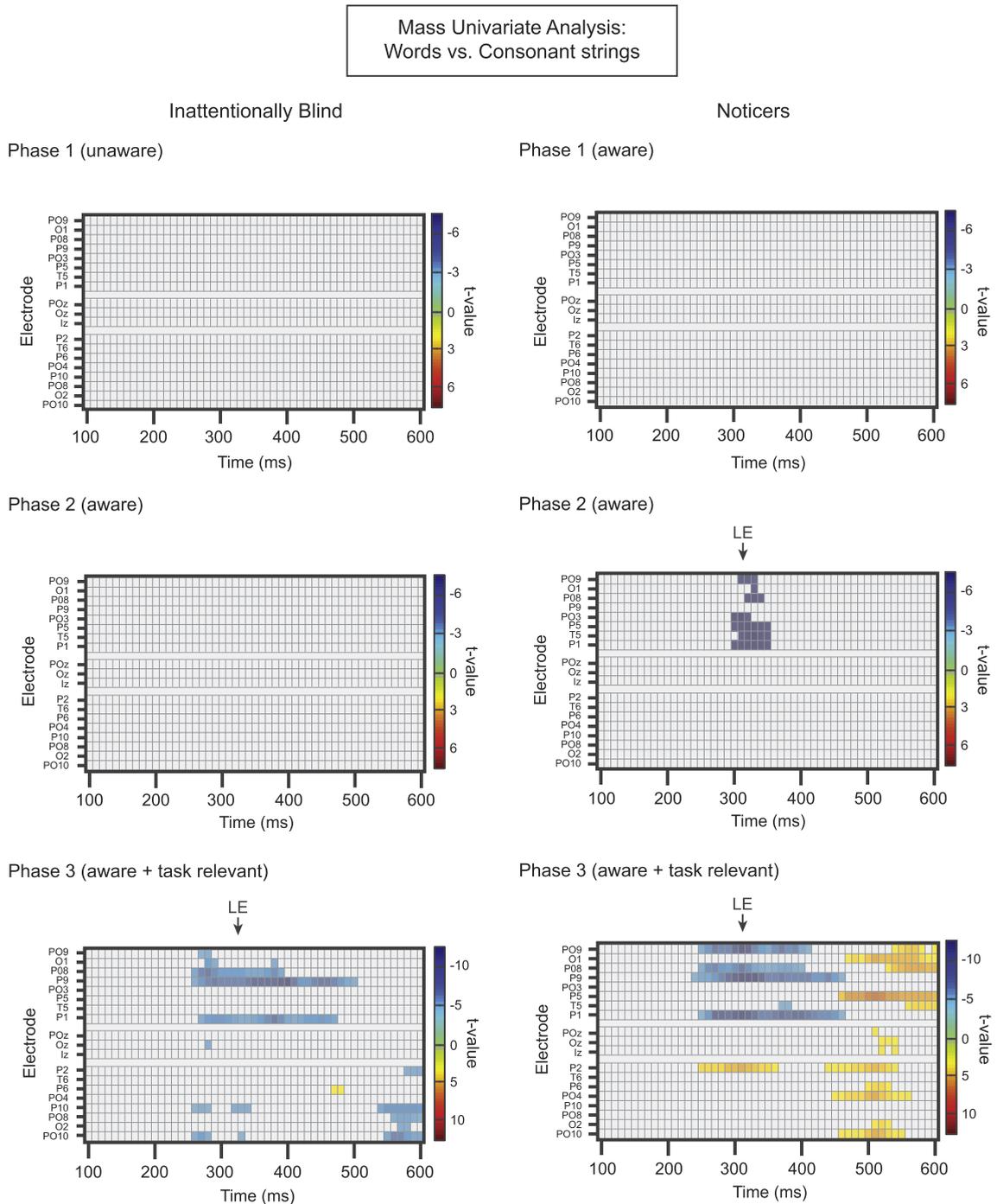


Fig. 4. Mass univariate results for the lexical effect (words versus consonant strings). Details are identical to Fig. 3. LE = lexical effect. In follow-up analyses using a less conservative statistical approach, the LE was also present in phase 2 for the inattentionally blind group and in phase 1 for the aware group (see main text for details).

4.1. Inattentional blindness

The results from this study as well as our previous studies using shapes and faces as stimuli may help inform our understanding of what types of processing do and do not occur during inattentional blindness. The emerging pattern of results suggests that both low-level and intermediate-level perceptual processing can occur during inattention. Low-level visual processing refers to the registration of basic sensory features such as orientation, contours, intersections, color, and motion. Intermediate-level processing refers to stages in which basic features are grouped, organized, segregated, etc. In Pitts et al. (2012), contour integration of oriented line segments

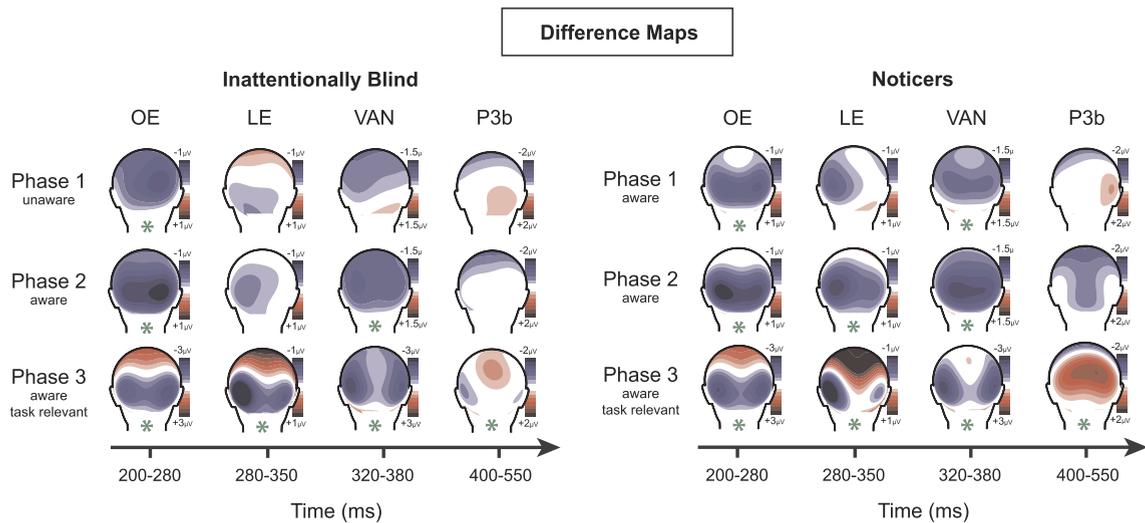


Fig. 5. Difference wave topographies over the posterior scalp for the four components of interest (each column) in the inattentively blind group (left) and the noticer group (right) across the three experimental phases (top to bottom). For the orthographic effect (OE), visual awareness negativity (VAN) and P3b, the maps show ERP differences for word forms minus scrambled. For the lexical effect (LE), the maps show ERP differences for words minus consonant strings. Asterisks under the maps indicate a statistically significant difference as assessed by the mass univariate analyses ($p < 0.01$).

was required to perceive geometric shapes, and ERPs suggested that this process remained intact during inattentional blindness. In the current study, ERPs differentiated between word forms and scrambled line segments during inattentional blindness. Both of these findings provide evidence for the formation of intermediate-level representations without attention. As discussed below, whether high-level (e.g., semantic) processing can occur during inattentional blindness is still debated, and the current study was not designed to test this possibility.

What doesn't seem to occur during inattention is phenomenal awareness of the unattended stimuli. The critical stimuli in our experiments were presented 200+ times, for reasonably long durations (300 ms), in the center of the screen, but subjects still failed to report seeing these stimuli and could not recognize them when shown examples (Pitts et al., 2012; Shafto & Pitts, 2015; current study). If this is correct, theories that posit a central role for attention in conscious perception (Dehaene et al., 2006; Prinz, 2012) should be favored over theories that allow for conscious perception in the absence of attention (Lamme, 2003; Tsuchiya & Koch, 2016).

4.2. Orthographic processing

In the current study, word forms were distinguished from scrambled lines during the interval 200–280 ms over the occipital scalp even in the absence of attention and awareness, suggesting that some level of orthographic processing takes place automatically and unconsciously. This is consistent with evidence from backwards masking studies that show orthographic priming effects even when the stimuli are not consciously seen (Dehaene et al., 2001; Holcomb & Grainger, 2006). In contrast to the typical distribution solely in the left hemisphere (Bentin et al., 1999; Holcomb & Grainger, 2006; Proverbio et al., 2004; Ruz et al., 2005; Simon, Bernard, Largy, Lalonde, & Rebai, 2004), in the current experiment the right hemisphere also exhibited orthographic processing differences. A possible reason for this discrepancy is that most studies that examine orthographic processing use linguistic tasks, such as lexical or rhyming decisions, which likely recruit the left-hemisphere networks specialized for language processing. In contrast, participants in the current study performed a non-linguistic visual tracking task in phases 1 and 2, a task that did not require, prime, or otherwise engage the left-lateralized language networks. The right hemisphere has shown differential activation for words, line drawings, and false-fonts when attention is occupied with a separate task (Appelbaum et al., 2009), and when the stimuli are degraded by visual noise (Ben-Shachar, Dougherty, Deutsch, & Wandell, 2007), indicating that the right hemisphere may be involved with shape extraction for word-form stimuli in certain circumstances. Indeed, in phase 3 of the current study, when attention was focused on the word forms to carry-out a linguistic task, the orthographic ERP effects became left-lateralized. Finally, the font used for the word forms in the current study lacked some of the features present in conventional, familiar fonts, such as explicit vertices, straight lines, parallel lines, and restricted angles. Right hemisphere activity may have been enhanced due to this unconventional stimulus presentation format (Cohen, Dehaene, Vinckier, Jobert, & Montavont, 2008; Hellige & Adamson, 2007; Mayall, Humphreys, Mechelli, Olson, & Price, 2001; Pammer, Hansen, Holliday, & Cornelissen, 2006).

4.3. Lexical processing

In the current study, ERPs elicited by words and consonant strings did not differ from each other during inattentional blindness, suggesting that lexical processing may require attention. While a number of previous studies have suggested that linguistic

processing, even up to the level of semantic analysis, may occur without awareness (Dehaene et al., 1998; Merikle, Smilek, & Eastwood, 2001) in almost all cases, a certain amount (or type of) attention was still allocated to the task-relevant word stimuli (e.g. Luck et al., 1996; Naccache, Blandin, & Dehaene, 2002; but see Mack & Rock, 1998). Studies employing the attentional blink along with measures of the semantically-sensitive N400 ERP component have produced mixed results (Batterink, Karns, Yamada, & Neville, 2010; Giesbrecht, Sy, & Elliott, 2007; Luck et al., 1996; Vogel, Luck, & Shapiro, 1998). To date, no previous study (including the current study) has manipulated semantic associations between words during inattention blindness while measuring the N400. This may be a fruitful avenue for future research.

A recent behavioral study, however, reported evidence for a semantic priming effect during inattention blindness (Schnuerch, Kreitz, Gibbons, & Memmert, 2016). In this experiment, Arabic numerals (1–4, 6–9) were presented during inattention blindness while the distracter task involved a magnitude judgment (greater than or less than 5). When the unseen numbers were incongruent with the task-relevant numbers of the distracter task, reaction times were significantly slower than congruent and neutral conditions. Schnuerch et al. (2016) interpret this finding as evidence for semantic processing during inattention blindness, although alternative explanations for this result have not yet been ruled out. For example, some studies suggest that while Arabic numerals activate semantic information (i.e. magnitude) even when subjects perform non-numerical tasks (Fias, 1996), written number words activate semantic information only when the task requires it (Fias, 2001; Ito & Hatta, 2003). While Schnuerch et al. (2016) report a second experiment in which the distracter stimuli were number words, these stimuli were always attended and consciously seen. It will be important to test whether the reaction time results they observed remain if number words are used as the critical (unseen) stimuli during inattention blindness. It is also unclear whether Schnuerch et al.'s (2016) findings for highly overlearned symbols (numerals) would extend to semantic processing of unpredictable words. For now, whether lexical-semantic processing can occur in the absence of attention is an interesting question that remains open for future research.

The current results appear to be inconsistent with Ruz et al.'s (2005) finding that words were distinguished from non-words in ERP recordings during an attentionally demanding distracter task on superimposed images. We suggest three possible explanations for this discrepancy. First, our distracter task could have been more difficult and attention-demanding, thus inhibiting higher-level linguistic processing. In the Ruz et al. (2005) study, participants needed to detect repetitions of pictures or words; in our study, participants had to track 12 rotating disks for a very slight change in luminance. Second, our stimuli contained more overall visual noise than Ruz et al.'s (2005) stimuli, potentially contributing to an even higher perceptual load in our experiment. This pattern is consistent with observations of the N400 component (related to semantic processing), which is attenuated or abolished under conditions of high perceptual load (McCarthy & Nobre, 1993). Finally, the way in which Ruz et al. (2005) confirmed that the words were unattended during the distracter task was to give a surprise word-recognition test at the end of the block. Participants recognized words presented during the unattended condition just as often as they claimed to have recognized foil stimuli (chance performance). Ruz et al. (2005) correctly label this manipulation “inattention amnesia” rather than inattention blindness because it is entirely possible that participants were aware of the words and consonant strings in the unattended condition, but were unable to recall the identity of the words during the surprise recognition test. In the current study, we used a much more inclusive measure and counted subjects as “aware” if they reported noticing the mere presence of words or consonant strings (even if they couldn't remember a single specific word). Although the issue of whether lexical-semantic processing can occur during inattention remains controversial, the current results tentatively suggest that at least a minimal amount of attention may be necessary.

4.4. VAN versus P3b as potential NCCs

In the current study, the VAN was absent during inattention blindness and present in all conditions in which participants reported awareness of the word forms, regardless of whether the reports were made immediately (as in the animal-word detection task of phase 3) or were delayed (as in the awareness assessments following phases 1 and 2). The P3b, on the other hand, was absent in three separate conditions in which participants confidently reported awareness of the word-form stimuli. In these conditions, subjects were performing the distracter task and thus did not have to carry-out task-relevant discriminations, hold information in working memory, or immediately report anything about the word forms. This pattern of results is consistent with our previous studies using shapes (Pitts et al., 2012) and faces (Shafto & Pitts, 2015) as critical stimuli. In all three cases, for shapes, faces, and words, the VAN correlated with awareness while the P3b correlated with task-relevance.

These findings are consistent with a recent proposal which places our current best estimate of the neural correlates of visual consciousness in posterior cortical areas at intermediate latencies (Koch, Massimini, Boly, & Tononi, 2016; Sandberg, Frässle, & Pitts, 2016). This estimate is at odds with predictions made by the global neuronal workspace theory, which posits that the P3b is a reliable neural signature of visual awareness (Dehaene, 2014; Dehaene & Changeux, 2011). By including no-report conditions (Tsuchiya et al., 2015) and isolating potential NCCs from closely related pre- and post-perceptual brain activity (Aru et al., 2012), the modified inattention blindness paradigm has proven useful in narrowing down the possibilities for potential NCCs (Pitts, Metzler, et al., 2014; Pitts, Padwal, et al., 2014).

Our findings concerning the VAN as a prime candidate for a reliable ERP index of conscious visual perception correspond very well with a number of results from other labs employing different paradigms to manipulate awareness (Busch et al., 2009; Koivisto & Revonsuo, 2010; Railo et al., 2011; Rutiku, Aru, & Bachmann, 2016; Sandberg et al., 2014). Together, this body of work may help guide future research that can investigate NCCs at a lower systems-level of analysis with more fine-grained tools (e.g., intracranial EEG, LFPs, multi-unit recordings, etc.). In other words, knowing where to look in space, when to look in time, and how to look in terms of carefully controlling potentially confounding factors may be useful in guiding future research aimed at identifying NCCs at the mechanistic level.

Despite this progress, however, it is important to remain cautious and to avoid coming to premature conclusions. As we have mentioned previously (Pitts, Metzler, et al., 2014; Pitts, Padwal, et al., 2014; Pitts et al., 2012), the current inattention paradigm, as well as other paradigms such as backward masking, attentional blink, change blindness, and bistable perception, may all fail to adequately distinguish between attention effects and awareness effects. These distinct, but closely related functions are very difficult to tease apart, and it remains possible that the VAN reflects a particular type of attentional process that is necessary for awareness but not identical (in this case the label “visual awareness negativity” would be premature and potentially misleading). Indeed, in the current inattention paradigm, attention and awareness co-vary, either both being absent (inattention blindness) or present (all aware conditions). The relationship between attention and awareness is an active area of research (Tsuchiya & Koch, 2016), and our working hypothesis is one of a single-dissociation: some types of attention (orienting, exogenous cueing) can influence perceptual processing in the absence of awareness, but awareness without attention is impossible, i.e. at least a minimal amount of attention is necessary for conscious perception (Cohen, Cavanagh, Chun, & Nakayama, 2012; Jackson-Nielsen, Cohen, & Pitts, 2016). Distinguishing between attention and awareness effects in the brain is a challenging endeavor, and new paradigms will be necessary to separately measure these two closely related processes.

4.5. VAN versus other ERP components

A possible path forward is to concentrate efforts on determining exactly what perceptual or cognitive function is indexed by the VAN. In addition to manipulating processes closely related to awareness such as attention and working memory and testing for the VAN, it may also be useful to design paradigms that can simultaneously measure the VAN along with other well-known ERP markers of attentional selection and working memory such as the N2pc (Luck & Hillyard, 1994; Luck & Kappenman, 2012) and contralateral delay activity (CDA) (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). Interestingly, the timing of the VAN falls directly in between the N2pc and the CDA, which are well-established signatures of attention and working memory, respectively. Our lab is currently adapting the inattention paradigm employed in the current study to permit concurrent measurements of N2pc and VAN by presenting critical stimuli in lateralized locations. It will be important to determine whether the N2pc and/or CDA can be elicited by stimuli that are attended and held in working memory despite not having been consciously perceived (Woodman & Luck, 2003). It will also be important to test whether certain interactions between attention and perceptual representations always lead to conscious experience, and thus cannot be separately manipulated and measured (Prinz, 2012).

While many negative-going ERP components over the posterior scalp at intermediate latencies (~200–400 ms) have been reported in the literature, two of these may be particularly relevant to furthering progress on understanding the processes that are reflected by the VAN: the selection negativity (SN) and the reversal negativity (RN). The SN was initially described as an ERP difference between target and non-target stimuli (Harter & Aine, 1984; Hillyard & Anllo-Vento, 1998), however, it is now clear that the SN can be elicited by non-target stimuli that share features to the target stimuli (Azizian, Freitas, Parvaz, & Squires, 2006; Pitts & Martinez, 2014), and it may even reflect a bilateral variant of the N2pc for stimuli presented at fixation (N2pb; see Luck & Hillyard, 1994). Indeed, many “ERPology” experiments remain to be carried-out on the SN, N2pc, and VAN.

Similarly, in the bistable perception literature, a negative-going ERP component recorded bilaterally over the posterior scalp (from ~200 to 300 ms), called the “reversal negativity” (RN) has been consistently linked with subjective perceptual changes, both during binocular rivalry (Britz & Pitts, 2011) and with ambiguous figures (Kornmeier & Bach, 2004; Pitts, Nerger, & Davis, 2007). We previously speculated that the RN might reflect updates to the contents of conscious perception (Pitts & Britz, 2011). Direct comparisons between the RN and VAN have only been attempted once, to our knowledge (Intaite, Koivisto, Ruksenas, & Revonsuo, 2010), but this question remains open for future research. Finally, research from the auditory domain may help inform our understanding of the VAN (Snyder, Yerkes, & Pitts, 2015). For example, an “awareness related negativity” (ARN) has been reported for auditory stimuli (Dykstra, Cariani, & Gutschalk, 2017; Wiegand & Gutschalk, 2012), and the links between this component and the VAN remain largely unexplored.

4.6. VAN and current theories of consciousness

Can the current findings along with those using the same paradigm on shape and face stimuli (Pitts, Padwal, et al., 2014; Pitts et al., 2012; Shafto & Pitts, 2015) help distinguish between leading theories of consciousness? At first glance, these results may appear to favor early sensory theories of consciousness such as the recurrent processing theory (Lamme, 2003, 2006, 2010, 2015) over late cognitive theories such as global neuronal workspace theory (Dehaene, 2014; Dehaene & Changeux, 2011; Dehaene, Kerszberg, & Changeux, 1998; Dehaene & Naccache, 2001; Dehaene et al., 2006). Indeed the VAN occurs earlier in time than the P3b, and the current series of experiments suggests that the VAN correlates with awareness while the P3b correlates with task-relevance. However, upon closer inspection, this set of results is not completely consistent with either theory, while several aspects of each theory seem to be clearly on the right track. For example, recurrent processing theory predicts NCCs at even earlier latencies than the VAN, and more importantly posits that whenever localized recurrent processing is observed, phenomenal awareness is present, regardless of whether subjects are able to report anything about their experience. The orthographic effect observed in the current study, as well as the Nd1 (shape effect) in one of our previous studies (Pitts et al., 2012), were both present during inattention blindness. The time course of these components was in the 200–300 ms range, which is later in time than the initial feedforward sweep of processing in the visual system. While it is not possible to distinguish between feedforward and recurrent processing with ERPs, the timing of these differences are highly suggestive of feedback (recurrency) playing a role. If this is true, these results would suggest that recurrent processing may be necessary but not sufficient for perceptual awareness, i.e. recurrent processing

was present even during inattention blindness. While one might argue in some instances that inattention blindness is actually inattentional amnesia (stimuli were briefly experienced but then rapidly forgotten), this is highly unlikely in the current paradigm. It would be quite surprising if subjects in this paradigm consciously experienced the critical stimuli hundreds of times but then forget about them by the time they were queried in the post-phase awareness assessments (see also: Cohen & Dennett, 2011; Ward & Scholl, 2015).

Similarly, it is possible that global neuronal workspace theory is correct in general, but has proposed at least one incorrect neural marker of workspace activity (P3b). In this case, the VAN may index the initial attentional boost that is required for perceptual representations to connect with the global workspace. Indeed, work on inattention blindness is largely consistent with global workspace theory in terms of the attentional requirements of consciousness (Dehaene et al., 2006). In this view, the early stimulus-specific effects (shape effect, N170, and orthographic effect) would reflect pre-conscious perceptual processing, and the VAN would be associated with cognitive access. After all, subjects in our inattention experiments were able to report what they saw at the end of the phase, and thus must have stored this perceptual information in memory to allow for the delayed report. Further research that combines this inattention paradigm with other brain measures such as fMRI are currently underway and may help test some of the other proposed signatures of global neuronal workspace activity such as wide-spread fronto-parietal activation.

Unfortunately, the VAN as currently understood cannot distinguish between existing theories of consciousness. The VAN might reflect a particular type of recurrent processing that is necessary and sufficient for awareness (Lamme, 2015), the initial entry of information into the global neuronal workspace (Dehaene, 2014), a specific type of information integration (Tononi & Koch, 2015), a perceptual model of attention (Graziano, 2013), attention to intermediate-level representations (Prinz, 2012), or an attentional probe of the multiple drafts (Dennett, 1991). Moving forward, it will be important to develop more refined and testable theories as well as new experimental paradigms that are better able to distinguish between theories.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.concog.2017.04.009>.

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