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ORIGINAL ARTICLE

When Conflict Cannot be Avoided: Relative Contributions of Early Selection and Frontal Executive Control in Mitigating Stroop Conflict

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Sirawaj Itthipuripat and Sean Deering both Equally contributed.

Abstract

When viewing familiar stimuli (e.g., common words), processing is highly automatized such that it can interfere with the processing of incompatible sensory information. At least two mechanisms may help mitigate this interference. Early selection accounts posit that attentional processes filter out distracting sensory information to avoid conflict. Alternatively, late selection accounts hold that all sensory inputs receive full semantic analysis and that frontal executive mechanisms are recruited to resolve conflict. To test how these mechanisms operate to overcome conflict induced by highly automatized processing, we developed a novel version of the color-word Stroop task, where targets and distractors were simultaneously flickered at different frequencies. We measured the quality of early sensory processing by assessing the amplitude of steady-state visually evoked potentials (SSVEPs) elicited by targets and distractors. We also indexed frontal executive processes by assessing changes in frontal theta oscillations induced by color-word incongruency. We found that target- and distractor-related SSVEPs were not modulated by changes in the level of conflict whereas frontal theta activity increased on high compared to low conflict trials. These results suggest that frontal executive processes play a more dominant role in mitigating cognitive interference driven by the automatic tendency to process highly familiar stimuli.

Key words: attention, conflict, frontal theta, SSVEP, Stroop

Introduction

Distraction caused by the inadvertent processing of task-irrelevant information, particularly when that information is

highly familiar and automatically analyzed, interferes with the speed and efficiency of decision-making (Stroop 1935; Jensen and Rohwer 1966; Pashler 1984; Lavie and Cox 1997; Wolfe 1998;

Hickey et al. 2010; Anderson et al. 2011; Eckstein 2011; Awh et al. 2012; Itthipuripat et al. 2015). When task-relevant and task-irrelevant information can be differentiated based on spatial position or low-level features (e.g., orientation and color) selective attention can facilitate decision-making by modulating the gain of sensory responses in visual cortex to bias processing in favor of the relevant stimulus (Cherry 1953; Broadbent 1958; Treisman 1969; Moran and Desimone 1985; Hillyard and Anlo-Vento 1998; McAdams and Maunsell 1999; Treue and Martinez-Trujillo 1999; Reynolds et al. 2000; Martínez-Trujillo and Treue 2002; Duncan et al. 2003; Störmer et al. 2009; Scolari et al. 2012; Störmer and Alvarez 2014; Itthipuripat, Ester et al. 2014; Itthipuripat, Garcia et al. 2014; Mayo and Maunsell 2016). Importantly, the magnitude of these early sensory modulations is closely related to behavioral performance (Mangun and Hillyard 1988; Andersen et al. 2012; Störmer et al. 2009, 2013; Itthipuripat and Serences 2016; Luo and Maunsell 2015; Itthipuripat, Garcia et al. 2013, Itthipuripat, Ester et al. 2014, Itthipuripat, Cha et al. 2017, 2018). While this type of “early selection” is supported by data from behavioral tasks that require the selective processing of low-level sensory features, the extent to which modulations of early sensory processing can support the resolution of conflict caused by highly-ingrained expectations is still in question. For example, in the classic Stroop and Eriksen flanker paradigms, competition arises because extensive experience with reading makes it difficult to ignore semantic information that is incompatible with other visual features (Stroop 1935; Eriksen and Eriksen 1974). In these situations, early selective attention to the task-relevant sensory stimulus might mitigate subsequent post-perceptual conflict by preventing or attenuating any semantic analysis and response planning associated with task-irrelevant stimuli (c.f., Coste et al. 2011; Appelbaum et al. 2011, 2012; Zavala et al. 2013).

Contrary to the early selection account, interference due to conflicting information is sometimes observed even when the conflicting information is presented at an unattended location or when it is rendered subjectively invisible via visual masking (Nieuwenhuis et al. 2001; Sumner et al. 2007; van Gaal et al. 2008, 2010, 2011; D’Ostilio and Garraux 2012; Jiang et al., 2016; Padro et al. 2015). These findings suggest that selective sensory processing may not play a substantive role in filtering out highly familiar and easily processed conflicting information before it reaches post-perceptual stages. This is more in line with “late selection” accounts, which posit that both incoming relevant and distracting sensory inputs receive extensive semantic analyses before response selection (Deutsch and Deutsch 1963; Duncan 1980; Yantis and Johnston 1990). Under this scenario, we hypothesized that frontal executive control networks are recruited to monitor and resolve conflict after the conflicting information has already been analyzed (Carter et al. 1998; Adelman et al. 2002; Botvinick et al. 1999, 2001, 2004; van Gaal et al. 2008, 2010, 2011; Cavanagh and Frank 2014).

In the present study, we evaluated the relative contributions of the early and late selection mechanisms to resolving cognitive conflict. We combined a stimulus-frequency tagging technique with a classic color-word Stroop paradigm (Stroop 1935; Jensen and Rohwer 1966), where task-relevant color-bar targets and task-irrelevant letter-string distractors were flickered at different frequencies (Fig. 1a). While human subjects were performing this task, we recorded scalp electroencephalography data (EEG), which allowed us to examine selective modulations of early visual responses via changes in steady-state visually evoked potentials (SSVEPs) elicited by targets and distractors

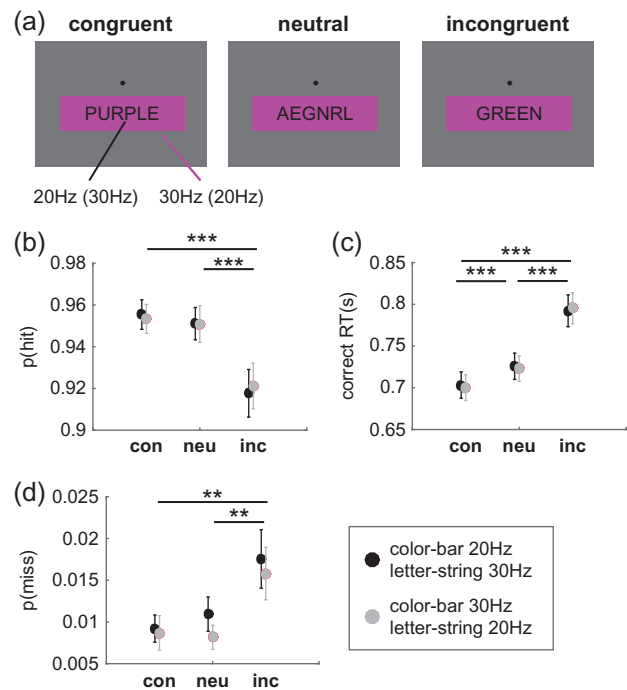


Figure 1. Task design and behavioral results. (a) An adapted version of the classical color-naming Stroop task, where the color-bar (task-relevant target) and the letter-string stimuli (task-irrelevant distractor) were flickered at different frequencies (20 Hz and 30 Hz, respectively and vice versa). (b) Hit rates, (c) correct RTs, and (d) miss rates differed across congruency conditions but did not differ across blocks where flicker-frequencies assigned to the color-bar and letter-string stimuli were counterbalanced. ** and *** show significant pair-wise differences between congruency conditions with P 's < 0.01 and <0.001. The data were averaged across all 30 subjects. Error bars show ± 1 within-subject SEM.

(Nordia et al. 2015). Following previous studies, we also measured frontal theta activity (4–7 Hz) as an index of the activation of frontal executive control mechanisms recruited by cognitive conflict (Cavanagh et al. 2011, 2012; Cavanagh and Frank 2014).

To the extent that filtering happens early in processing, we should observe enhanced SSVEPs for targets (color bars) and reduced SSVEPs for highly familiar distractors (i.e., letter strings). There should be minimal modulations in frontal theta band power, since early sensory modulations should prevent the semantic analyses of distractors and corresponding cognitive conflict from occurring. However, if cognitive conflict is resolved primarily via late selection mechanisms, there should be little modulation of early visual SSVEPs and we should instead observe an increase in frontal theta power in response to stimulus conflict.

Materials and Methods

Subjects

Thirty-one neurologically healthy human volunteers (13 females, 4 left-handed, 18–44 years old) with normal or corrected-to-normal vision were recruited from the University of California, San Diego (UCSD) community. Each volunteer provided written informed consent in accordance with UCSD Institutional Review Board guidelines (IRB#110 176), and the experiment was conducted under the protocol that followed the Declaration of Helsinki. Subjects were compensated \$15 per hour for participation in the study. Data from one subject were

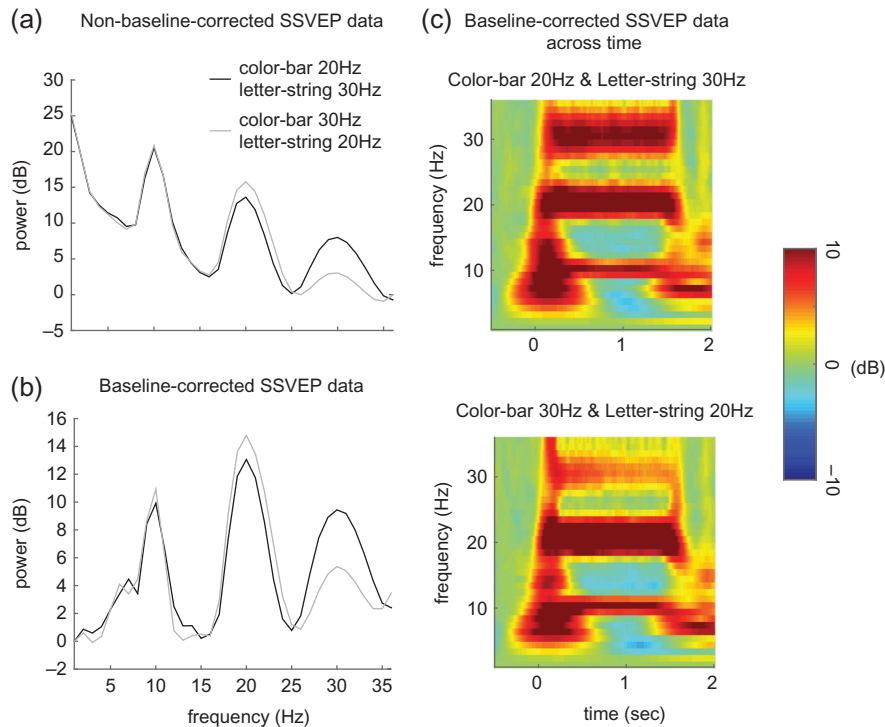


Figure 2. Steady-state visually evoked potentials (SSVEPs) elicited by the flickering color-bar and letter-string stimuli obtained from the occipital electrodes. The data were averaged across all 30 subjects. (a) The non-baseline-corrected power spectrums from 0 to 1500 ms stimulation period show the $1/f$ pattern with two SSVEP peaks at 20 and 30 Hz for both types of stimulus-frequency assignments. (b) Same as (a) but the data were baseline-corrected to remove the $1/f$ noise. (c) Same as (b) but plotted across each time point.

excluded due to excessive EEG blinks, eye and head movement artifacts (>84% of trials), leaving data from 30 subjects in the final behavioral and EEG analyses.

Stimuli and Experimental Design

Stimuli were presented using MATLAB (Mathworks Inc., Natick, MA) and the Psychophysics Toolbox (version 3.0.8; Brainard, 1997; Pelli, 1997) on a PC running Microsoft Windows XP. Subjects were seated 60 cm from a CRT monitor (with a dark gray background of $4.11 \text{ cd/m}^2 \pm 0.12 \text{ SD}$, 60 Hz refresh rate) in a sound-attenuated and electromagnetically shielded chamber (ETS Lindgren). The entire experiment (EEG preparation, experimental tasks, and breaks) lasted approximately 2-2.5 h.

Like many previous Stroop studies that required manual responses instead of verbal responses (e.g., Appelbaum et al. 2012; Krebs et al. 2010, 2013; van den Berg et al. 2014; Donohue et al. 2013, 2016), subjects first underwent a stimulus-response mapping task in which they learned to associate the physical colors of color-bar stimuli (i.e., green, yellow, orange, and purple with RGB values of [0 170 0], [173 145 0], [220 120 0], and [230 0 255], respectively; iso-luminance of $14.10 \text{ cd/m}^2 \pm 0.72 \text{ SD}$) with 4 buttons on a numeric keypad (“7”, “4”, “1”, and “0”), which they pressed using their index, middle, ring, and little fingers of their right hand, respectively. Each trial began with the presentation of the color-bar stimulus (size = $4.30^\circ \times 21.70^\circ$ visual angle), which appeared 2.39° visual angle below a central black fixation dot (radius = 0.38° visual angle). Each color-bar stimulus was presented for 1000 ms, and participants were instructed to report its physical color as quickly and accurately as possible before the stimulus disappeared. 300 ms following the stimulus offset, subjects received feedback on their

performance for that trial (“C” for correct responses, “I” for incorrect responses, and “M” for misses) for 200 ms. The inter-trial interval was randomly drawn from the uniform distribution of 500–1500 ms. Each subject completed one block of the stimulus-response mapping task, which consisted of 144 trials in total and lasted approximately 6 min (36 trials per each color; trial order was pseudo-randomized).

Immediately after completing the stimulus-response mapping task, subjects performed an adapted version of the color-naming Stroop task (Fig. 1a). They were instructed to fixate at a central fixation point while attending to the color-bar stimulus and ignoring the letter-string stimulus (all letters were capitalized; font type = “Arial”; font size = 3.34° visual angle in height), which appeared over of the color-bar stimulus. The letter-string stimulus could be a non-word (i.e., neutral; e.g., color-letter = purple-AEGNRL) or a word that was semantically congruent (e.g., color-letter = purple-PURPLE) or incongruent (e.g., color-letter = purple-GREEN) with respect to the physical color of the color-bar stimulus. To concurrently monitor sensory responses evoked by the color-bar and letter-string stimuli, the two stimuli were flickered at different frequencies for 1500 ms (20 Hz color-bar and 30 Hz letter-string or 30 Hz color-bar and 20 Hz letter-string; the frequency assignments were counterbalanced block-by-block). This stimulus-frequency-tagging technique allowed us to obtain steady-state visually evoked potentials (SSVEPs) elicited by the color-bar and letter-string stimuli (relevant and irrelevant stimuli, respectively). The flicker frequencies of 20 Hz and 30 Hz were chosen based on previously established methods in order to restrict SSVEP measurements to entrained activity in the visual cortex and to avoid spectral overlap with intrinsic theta and alpha oscillations (see Fig. 2; e.g., Müller et al. 1998; O’Connell et al. 2012; Bridwell et al. 2013; Garcia et al. 2013; Itthipuripat,

Garcia et al. 2013; Itthipuripat, Garcia et al. 2014). Participants were instructed to report the physical color of the color-bar stimulus as quickly and accurately as possible. The size, luminance and RGB values of the color-bar stimuli, feedback duration, and ITI were identical to those used in the stimulus-response mapping task. Subjects completed 4 blocks of the Stroop task where color bar and letter-string stimuli were flashed at 20 Hz and 30 Hz and 4 blocks where they were flashed at 30 Hz and 20 Hz (the order of block types were counterbalanced across subjects). Each block contained 144 trials (48 congruent trials, 48 neutral trials, and 48 incongruent trials), and each block lasted about 7.2 min.

Statistical Analysis of Behavioral Data

For each subject, we computed hit rates, mean response times on correct trials (correct RTs), and miss rates on congruent, neutral, and incongruent trials separately for the blocks that had different frequency assignments to the color-bar and letter-string stimuli. The within-subject standard error of the mean (SEM) was also calculated by removing the mean value of each congruency condition and each frequency assignment from the individual subject data before computing the SEM (Loftus and Masson, 1994). We present within-subject instead of between-subject SEM so that the data presentation aligns with within-subject statistical analyses we performed. Specifically, we performed repeated-measures ANOVAs with within-subject factors of congruency and frequency assignment to test the main effects of these two factors on hit rates, correct RTs, and miss rates. Post-hoc paired t-tests (2-tailed) were then used to test differences in hit rates, correct RTs, and miss rates between the congruent and incongruent conditions, between the congruent and neutral conditions, and between the neutral and incongruent conditions, respectively. We used the Bonferroni method to correct for multiple comparisons with the corrected threshold of 0.05.

EEG Data Acquisition

EEG data were recorded with a 64 + 8 electrode Biosemi ActiveTwo system (Biosemi Instrumentation) using a sampling rate of 512 Hz. Two reference electrodes were placed on the left and right mastoids. Blinks and vertical eye movements were monitored using 4 external electrodes affixed above and below the eyes. Horizontal eye movements were monitored using another pair of external electrodes affixed near the outer canthi of the left and right eyes. The EEG data were referenced on-line to the CMS-DRL electrode and the data offsets in all electrodes were maintained below 20 μ V (a standard criterion for this active electrode system).

EEG Data Preprocessing and Analysis

EEG data were preprocessed using a combination of EEGLab11.0.3.1b (Delorme and Makeig, 2004) and custom MATLAB scripts. The continuous EEG data were first re-referenced to the algebraic mean of the left and right mastoid electrodes, then filtered by applying 0.25-Hz high-pass and 55-Hz low-pass Butterworth filters (third order). Next, the continuous EEG data were segmented into epochs extending from 1000 ms before to 2500 ms after trial onset. Independent component analysis (ICA) was then applied to remove prominent eye blink artifacts (Makeig et al. 1996). Trials containing residual eye movements, muscle activity, drifts, and other artifacts were removed using threshold

rejection and visual inspection, which resulted in the removal of $7.79\% \pm 8.87$ SD of trials across all 30 subjects.

Next, we wavelet-filtered the artifact-free EEG data on a trial-by-trial basis using Gaussian filters centered at 1–40 Hz (1-Hz steps) with a fractional bandwidth of 0.2. This method yielded complex coefficients of the trial-by-trial EEG data in each of these frequency bands (see similar methods in Canolty et al. 2007; Roach and Mathalon 2008; Itthipuripat, Wessel et al. 2013; Freeman et al. 2016). We first computed SSVEP responses across all experimental conditions by averaging the complex coefficients across trials for each frequency and then computed the power of the trial-averaged complex coefficients using the squared complex magnitude. We then transformed the SSVEP into dB units. Note that averaging the complex numbers before calculating power yields the same result as averaging the time-domain EEG data across trials and then applying the wavelet filter. Finally, we baseline-corrected SSVEP power across time for each condition by subtracting the mean amplitude 500–200 ms before stimulus onset to remove 1/f noise. As shown in Figure 2, we observed SSVEP signals peaking at the driving stimulus frequencies (20 Hz and 30 Hz) for both types of stimulus-frequency pairings. Note that we also observed high alpha power in all plots in Figure 2, which likely reflects an alpha phase reset induced by stimulus onset. In turn, the alpha phase reset that is time-locked to the onset of the stimulus renders alpha oscillations partially phase-locked to the stimulus presentation. This observation has been made in several past studies, where the visual stimuli were large and centrally presented (e.g., Ding et al. 2006; Sauseng et al. 2007). Importantly, our SSVEP analysis should be minimally confounded by this alpha reset because the driving stimulus frequencies were much higher than alpha frequencies.

After verifying that we obtained robust SSVEP responses (Fig. 2), we next computed the SSVEP response separately in each experimental condition. First, the trial-by-trial complex coefficients (obtained from the wavelet filter described above) at the driving frequencies of 16–24 Hz (centered at the 20 Hz flicker frequency) and 26–34 Hz (centered at the 30 Hz flicker frequency) for individual trials were sorted into bins based on the driving stimulus (color-bar or letter-string) and semantic congruence (congruent, neutral, or incongruent). We included a range of frequencies around the driving SSVEP frequency so that the number of frequency bins matched that the number of frequency bins in the theta analysis (see below). For each congruency condition, the data from correct trials were also sorted by RTs into fast and slow bins using a median split. The sorted complex coefficients were then averaged across trials and the power of SSVEP signals was computed based on the squared complex magnitude and transformed into dB units. Then, we baseline-corrected SSVEP amplitude across time for each condition by subtracting the mean amplitude 500–200 ms before the stimulus onset.

To obtain the power of endogenous theta oscillations in the EEG data, we computed the power of the coefficient values in dB units on a trial-by-trial basis from 1 to 9 Hz. Next, the single-trial data were sorted based on congruency and RT, locked to stimulus onset, baseline-corrected from 500 to 200 ms before the stimulus onset, and averaged across trials in each experimental bin. In addition, to examine theta modulations around response onset, single trial theta data that were baseline-corrected were realigned to response onset and averaged across trials in each experimental bin. Because we displayed the stimuli at the center of the screen, the SSVEP, and theta data were obtained from the central occipital electrodes (O1, Oz, and O2) and central frontal electrodes (F1, Fz, and F2), respectively.

These electrodes have also been used as standard electrodes of interest to analyze SSVEP and theta data (Andersen et al. 2012; Cavanagh et al. 2011, 2012; Störmer et al. 2013; Itthipuripat, Wessel et al. 2013; Norcia et al. 2015; Freeman et al. 2016). The within-subject SEM of the SSVEP and theta data was also calculated by removing the mean power value of each congruency condition and each RT condition from the individual subject data before computing the SEM (Loftus and Masson, 1994).

Statistical Analysis of EEG Data

For statistical evaluation of the data, we performed cluster-based permutation testing via FieldTrip (Oostenveld et al., 2011; Maris and Oostenveld 2007). Using this statistical approach, the SSVEP and theta data were compared across the following conditions independently across frequencies and time points: fast incongruent versus fast congruent, fast incongruent versus fast neutral, fast neutral versus fast incongruent, slow incongruent versus slow congruent, slow incongruent versus slow neutral, slow neutral versus slow incongruent, slow versus fast incongruent, slow versus fast neutral, and slow versus fast congruent trials. Since the cluster-based permutation tests suggested no SSVEP changes in the direction predicted by the early selection account, we also performed post-hoc Bayes factor tests on the SSVEP data (Edwards et al. 1963; Wagenmakers 2007; Rouder et al. 2009; Rungtatsametaweemana et al. 2018). The reported Bayes factors indicate the probability of the data given H1 (i.e., there was a congruency or an RT effect in the expected direction according to the early selection account) relative to H0 (i.e., there was no congruency or RT effect in the expected direction). There is no fixed threshold to determine significance; however, a Bayes factor >3 generally indicates positive evidence in favor of H1, whereas a value <0.33 is generally considered evidence for H0.

Results

Behavioral Results

Consistent with many previous studies employing variants of the Stroop task, incongruent color-word pairings led to significant effects on hit rates, correct RTs, and miss rates ($F(2, 58)$'s = 23.91, 131.61, and 8.53, respectively, with all P 's < 0.001 (Fig 1b-s) (Stroop 1935; Jensen and Rohwer 1966; Liotti et al. 2000; West and Alain 2000; Zysset et al. 2001; Atkinson et al. 2003; Kane and Engle 2003; Hanslmayr et al. 2008; Huster et al. 2009; Coderre et al. 2011; Appelbaum et al. 2009, 2012; Caldas et al. 2012; Krebs et al. 2010, 2013; van den Berg et al. 2014; Donohue et al. 2013, 2016). Post-hoc t -tests revealed that hit rates in the incongruent condition were significantly lower than hit rates in the neutral and congruent conditions ($t(29)$'s = 5.84 and 4.85, respectively, both P 's < 0.001 , Bonferroni-corrected), with no significant difference between the congruent and neutral conditions ($t(29) = 0.97$, $P = 0.340$). Correct RTs in the incongruent condition were significantly longer than correct RTs in the neutral and congruent conditions ($t(29)$'s = 10.14 and 12.89, respectively, with both P 's < 0.001 , Bonferroni-corrected). Correct RTs in the neutral condition were also significantly longer than correct RTs in the congruent condition ($t(29) = 8.55$, $P < 0.001$, Bonferroni-corrected). Miss rates in the incongruent condition were also higher than miss rates in the neutral and congruent conditions ($t(29)$'s = 3.14 and 3.00, respectively, with both P 's < 0.01 , Bonferroni-corrected) with no difference between the neutral and congruent conditions ($t(29) = 0.55$, $P = 0.587$). In addition, there were no differences in hit rates, correct RTs, or miss

rates across trials that contained a 20-Hz flickering color-bar and 30-Hz flickering letter-string and trials that contained 30-Hz flickering color-bar and 20-Hz flickering letter-string ($F(1, 29)$'s = 0.03, 0.10, 1.80, P 's = 0.87, 0.76, and 0.19, respectively).

EEG Results

Target-Related and Distractor-Related SSVEPs

Overall, there were robust target-related and distractor-related SSVEPs that peaked at the driving stimulus flicker frequencies over occipital electrodes (Fig. 2). However, the SSVEP results are inconsistent with the early selection account, which predicts higher target-related SSVEP power and lower distractor-related SSVEP power on congruent trials compared to neural and incongruent trials and on fast incongruent trials compared to slow incongruent trials. For the target-related SSVEPs, there were no significant SSVEP differences across fast congruent, fast neutral, and fast incongruent trials that passed the corrected significance threshold using the cluster-based permutation method (Fig. 3). For slow trials, there were also no differences between the incongruent and congruent trials or between the neutral and congruent trials. Although there was a significant difference in target-related SSVEP power between the slow incongruent and slow neutral trials, the SSVEP modulation was in the opposite direction compared to predictions of the early selection account. In addition, we observed no difference in target-related SSVEP power between fast and slow trials from any congruency condition. Similarly, for the distractor-related SSVEPs, we observed no difference across different congruency conditions on either fast or slow trials (Fig. 4). Finally, there were no differences in target-related SSVEP power between fast and slow trials from any congruency condition.

Frontal Theta Activity

Overall frontal theta results are consistent with the late selection account, which predicts a general increase in frontal theta power in response to conflict on slow incongruent trials (Figs 5 and 6). First, for fast trials, we observed no differences between mid-line frontal theta power across the congruent, neutral, and incongruent conditions for both stimulus-locked and response-locked data. In contrast, on slow trials, we found that frontal theta power increased in the incongruent compared to the neutral and congruent conditions. These results were significant only for the stimulus-locked but not in the response-locked analyses. This suggests that conflict-induced modulations of frontal theta power on slow incongruent trials compared to slow neutral and slow congruent trials were driven by stimulus-stimulus rather than stimulus-response conflict.

As predicted by the late selection account, we also observed increased frontal theta power on slow compared to fast incongruent trials. Like the results reported in the previous paragraph, this significant result was only found in the stimulus-locked but not in the response-locked data, suggesting that this frontal theta modulation in the incongruent condition was driven by stimulus-stimulus conflict rather than stimulus-response conflict. In addition, we found that frontal theta power increased on slow compared to fast neutral/congruent trials. However, the results were significant for both stimulus-locked and response-locked data, suggesting that the theta increase is also tied to stimulus-response conflict that may occur near response onset. These findings are consistent with the fact that there was no semantic conflict between color-bar and letter-string stimuli in the neutral and congruent conditions.

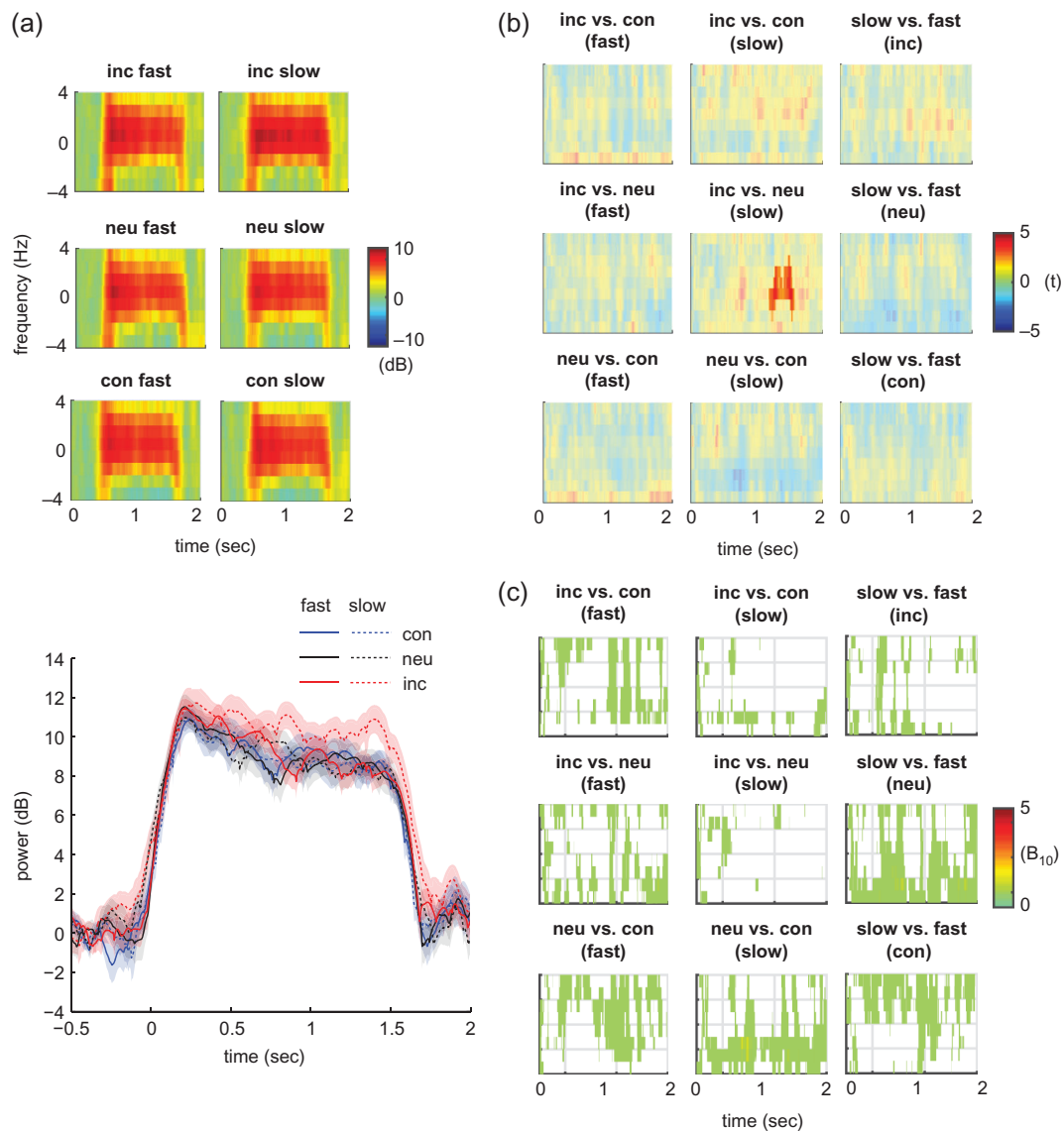


Figure 3. Steady-state visual evoked potentials induced by color-bar stimuli (target-related SSVEPs), averaged across all 30 subjects. (a-Top) Target-related SSVEP power from the mid-line occipital electrodes sorted into congruent, neutral, and incongruent conditions separately for fast and slow trials (left and right columns, respectively). Zero-Hz is the center of the stimulus flicker frequency. (a-Bottom) The SSVEP data at the flicker frequency shown in the top panel. Error bars show ± 1 within-subject SEM. (b) Statistical comparisons between congruency conditions in fast and slow trials as well as statistical comparisons between slow and fast trials for individual congruency conditions (left, middle, and right columns, respectively). The untinted areas show significant differences from cluster-based permutation tests with a corrected alpha threshold of 0.05 (Maris and Oostenveld 2007). Inconsistent with the early sensory modulation account, the target-related SSVEP power is not lower on slow incongruent compared to congruent, neutral, or fast incongruent trials. (c) Bayes factors suggest that that this null result is robust. We only plot Bayes factors for data points where the direction of SSVEP modulations match the prediction of the alternative hypothesis that is in support of the early selection account, i.e., white color presents data points where the modulation is going in the opposite direction to predictions of the early selection account or t values in (b) > 0 .

Discussion

The present study evaluated the relative contributions of early sensory modulation and frontal executive control to the efficiency of decision making in the face of cognitive conflict. We developed a novel version of the Stroop task where targets (i.e., color bars) and distractors (letter strings) were flickered at different frequencies to concurrently measure the modulations of target-evoked and distractor-evoked SSVEPs. We found no changes in target-related or distractor-related SSVEPs either as a function of congruency or RT in the predicted direction. Instead, we observed an increase in frontal theta power

induced by semantically incongruent stimuli on slow trials. Our results are thus inconsistent with early selection accounts and instead suggest a more dominant role of late frontal executive control in resolving cognitive conflict induced by the processing of highly familiar stimuli.

Even though we found robust behavioral interference that is comparable or larger than many previously reported attention studies that did find changes in SSVEPs, we observed a compelling null result of congruency and RT, counter to the early selection account (see a similar logic discussed in Rungratsametaweemana et al. 2018). Importantly, the null SSVEP results were not due to a lack of experimental power to elicit SSVEPs because we were able

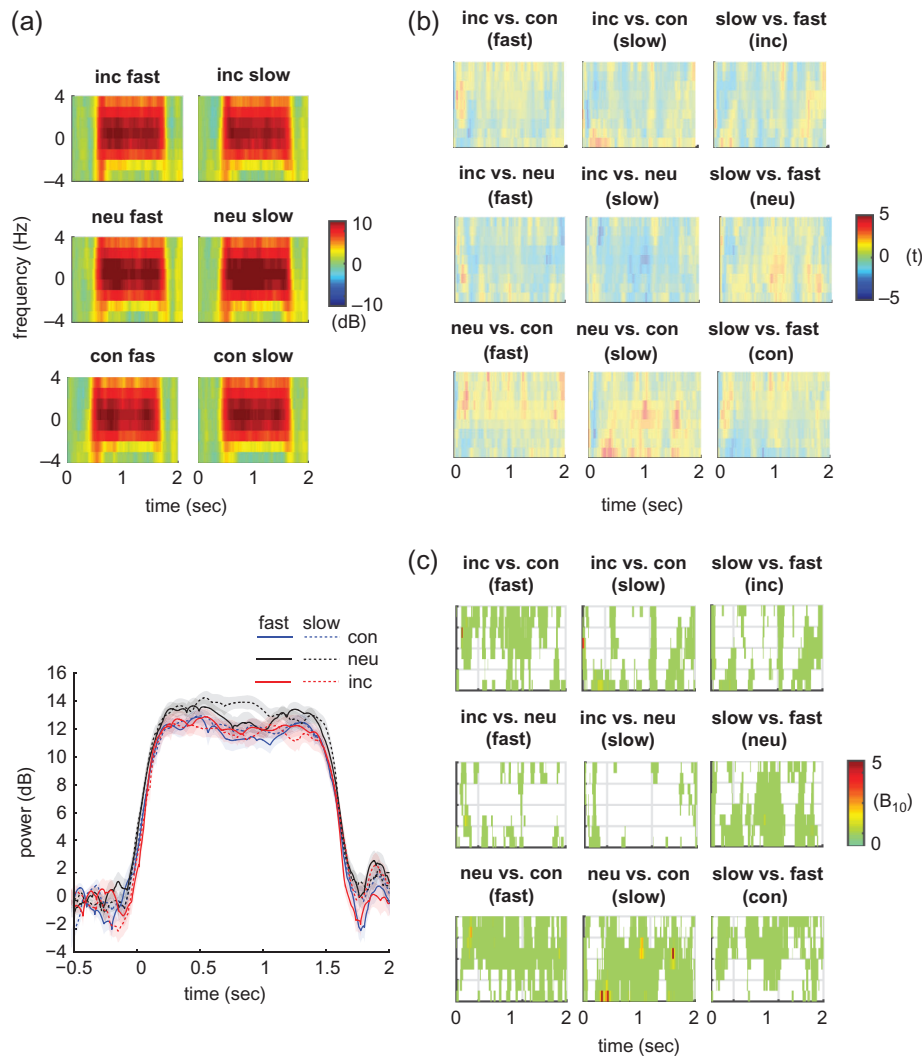


Figure 4. Steady-state visual evoked potentials induced by letter-string stimuli (distractor-related SSVEPs), averaged across all 30 subjects. (a-Top) Distractor-related SSVEP power from the mid-line occipital electrodes sorted into congruent, neutral, and incongruent conditions separately for fast and slow trials (left and right columns, respectively). Zero-Hz is the center of the stimulus flicker frequency. Zero-Hz is the center of the stimulus flicker frequency. (a-Bottom) The SSVEP data at the flicker frequency shown in the top panel. Error bars show ± 1 within-subject SEM. (b) Statistical comparisons between congruency conditions on fast and slow trials as well as statistical comparisons between slow and fast trials for individual congruency conditions (left, middle, and right columns, respectively). There is no significant difference in any of the comparisons based on cluster-based permutation tests with a corrected alpha threshold of 0.05 (Maris and Oostenveld 2007). Inconsistent with the early sensory modulation account, target-related SSVEP power is not higher on slow incongruent compared to congruent, neutral, or fast incongruent trials (c) Bayes factors suggest that the null results are robust. As in Figure 2, we only plot Bayes factors for data points where the direction of SSVEP modulations matches the prediction of the alternative hypothesis that is in support of the early selection account, i.e., white color presents data points where the modulation is going in the opposite direction to predictions of the early selection account or t values in (b) < 0 .

to obtain robust SSVEP signals for both targets and distractors, and they were also precisely tuned to their respective flicker frequencies (Figs 2, 3 and 4). Finally, the null result is also not likely due to general insensitivity of SSVEPs to early sensory modulations as many past studies have shown that selective attention alters the magnitude of SSVEP responses (Müller et al. 1998, 2003, 2006; Andersen et al. 2008; Andersen and Müller 2010; Störmer and Alvarez 2014; Itthipuripat, Garcia et al. 2014; Kim et al. 2007, 2011, 2017).

The null result here instead suggests a more dominant role for late selection when trying to attenuate the influence of highly-familiar and easily processed distractors (Deutsch and Deutsch 1963; Duncan 1980; Yantis and Johnston 1990). Since the full semantic analysis of the distractor is expected under late selection models, semantic incongruity between color bars and the

letter strings may not be avoidable and it cannot be mitigated early as the stimuli are being processed. Instead, our data suggest that the brain resolves such conflict by recruiting the frontal executive control network to carefully monitor conflict as it is occurring so that appropriate responses can be selected (Carter et al. 1998; Botvinick et al. 1999, 2001, 2004; Cavanagh and Frank 2014). Consistent with this idea, we observed an increase in frontal theta amplitude in the slow incongruent condition—an index for frontal executive control induced by cognitive conflict (Cavanagh et al. 2011; Cavanagh and Frank 2014). Moreover, this modulation of frontal theta was significant only in the stimulus-locked but not in the response-locked data (Figs 5 and 6), consistent with the idea that the increased theta on incongruent trials is driven by stimulus-stimulus rather than stimulus-response conflict, which may occur in other types of tasks (e.g., Eriksen flanker and Simon

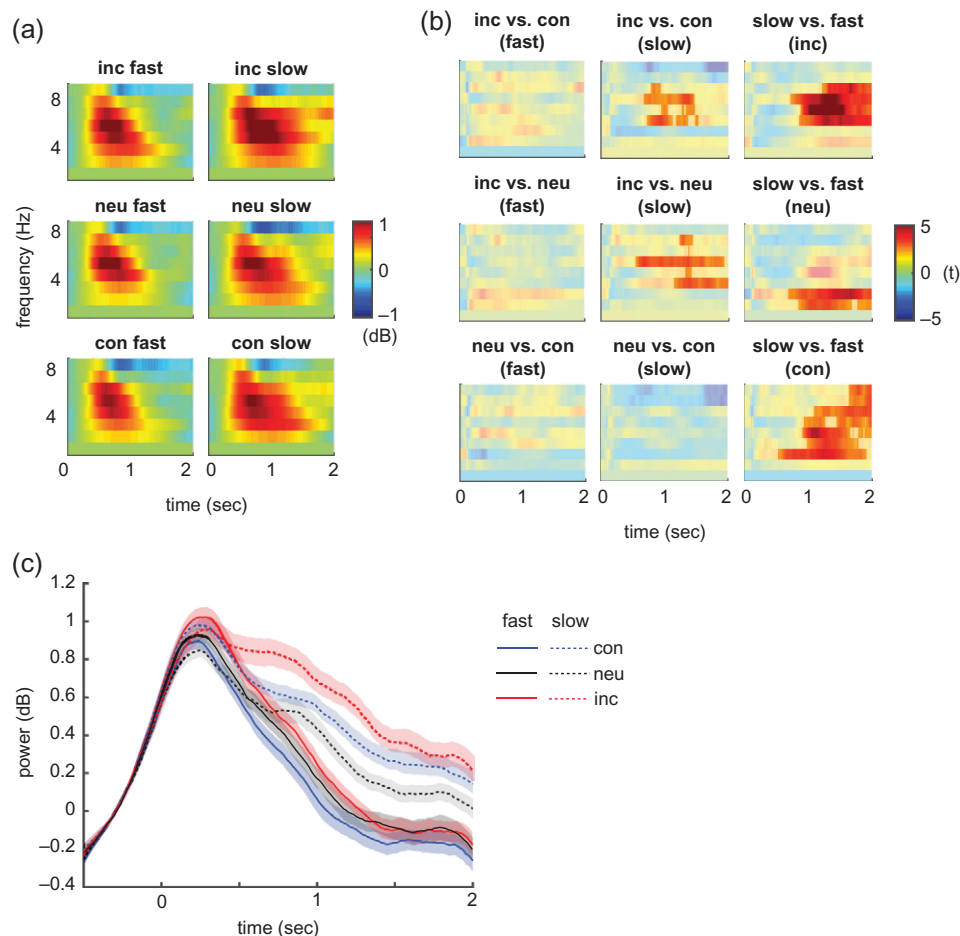


Figure 5. Stimulus-locked frontal theta power averaged across 30 subjects. (a) The event-related time frequency plots showing mid-line frontal theta oscillation induced by congruent, neutral, and incongruent conditions in fast and slow trials (left and right columns, respectively). (b) Statistical comparisons between congruency conditions on fast and slow trials as well as statistical comparisons between slow and fast trials for individual congruency conditions (left, middle, and right columns, respectively). The untinted areas show significant differences based on cluster-based permutation tests with a corrected alpha threshold of 0.05 (Maris and Oostenveld 2007). Frontal theta power is higher on incongruent compared to congruent and neutral neutral conditions only in slow trials. Theta power is generally higher on slower than fast trials irrespective of congruency condition. (c) same as (a) but the data were averaged across 3–8 Hz. Error bars show ± 1 within-subject SEM.

tasks). That said, interpreting this null result should be done with caution. While the lack of SSVEP modulations suggests that sensory inputs in early visual cortex are unaltered by cognitive conflict, relatively early selection may still happen after processing in early visual cortex but before the operation of late selection mechanisms that we assume are mediated by frontal cortex.

Even though there was no semantic conflict on the slow congruent/neutral trials, we also observed frontal theta increases in these conditions. However, unlike the RT effect on the frontal theta amplitude on incongruent trials, the theta increases on slow congruent/neutral trials happened at a lower and non-overlapping theta frequency and occurred around the time of response onset (Fig. 6). This suggests that increased theta in these conditions might be due to other attributes of frontal executive function including error detection and response inhibition occurring around the time of motor execution (D'Esposito et al. 1995; Curtis and D'Esposito 2003; Kane and Engle 2003; Ridderinkhof et al. 2004; Cavanagh et al. 2011, 2012; Itthipuripat, Wessel et al. 2013; Aron et al. 2004, 2014; Cavanagh and Frank 2014; Wessel and Aron 2017).

Interestingly, the pattern of frontal theta results is similar to the modulations of theta activity recorded from the subthalamic nucleus (STN) in humans performing an Eriksen flanker

task (Zavala et al. 2013). The similarity of the results recorded in scalp electrodes over frontal cortex and modulations recorded directly from the STN raises the possibility that areas of frontal cortex and the basal ganglia rely on long-range communication operating in theta frequencies to support their putative functions in cognitive control and cognitive interference tasks (cf. Cavanagh et al. 2011; Itthipuripat, Wessel et al. 2013; Cavanagh and Frank 2014; Zavala et al. 2013, 2014, 2015). In addition, Zavala et al. (2013) noted an absence of differences in STN theta activity and RTs between fast incongruent trials and all congruent trials, which they postulated might be due to subjects successfully suppressing irrelevant sensory signals on fast incongruent trials, thus reducing conflict generated by the distractors. However, in the present study, no changes in SSVEP signals were observed across these conditions, calling into question this interpretation of their data and suggesting instead that conflict is resolved by late selection and frontal control mechanisms. Our results are thus in agreement with the idea that the speed and efficiency of decision making during higher-order cognitive conflict is more reliant upon interactions between the frontal executive control network and sub-regions of the basal ganglia than modulations of low-level sensory processing.

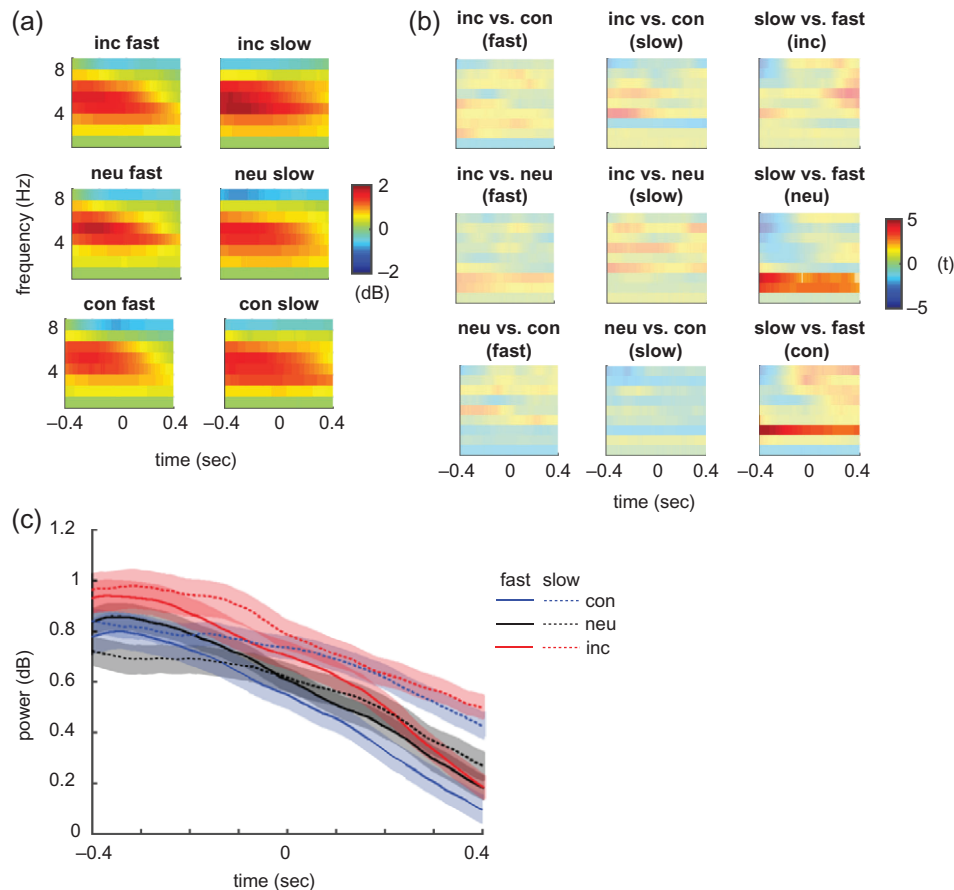


Figure 6. Response-locked frontal theta power averaged across 30 subjects. (a) The data are sorted into congruent, neutral, and incongruent conditions separately for fast and slow trials (left and right columns, respectively). (b) Statistical comparisons between congruency conditions on fast and slow trials as well as statistical comparisons between slow and fast trials for individual congruency conditions (left, middle, and right columns, respectively). The untinted areas show significant differences based on cluster-based permutation tests with a corrected alpha threshold of 0.05 (Maris and Oostenveld 2007). No difference was observed across congruency conditions in the response-locked data. Response-locked theta power is higher on slow compared to fast trials only in neutral and congruent conditions, but not in the incongruent condition. (c) same as (a) but the data were averaged across 3–8 Hz. Error bars show ± 1 within-subject SEM.

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Notes

S.I. conceived and implemented the experiments, analyzed the data, wrote the first draft of the manuscript, and co-wrote the manuscript. S.D. collected and analyzed the data and co-wrote the manuscript. J.T.S. conceived and supervised the project and co-wrote the manuscript. We thank Greg L. Appelbaum and Nuttida Rungratsameetaweemana for useful comments. *Conflict of Interest:* None declared.

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