

Steady-state Signatures of Visual Perceptual Load, Multimodal Distractor Filtering, and Neural Competition

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Abstract

■ The perceptual load theory of attention posits that attentional selection occurs early in processing when a task is perceptually demanding but occurs late in processing otherwise. We used a frequency-tagged steady-state evoked potential paradigm to investigate the modality specificity of perceptual load-induced distractor filtering and the nature of neural-competitive interactions between task and distractor stimuli. EEG data were recorded while participants monitored a stream of stimuli occurring in rapid serial visual presentation (RSVP) for the appearance of previously assigned targets. Perceptual load was manipulated by assigning targets that were identifiable by color alone (low load) or by the conjunction of color and orientation (high load). The RSVP task was performed alone and in the presence of task-irrelevant visual and auditory distractors. The RSVP stimuli, visual distractors,

and auditory distractors were “tagged” by modulating each at a unique frequency (2.5, 8.5, and 40.0 Hz, respectively), which allowed each to be analyzed separately in the frequency domain. We report three important findings regarding the neural mechanisms of perceptual load. First, we replicated previous findings of within-modality distractor filtering and demonstrated a reduction in visual distractor signals with high perceptual load. Second, auditory steady-state distractor signals were unaffected by manipulations of visual perceptual load, consistent with the idea that perceptual load-induced distractor filtering is modality specific. Third, analysis of task-related signals revealed that visual distractors competed with task stimuli for representation and that increased perceptual load appeared to resolve this competition in favor of the task stimulus. ■

INTRODUCTION

A long-standing debate in the attention literature has focused on the level of processing at which attentional selection occurs. Early selection theories argued that perceptual systems select information at the earliest levels of processing (e.g., Broadbent, 1958), whereas late selection theories posited that essentially all information is processed to a semantic level and only then filtered by some attentional mechanism (e.g., Deutsch & Deutsch, 1963). There is evidence in favor of both early and late selection, but neither class of theories adequately accounts for all empirical results (Driver, 2001). A more contemporary theory of selective attention offers a resolution to the locus of selection debate. Perceptual load theory proposes that the locus of selection is not fixed but is instead dependent on the perceptual demands of a task (Lavie, 1995; Lavie & Tsai, 1994). The term *perceptual load* refers to the attentional demands required to make a perceptual discrimination (Lavie, 1995, 2005; Lavie & De Fockert, 2003; Lavie & Tsai, 1994). The theory suggests that a task with low perceptual load imposes little demand on attention and leaves attentional resources available to fully process other stimuli and, in this case, selection occurs late in processing. On the other hand, high perceptual load imposes greater demands on attention and leaves fewer at-

tentional resources available to process other task-irrelevant stimuli. Thus, under high load, selection occurs early in processing (i.e., at the sensory level). For example, one common manipulation of perceptual load compares the detection of a feature singleton (e.g., color) versus a feature conjunction (e.g., color and orientation). Detecting a single feature is considered to be of low perceptual load, and therefore any task-irrelevant distractor stimuli are still fully perceptually processed. However, the detection of a feature conjunction is considered to be of high perceptual load, requires more attentional resources, and leaves fewer resources available for the processing of irrelevant distractors.

Much of the behavioral evidence in favor of perceptual load theory has come from response competition paradigms (Lavie & Cox, 1997; Lavie, 1995; Lavie & Tsai, 1994). In these experiments, a speeded choice response must be made to discriminate two target stimuli (e.g., “X” or “Z”). The targets are flanked by response-congruent or response-incongruent distractor stimuli. For example, in a configuration containing the target stimulus “Z,” a flanking “Z” would be response compatible whereas a flanking “X” would be response incompatible. The typical result in such a paradigm reveals a significant incompatibility effect (Eriksen & Eriksen, 1974) such that response-incompatible distractors slow the target discrimination response compared with response-compatible distractors. However, studies of perceptual load have found that the magnitude (or even existence) of such interference effects is depen-

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dent on the level of perceptual load imposed by the task. Specifically, if the perceptual load of the task is increased, then little to no interference effect is found (Lavie & Cox, 1997; Lavie, 1995; Lavie & Tsal, 1994). In contrast, under conditions of low perceptual load, typical interference effects are present. Together, these results suggest that early sensory-level filtering of distractors occurred under conditions of high load, whereas distractors were fully processed under low-load conditions.

Neurophysiological studies also support the idea that perceptual load decreases sensory-level processing of task-irrelevant information. ERP studies have shown that increasing the perceptual load of a task causes a reduction in the amplitude of the early visual P1 component to irrelevant distractor stimuli (Handy, Soltani, & Mangun, 2001; Handy & Mangun, 2000). These results are indicative of increased task-irrelevant distractor filtering within extrastriate visual areas under high-load conditions. A number of neuroimaging studies have also demonstrated load-dependent reductions in brain activity in response to irrelevant visual distractor stimuli (Schwartz et al., 2005; Pinsk, Doniger, & Kastner, 2004; O'Connor, Fukui, Pinsk, & Kastner, 2002). Rees, Frith, and Lavie (1997) showed that increasing the visual perceptual load of a task caused a reduction in the processing of task-irrelevant background motion in human MT+. Studies using functional retinotopic mapping have further demonstrated that increased perceptual load results in increased filtering of peripheral visual distractor throughout the visual hierarchy (i.e., V1, V2, V3, V4; Schwartz et al., 2005; Pinsk et al., 2004; O'Connor et al., 2002).

Behavioral and neurophysiological studies have provided considerable support for the general propositions of perceptual load theory (i.e., that increased perceptual load reduces sensory-level processing of within-modality distractors). However, a number of critical questions regarding the limitations and neural mechanisms of perceptual load remain.

Is Distractor Filtering Modality Specific?

One question that persists within the perceptual load literature is whether perceptual load within one sensory modality affects the processing of distractors within another modality. Some psychophysical evidence has suggested that perceptual load within one modality has no bearing on the processing of distractors in another. Rees, Frith, and Lavie (2001) demonstrated that the perceived duration of the MAE induced by irrelevant visual background motion was significantly reduced by increased load in a visual task but was unaffected by manipulations of load in an auditory task. This suggested that the effects of perceptual load were confined to the modality within which load was manipulated (i.e., perceptual load-induced distractor filtering is modality specific). However, another study using similar perceptual measures but using very different load tasks found that increased load in an auditory task reduced MAE duration with the same

efficacy as that of a visual task, suggesting that the effects of perceptual load are cross modal (i.e., perceptual load-induced distractor filtering is modality general; Houghton, Macken, & Jones, 2003). Such contradictory results are also apparent in neuroimaging studies. Rees et al. also conducted a neuroimaging study and found that load in a visual task modulated the response of MT+ to irrelevant background motion whereas increased load in an auditory task had no effect on activity within MT+. In contrast, Berman and Colby (2002) reported that increased perceptual load in both visual and auditory tasks could modulate the response to irrelevant background motion within MT+. Simple methodological differences are likely the source of some discrepancies in the literature (Lavie, 2005), but the existence (or otherwise) of cross-modal effects of perceptual load remains unresolved.

Do Irrelevant Distractors Affect the Processing of Task Stimuli?

To date, examinations of perceptual load theory have concentrated almost exclusively on how increased perceptual load affects the processing of distractors. Although certainly an imperative question, it explores only one side of the target–distractor relationship. It is equally important to understand how the presence of distractors affects the processing of task stimuli and how that interaction is influenced by manipulations of perceptual load.

A neural mechanism likely to contribute to the effects of distractors on task stimulus processing, at least within the visual modality, is that of neural competition. Stimuli that fall within the same visual receptive field compete for representation and mutually suppress each other's response (Rolls & Tovee, 1995; Miller, Gochin, & Gross, 1993; Moran & Desimone, 1985). These mutually suppressive–competitive interactions are such that the neural response to paired stimuli is reduced relative to the summed response of each stimulus presented alone in the receptive field (Rolls & Tovee, 1995; Miller et al., 1993; Moran & Desimone, 1985). The biased competition model of visual attention posits that the action of visual attention is to bias this neural competition in favor of one stimulus over another through top–down feedback (Duncan, 1996, 2006; Reynolds, Chelazzi, & Desimone, 1999; Desimone, 1998; Desimone & Duncan, 1995; Moran & Desimone, 1985). A number of fMRI studies have demonstrated neural competition within the human visual system (Fuchs, Andersen, Gruber, & Müller, 2008; Beck & Kastner, 2005, 2007; Kastner et al., 2001; Kastner, De Weerd, Desimone, & Ungerleider, 1998) and have further shown that such visual competition is modulated by selective attention in accordance with the biased competition model of attention (Fuchs et al., 2008; Beck & Kastner, 2005; Kastner et al., 1998).

Torrallbo and Beck (2008) have recently proposed that perceptual load may be the result of local competitive interactions in visual cortical areas. Using spatial separation to manipulate visual competition, they found that distractor

incompatibility effects decreased as spatial separation between items in a search array decreased. Thus, the standard effects of perceptual load appear to be attributable to visual competition between items. Torralbo and Beck suggest that visual competition is the neural basis of perceptual load such that increased competition between stimuli causes the perceptual load of a task to increase. Because of the increased competition between stimuli a stronger top-down bias signal is required to resolve the increased competition in favor of the target stimulus. It is this enhanced biasing signal that leads to the filtering of irrelevant distractor stimuli. This biased competition hypothesis of perceptual load provides a viable underlying neural mechanism of the phenomenon and forms an important theoretical framework.

Neural competition and top-down biasing of visual processing appear to be basic mechanisms of selective attention, and competitive interactions between distractor and task stimuli may play a role in the observed effects of perceptual load. However, neurophysiological evidence of neural competition between distractor and task stimuli in a perceptual load paradigm has yet to be demonstrated, and the effect of perceptual load on such competitive interactions remains an open question.

The Current Study

We investigated the two aforementioned issues of perceptual load theory using a steady-state evoked potential (SSEP) technique. When stimuli are modulated at a constant frequency, their corresponding neural response becomes entrained to the frequency of modulation and can be measured from the frequency spectrum of the scalp-recorded EEG (Regan, 1977, 1989). For example, a checkerboard stimulus contrast reversed at 10.0 Hz will induce a clear 10.0-Hz peak in the frequency domain at occipital electrodes. Although time domain information is lost, the use of SSEPs has the advantage of allowing multiple stimuli to be monitored simultaneously and independently in the frequency domain. That is, modulating individual stimuli at unique frequencies (frequency tagging) yields a distinct frequency domain signature for each stimulus (Ding, Sperling, & Srinivasan, 2006; Müller, Malinowski, Gruber, & Hillyard, 2003; Morgan, Hansen, & Hillyard, 1996). Here, we used such a frequency tagging approach to simultaneously measure task-related and distractor-related neural signatures in a task that varied in perceptual load.

Here we recorded EEG while participants performed a rapid serial visual presentation (RSVP) task. The task required participants to monitor a central RSVP stream for two predesignated target stimuli. The perceptual load of this task was varied between blocks by manipulating which stimuli were assigned as targets. In a low perceptual load condition, the target was defined simply by color, whereas in a high-load condition, targets were defined by a conjunction of color and orientation. The RSVP task was performed in isolation as well as in the presence of irrelevant visual and auditory distractors. Task and distractor stimuli were fre-

quency tagged by modulating each class of stimulus (i.e., RSVP stream, visual distractors, auditory distractors) at a unique frequency. Stimuli were presented at 2.5 Hz (RSVP task), 8.5 Hz (visual distractors), or 40.0 Hz (auditory distractors). Using this SSEP frequency-tagging method signals from each type of stimulus could be independently examined for changes in cortical processing associated with cross-modal distractor filtering and neural-competitive interactions between task and distractor.

METHODS

Participants

Twenty undergraduate participants (4 women, age $M = 19.5$, $SD = 1.2$) were recruited from the Georgia Institute of Technology. Participants reported normal or corrected-to-normal vision. All participants gave informed consent and received extra credit toward a psychology course for their participation.

Stimuli and Procedure

Testing was conducted in an electrically shielded, sound-attenuating chamber under low levels of illumination. Stimuli were controlled by the Presentation software package (Neurobehavioral Systems, Albany, CA) and were presented on a 21-in. CRT monitor. A chin rest maintained a viewing distance of 57 cm.

The perceptual load task was adapted from Parks, Hilimire, and Corballis (2009) and was similar to that used in a previous fMRI investigation (Schwartz et al., 2005). The task required a rapid central stream of stimuli to be monitored for the occurrence of particular targets. Stimuli were crosses ($0.8^\circ \times 0.8^\circ$) that varied in color (red, green, violet, or blue) and orientation (upright or inverted). Cross stimuli were positioned at fixation and occurred in RSVP at a rate of 2.5 Hz (one every 400 msec). During each trial, a total of 13 crosses were presented over a 5.2-sec period. Participants were assigned two target crosses and were instructed to count the occurrences of those targets within a trial. The attentional demands of the RSVP task were manipulated between two conditions of perceptual load. In the low-load condition, participants monitored the stream for any red target (i.e., upright or inverted red crosses). Thus, targets were easily discriminable, and their identification placed little demand on attention (Lavie, 1995). In the high-load condition, targets were upright green and inverted violet crosses. Here, the identification of targets required both color and orientation to be resolved, a task highly demanding of attention (Lavie, 1995). Crucially, stimulus parameters remained constant between low-load and high-load conditions, and only attentional demands were manipulated through the assignment of different targets. In a given trial, either two or three target crosses were presented. Cross order within the RSVP stream was randomly determined with the ex-

ception that two target crosses could not appear sequentially. At the end of a trial, participants were prompted to indicate the number of targets by white text reading “2 or 3?” Responses were given using the left (for “2”) and right (for “3”) control keys of a standard PC keyboard.

To investigate the effects of perceptual load on distractor filtering, the presence of irrelevant visual and auditory distractors was systematically manipulated in four conditions. The central RSVP task was performed in all conditions. V+ indicates the presence of a visual distractor and V− its absence. Similarly, A+ and A− indicate the presence or absence of an auditory distractor, respectively. In one condition, V−A−, the RSVP task was performed in isolation. This condition was termed V−A− because both visual and auditory distractors were absent. Measurement of SSEPs during the perceptual load task in isolation served as a baseline and allowed the assessment of task-related neural changes because of the presence of distractors. In a second condition, task-irrelevant visual distractors were paired with the RSVP task (V+A− condition). Here, two “dartboard” wedges were positioned in the left and right hemifields (10.5° wide; varying linearly in height from 4.3° to 24.5°). The two wedges always reversed in contrast at a rate of 8.5 Hz, and their reversals were in phase. Task-irrelevant auditory distractors were paired with the RSVP task in the V−A+ condition. Auditory distractors were 500 Hz tones that sinusoidally modulated in amplitude between 0 and 70 dB SPL at a rate of 40 Hz. These parameters were chosen on the basis of previous research that has demonstrated that a 40-Hz amplitude-modulated signal can be influenced by auditory selective attention (Ross, Picton, Herdman, & Pantev, 2004; Tiitinen et al., 1993). A final condition paired both auditory and visual distractors with the RSVP task (V+A+). This condition allowed assessment of whether distraction and filtering increased in the presence of more than one distractor. Before experimentation, subjects were instructed that distractors were irrelevant to the task at hand and should be ignored. The configuration of task and distractor stimuli is depicted in Figure 1.

Participants performed eight practice trials consisting of one trial of each combination of load condition and level of distraction. Practice trials were followed by 12 blocks of 32 trials, alternating between low load and high load. Before each block, participants were assigned the high- or low-load targets to which they were to attend. The order of low- and high-load blocks was counterbalanced between participants. Each block contained eight V−A−, V+A−, V−A+, and V+A+ trials, the presentation of which was randomized within blocks.

Electrophysiological Recording and Analysis

EEG data were acquired from 30 scalp-recorded channels using a BioSemi ActiveTwo amplifier (Amsterdam, Netherlands). Electrodes were positioned according to the extended 10–20 system. Electrode positions were

AF3/4, FC1/2, FC5/6, F7/8, F3/4, Fz, C3/4, Cz, CP1/2, CP5/6, P7/8, PO3/4, P3/4, Pz, T7/8, O1/2, and Oz. The ActiveTwo system requires the placement of two additional electrodes that replace traditional reference and ground: common mode sense (CMS) and driven-right leg (DRL). The CMS electrode was positioned halfway between Cz and C3, and the DRL electrode was positioned halfway between Cz and C4 electrodes. EOG was formed from a pair of electrodes positioned above and below the left eye (for vertical EOG) and from a pair of electrodes positioned on the outer canthi of the left and right eyes (for horizontal EOG).

Continuous EEG data were acquired in reference to the CMS electrode and were sampled at a rate of 1024 Hz. Off-line, data were rereferenced to the average of all scalp-recorded channels. Channels identified by the experimenter as excessively noisy were dropped before the formation of the average reference. Continuous EEG was digitally band-pass filtered from 0.5 to 50 Hz using a zero-phase-shift Butterworth filter (−12 dB/octave). Data were divided into segments of 4000 msec (4096 data points) beginning 600 msec after the onset of the RSVP task and terminating 600 msec before trial termination. The first and the last 600 msec were excluded for three key reasons. First, these points were excluded to ensure that the data submitted to

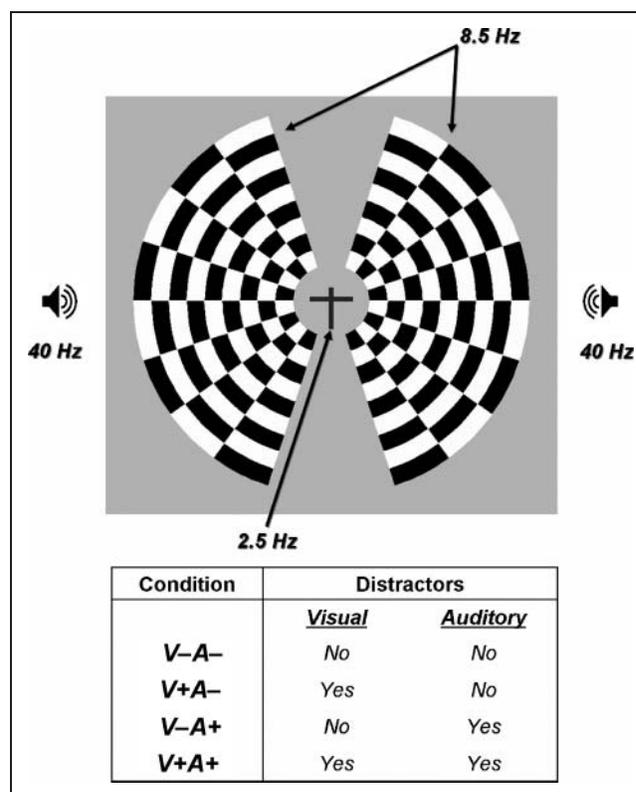


Figure 1. In four conditions, the central RSVP task (2.5 Hz) was performed in isolation as well as in the presence of irrelevant visual and auditory distractors. Visual distractors were peripheral “dartboard” wedges that contrast reversed at a rate of 8.5 Hz. Auditory distractors consisted of a 500-Hz tone amplitude modulated at 40.0 Hz.

frequency analysis had enough time to achieve steady state. Second, this was done so that exactly 4096 data points would remain because the number of data points must be a power of two for the fast Fourier transform algorithm. Lastly, the early and the late data points were omitted to avoid transient responses from stimulus onsets and offsets. Individual segments were corrected for ocular artifacts using the method of Gratton, Coles, and Donchin (1983). Segments were then submitted to a linear detrend using the first and the last 100 msec of the segment and were then centered about zero by setting the average of the entire segment to zero. Individual segments containing activity that exceeded $\pm 150 \mu\text{V}$ in any scalp-recorded channel were considered to contain artifacts and were rejected from analysis. On average, 8.0% of trials were rejected on the basis of these criteria. Individual segments were averaged in the time domain for each level of perceptual load and distraction. Time-averaged data from each condition of load and distraction were submitted to a fast Fourier transform with a 10% Hanning window. Resultant frequency domain signal amplitude was expressed in voltage (μV).

Analysis and Interpretation of Frequency Domain EEG Signals

Separate statistical analyses were conducted for frequency domain signals of visual distractors, auditory distractors, and the task-relevant RSVP stream. For each class of stimulus, signal amplitude at the fundamental frequency of modulation was extracted from frequency domain data and analyzed using a repeated measures ANOVA on a pre-selected set of electrode positions. Each class of signal was assessed at a different set of electrode positions. Scalp distributions were used to select electrode sites for analysis by choosing those electrodes that displayed the greatest signal strength in the grand average of all conditions. For all statistical analyses, follow-up ANOVAs and *t* tests were conducted where appropriate. ANOVAs with more than one degree of freedom were Huynh–Feldt corrected for violations of sphericity. Corrected degrees of freedom are rounded to the closest integer value whenever reported. An alpha value of .05 was accepted as statistical significance for all ANOVAs and comparisons.

To determine whether perceptual load leads to modality-specific or modality-general distractor filtering, SSEP amplitude for irrelevant visual (8.5 Hz) and auditory (40.0 Hz) distractor signals was assessed for evidence of signal reduction under high visual load. Analysis of visual distractor signals was done with a $3 \times 2 \times 2$ omnibus ANOVA having factors of electrode (O1, Oz, or O2), load (high or low), and distractor (V+A– or V+A+). Auditory distractor signals (40.0 Hz) were analyzed with a $4 \times 2 \times 2$ ANOVA having factors of electrode (FC1, FC2, Fz, Cz), load (high or low), and distractor (V–A+ or V+A+). If load-induced distractor filtering is modality general, then both visual (8.5 Hz) and auditory (40.0 Hz) signals would be expected to exhibit amplitude reductions (reduced distractor pro-

cessing) under high perceptual load. If distractor filtering is modality specific, then amplitude reductions would be expected only with visual distractors and no change should be present for auditory distractor signals.

The RSVP task occurs at a unique frequency of 2.5 Hz. Thus, the 2.5-Hz frequency domain EEG signature reflects task-specific processing and can be assessed for modulations in the processing of task stimuli. RSVP task signals clearly exhibited a bilateral posterior scalp distribution as well as a frontocentral distribution. Separate omnibus ANOVAs were conducted on posterior and anterior distributions to examine changes in RSVP task signals. The posterior omnibus was a $5 \times 2 \times 2 \times 2$ ANOVA with factors of electrode (O1, Oz, O2, P7, and P8), load (high or low), visual distractor (present or absent), and auditory distractor (present or absent). The anterior omnibus was identical to the posterior analysis except that the electrode factor had four levels (FC1, FC2, Fz, and Cz) rather than five.

A question of interest was whether distractor stimuli affect the processing of task-relevant stimuli. Frequency tagging of the RSVP task allows the associated neural signature to be tracked in conjunction with distractor signals. Thus, task-related cortical signals can be compared in the presence and absence of distractor stimuli and assessed for changes in amplitude related to distractors (allowing an assessment of neural competition between task and distractors). If task and distractor stimuli were competing for representation, then task-related signal strength should decrease in the presence of visual distractors because of mutually suppressive effects of neural competition.

RESULTS

Behavioral Data

Accuracy data from the RSVP task were submitted to a $2 \times 2 \times 2$ repeated measures ANOVA with factors of load (low or high), visual distractor (present or absent), and auditory distractor (present or absent). Overall accuracy in the RSVP task was significantly greater for low visual load ($M = 96.4\%$, $SD = 4.2\%$) than for high visual load ($M = 77.2\%$, $SD = 10.7\%$) as evidenced by a main effect of load, $F(1, 19) = 109.73$, $p < .0001$. Performance in the central RSVP task was affected by the presence of irrelevant visual distractors, as supported by a main effect of visual distractor, $F(1, 19) = 6.82$, $p < .05$. The presence of a Load \times Visual Distractor interaction, $F(1, 19) = 11.25$, $p < .005$, further indicated that the effect of visual distractors on performance was a function of the level of perceptual load. Follow-up *t* tests were conducted within each level of load (low and high) and compared performance in the absence of visual distractors with that in the presence of visual distractors. These tests revealed that RSVP performance was unaffected by visual distractors under low load, $t(19) = -1.38$, $p > .18$, but was significantly impaired by the presence of visual distractors under high load, $t(19) = 3.38$, $p < .005$. The nature of this Load \times Visual Distractor

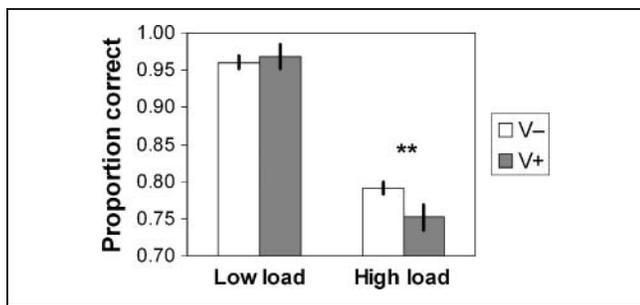


Figure 2. Effects of irrelevant visual distractors on behavioral performance as a function of perceptual load. Double asterisks (**) denote significance at the .01 level. Error bars represent 95% within-subjects confidence intervals (Loftus & Masson, 1994).

interaction is illustrated in Figure 2. Auditory distractors had no bearing on RSVP performance ($p > .75$).

Steady-state EEG Data

Visual Distractor—8.5 Hz

Manipulation of perceptual load in the central RSVP task had a significant effect on the processing of irrelevant peripheral visual distractors. The omnibus analysis revealed a significant Electrode \times Load interaction, $F(2, 32) = 6.28, p < .01$. Follow-up t tests performed at each electrode site revealed that, relative to low load, 8.5-Hz signal strength was reduced under high perceptual load at electrodes Oz and O2, $t(19) = 3.26, p < .005$, and $t(19) = 2.98, p < .01$, respectively. No significant effect of load was present at electrode O1, $t(19) = 1.50, p > .15$. Scalp

maps and effects of perceptual load on the 8.5 Hz visual distractor signals are shown in Figure 3.

Auditory Distractor—40.0 Hz

The omnibus ANOVA for 40.0-Hz auditory distractor signals revealed no main effects or interactions with perceptual load (all $ps > .27$). See Figure 4 for scalp distributions and plots of 40.0-Hz signal amplitude as a function of visual perceptual load.

RSVP Perceptual Load Task—2.5 Hz

The scalp distribution of the 2.5-Hz RSVP task signal is shown in Figure 5A. The posterior omnibus of the task-related 2.5-Hz signal revealed a significant Electrode \times Load \times Visual Distractor interaction, $F(4, 54) = 3.65, p < .05$. Five follow-up 2×2 ANOVAs were conducted within each electrode and had factors of load (high or low) and visual distractor (present or absent). Each electrode analyzed exhibited a significant main effect of visual distractor: O1, $F(1, 19) = 17.84, p < .0005$; Oz, $F(1, 19) = 14.17, p < .005$; O2, $F(1, 19) = 7.17, p < .05$; P7, $F(1, 19) = 4.57, p < .05$; and P8, $F(1, 19) = 7.13, p < .05$. At each electrode, the main effect of visual distractor was such that the 2.5-Hz signal strength was attenuated in the presence of irrelevant visual distractors (Figure 5B). A single occipital-temporal electrode (P8) exhibited a significant Load \times Visual Distractor interaction, $F(1, 19) = 16.30, p < .01$. This interaction was such that visual distractors significantly attenuated signal strength under low perceptual load, $t(19) = 3.87, p < .005$,

Figure 3. Effects of visual perceptual load on irrelevant visual distractor signals (8.5 Hz). (A) The 8.5-Hz amplitude peaked over occipital electrodes. Time domain signals were extracted using a band-pass method. (B) The 8.5-Hz signal amplitude was significantly attenuated under high perceptual load at electrodes Oz and O2. Double asterisks (**) denote significance at the .01 level. Error bars represent 95% within-subjects confidence intervals.

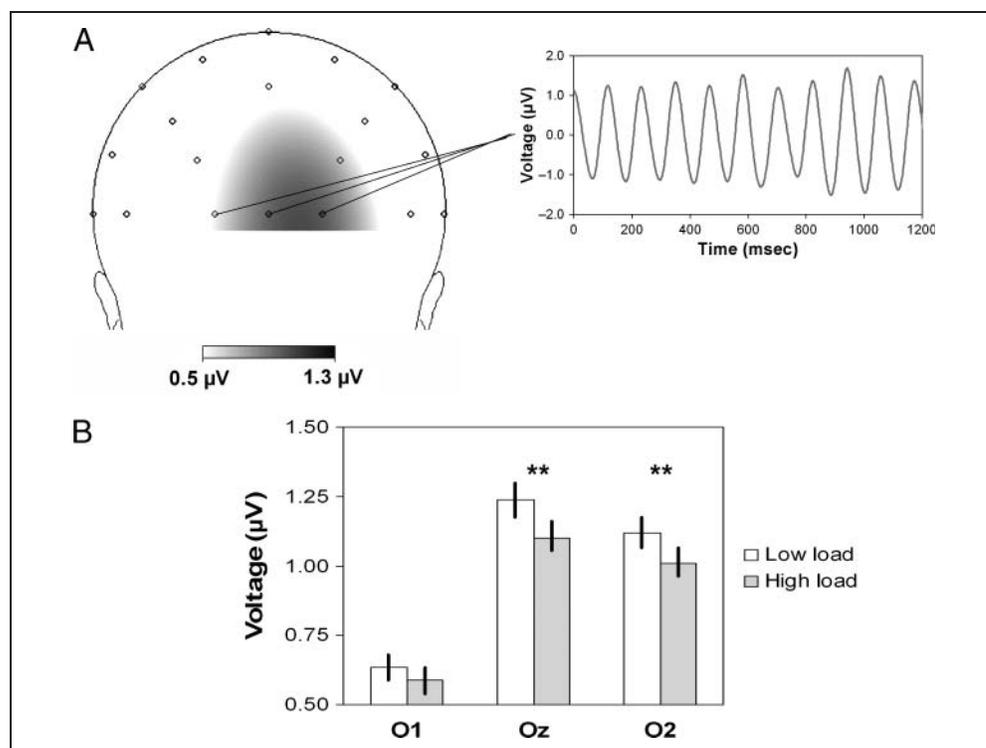
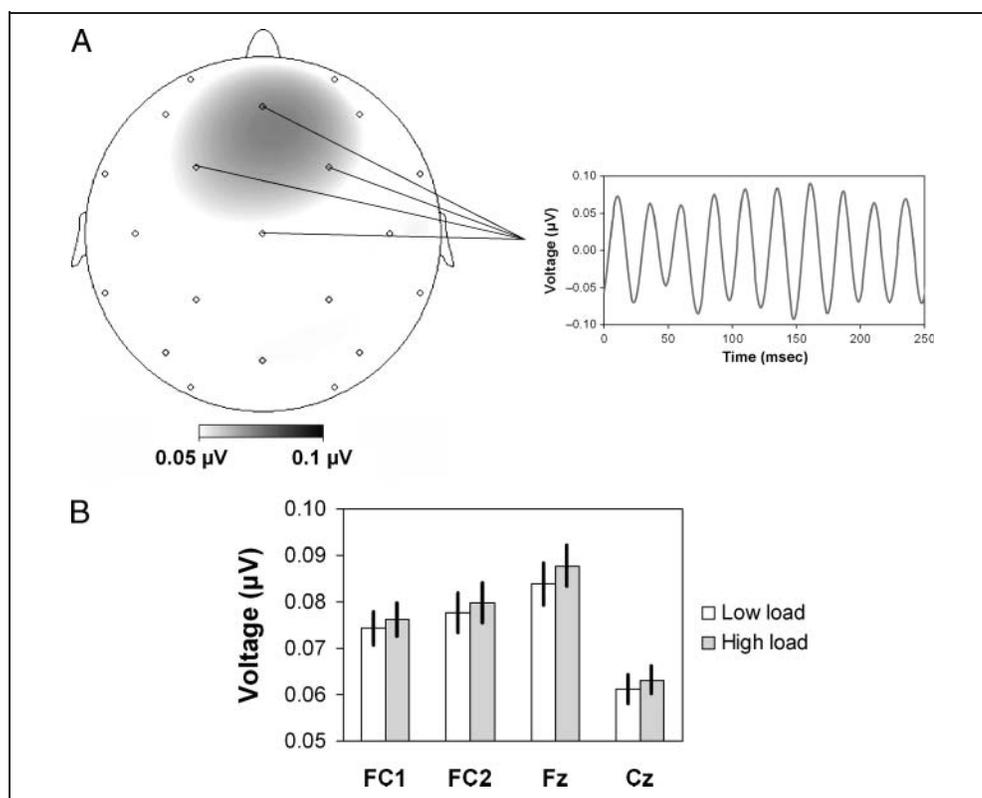


Figure 4. Effects of visual perceptual load on irrelevant auditory distractor signals (40.0 Hz). (A) Auditory distractor signals exhibited a typical frontocentral distribution. (B) Visual load had no effect on auditory distractor signal amplitude. Error bars represent 95% within-subjects confidence intervals.



but had no effect on signal strength with high perceptual load, $t(19) = 1.15, p > .26$ (Figure 5C).

The anterior omnibus revealed significant Electrode \times Visual Distractor and Load \times Visual Distractor interactions, $F(3, 37) = 5.93, p < .01$, and $F(1, 19) = 5.84, p < .05$, respectively. The effect of visual distractors on RSVP 2.5-Hz signals was further examined by conducting a t test within each electrode of interest that compared signal strength in the absence of distractors to that in the presence of visual distractors. Electrode sites FC1, FC2, Fz, and Cz each exhibited a reduction in signal power in the presence of peripheral visual distractors, $t(19) = 5.50, p < .00005$, $t(19) = 4.16, p < .001$, $t(19) = 3.08, p < .01$, and $t(19) = 4.33, p < .0005$, respectively (Figure 5B). The Load \times Visual Distractor interaction resulted from a greater distractor-related reduction in signal strength under low load (mean difference = 0.096, $SE = 0.022$), $t(19) = 4.33, p < .0005$, than under high load (mean difference = 0.059, $SE = 0.012$), $t(19) = 4.75, p < .0005$ (Figure 5C).

DISCUSSION

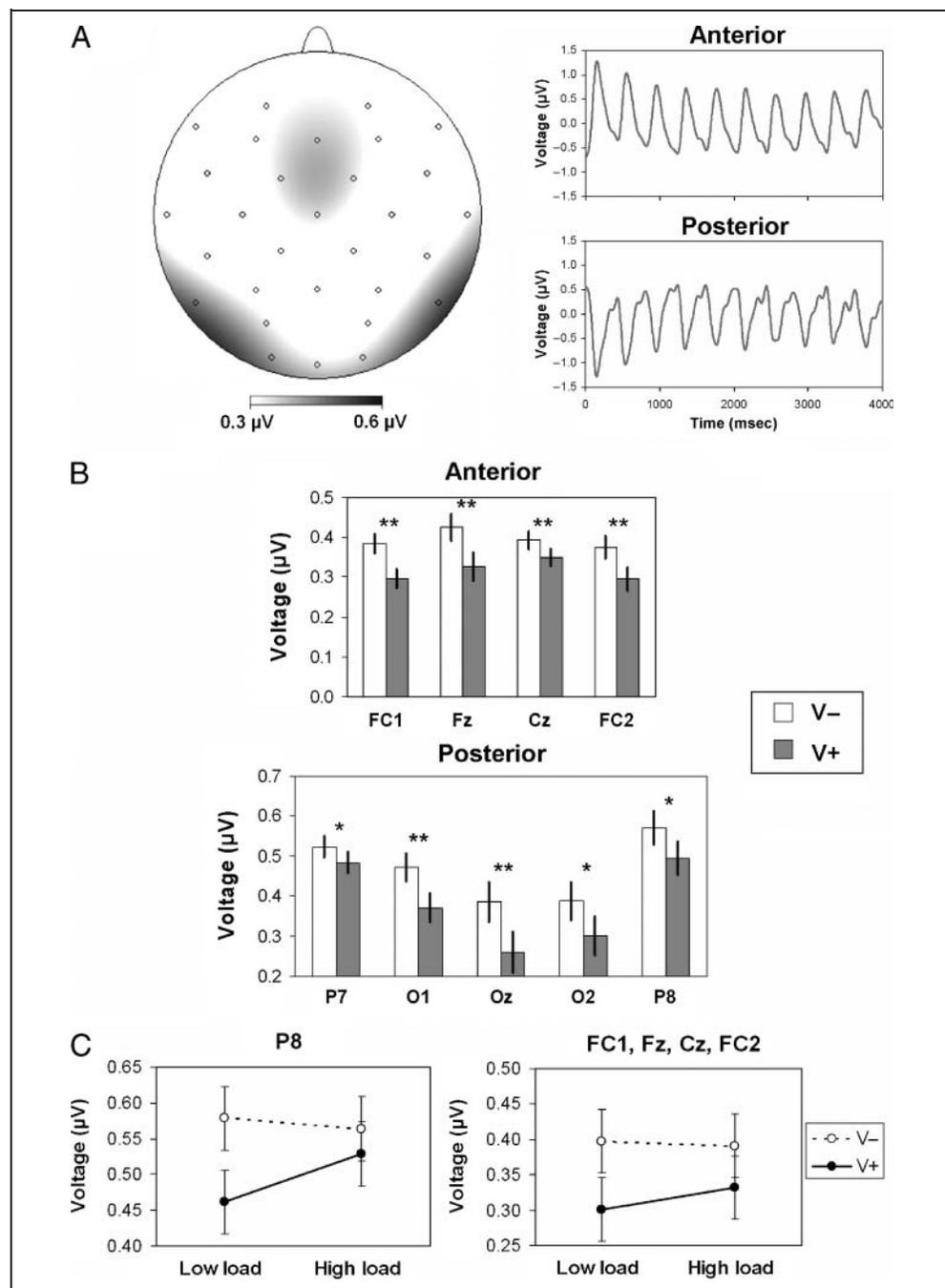
We used a frequency-tagging SSEP paradigm to examine the neural mechanisms of perceptual load. Participants performed a central RSVP task that varied in perceptual load (low or high). This task was performed in isolation or in the presence of irrelevant visual or auditory distractor stimuli. Task-related stimuli, visual distractors, and auditory distractors were each modulated at unique frequencies of

2.5, 8.5, and 40.0 Hz, respectively. Frequency tagging each stimulus of interest in this manner allowed neural signals associated with each to be tracked simultaneously in the frequency domain. Using this technique, changes in the entrained neural response could be measured independently for both distractor and task stimuli. We examined two major issues regarding the neural underpinnings of perceptual load. First, we investigated whether the distractor filtering induced by increased perceptual load is confined to a single sensory modality or is cross modal in nature. Specifically, we assessed how visual perceptual load affected the sensory response to within-modality visual distractors and between-modality auditory distractors. A second question focused on whether distractor stimuli affected the processing of task-relevant stimuli. We sought to determine if the presence of irrelevant visual or auditory distractors interfered with processing of RSVP task stimuli and how such effects interacted with the level of perceptual load. Task-related signal strength was assessed for modulations associated with the presence of visual or auditory distractor stimuli. Such effects were evaluated in the context of visual competition and the biased competition model of attention.

Is Distractor Filtering Modality Specific?

Investigations of cross-modal interactions of perceptual load have yielded somewhat discrepant results. Some studies have indicated that the distractor filtering induced by perceptual load is modality general and that increased load

Figure 5. Effects of load and visual distractors on task-related signals of the RSVP task (2.5 Hz). (A) Task-related signals exhibited a scalp distribution concentrated over bilateral occipital-temporal and frontocentral electrodes. (B) In the presence of visual distractors (V+), 2.5 Hz task-related signal strength was suppressed at posterior and anterior electrodes relative to when visual distractors were absent (V-). These findings are consistent with the occurrence of neural competition between task and visual distractor stimuli. Single asterisk (*) denotes significance at the .05 level, whereas double asterisks (**) denote significance at the .01 level. (C) Signal suppression induced by the presence of visual distractors interacted with perceptual load. Signal suppression occurred with low load but not with high load, suggesting that increased perceptual load acted to resolve task-distractor competition. All error bars represent 95% within-subjects confidence intervals.



in one sensory modality introduces distractor filtering in that modality as well as others (Houghton et al., 2003; Berman & Colby, 2002). Others have suggested that the effects of perceptual load are modality specific and affect distractor filtering only within the modality in which load is manipulated (Rees et al., 2001). Our analysis of frequency-tagged distractor signals is in agreement with the latter proposal. Entrained neural responses to within-modality visual distractors were clearly modulated by perceptual load. Signal strength of frequency-tagged 8.5-Hz peripheral visual distractors decreased significantly under high visual load. This result demonstrates a clear within-modality effect of distractor filtering and is consistent with a number

of previous neurophysiological examinations of perceptual load in the visual modality (Schwartz et al., 2005; O'Connor et al., 2002; Handy et al., 2001; Handy & Mangun, 2000). Unlike visual distractors, between-modality auditory distractor signals (40.0 Hz) did not modulate with increased visual perceptual load. Auditory steady-state signal strength remained unchanged between low and high load in the visual RSVP task, a result that suggests auditory distractor processing was unaffected by manipulations of perceptual load in the visual modality.

The findings of the current experiment are consistent with the idea that the distractor filtering induced by perceptual load is modality specific and not cross modal in nature.

However, several limitations and alternate possibilities must also be considered. First, modulation of auditory distractor signals may not have been apparent because the rate of stimulus modulation selected for frequency tagging (40.0 Hz) was not within a suitable frequency range to reveal attentional modulation. There has been some evidence that the effect of attention on steady-state signals is dependent on the selected frequency of stimulus modulation (Ding et al., 2006). We do not believe our selection of a 40-Hz amplitude-modulated tone can explain the lack of attentional modulation as several previous investigations have demonstrated that the 40-Hz auditory steady-state response does modulate with attention (Saupe, Widmann, Bendixen, Müller, & Schröger, 2009; Ross et al., 2004; Tiitinen et al., 1993). It should be noted that these studies presented 40-Hz stimuli over a shorter interval (<1.0 sec) than that used here (5.2 sec). Second, auditory distractor modulation may have been absent because the manipulation of visual load in our experiment was simply not strong enough. Perhaps modulation of auditory processing would have been apparent had the visual RSVP task been more demanding of attention. Such an explanation seems rather unlikely. The load manipulation in the RSVP task had a considerable effect on behavioral performance (96.4% accurate under low load vs. 77.2% under high load) and was demanding enough to induce a significant reduction in 8.5-Hz visual distractor signal strength. Thus, the load manipulation was of appropriate difficulty to affect within-modality distractor processing. There is no reason to assume that the task was insufficient to affect processing in the auditory domain. Third, visual distractor signals were of considerably greater amplitude than their auditory counterparts, and there may have been a bias to detect changes in visual distractors because of this magnitude difference. However, signal amplitudes of auditory steady-state responses were stable and reliable, and there were no trends in mean amplitude suggesting a failure to detect a reduction in amplitude with increased visual load (Figure 4). Although the absolute amplitude of visual and auditory distractor signals did differ substantially these differences reflect differences in the response of distinct neural populations given the chosen stimulus and task parameters. Thus, it is the relative change in amplitude that is informative rather than absolute amplitude. Last, the lack of modulation in auditory distractor signals may be attributable to differences in the underlying neural origins of auditory and visual steady-state responses. The scalp-recorded visual steady-state response originates from sources in primary visual cortex as well as a number of higher order extrastriate visual areas (Di Russo et al., 2006). The 40-Hz auditory steady-state response originates largely from sources in the hindbrain and primary auditory area (Herdman et al., 2002). Thus, the visual steady state reflects activity from higher level association cortex more so than that of the auditory steady-state response. As such, the auditory steady state may be less likely to exhibit attentional modulation because of its lower level

neural origins. Although previous examinations have demonstrated modulation of the auditory steady-state response (Saupe et al., 2009; Ross et al., 2004; Tiitinen et al., 1993), if visual load were to affect auditory processing in an area higher than primary auditory cortex, it would be immeasurable with the 40-Hz auditory steady state. Thus, it remains possible that auditory processing was affected by our manipulation of visual load but did not manifest until a stage of auditory processing beyond the primary auditory area.

No evidence of cross-modal auditory distractor filtering was apparent in the present examination. However, we have recently demonstrated a cross-modal EMG effect of perceptual load (Parks et al., 2009). Using a visual RSVP task nearly identical to that used here, high visual load was found to attenuate the amplitude of an auditory-evoked micro-reflex (the postauricular reflex [PAR]). It is unclear why cross-modal effects were observed in an overt muscular response but not within the CNS. The PAR is mediated through several brainstem nuclei earlier in the auditory pathway than in the major sources of the auditory steady-state response (Herdman et al., 2002; Hackley, Woldorff, & Hillyard, 1987). It is puzzling that cross-modal effects of visual perceptual load were present in a response generated by brainstem nuclei but were not apparent in a measure that reflects cortical sensory processing. One possibility is that feedback from some later stage of cortical processing actively modulates the PAR reflex arc (Parks et al., 2009), although this proposal is purely speculative.

Do Irrelevant Distractors Affect the Processing of Task Stimuli?

The effect of distractor stimuli on the processing of task-relevant stimuli remains an open question in the perceptual load literature and is of considerable importance as it will more fully reveal the neural dynamics that underlie perceptual load and associated distractor filtering. We investigated this issue by examining how the presence of irrelevant visual or auditory distractors impacted task-related steady-state signal strength.

Our results fit well within the framework of neural competition and the biased competition model of attention. Consistent with the mutually suppressive effects of neural competition, task-related 2.5-Hz signal strength was reduced when the RSVP task was performed in the presence of visual distractors compared with when the task was performed in isolation. This suppressive effect was present at each of the electrodes analyzed and was unique to visual distractors. Auditory distractor stimuli had no discernible effect on the 2.5-Hz signal amplitude. The attenuation of 2.5-Hz RSVP signal amplitude in the presence of peripheral checkerboards implies that visual distractors and task stimuli competed for representation within cortex.

Analyses of task-related cortical signals focused on both a posterior and frontocentral distribution of the 2.5-Hz steady-state signal. The presence of signal suppression at posterior electrodes suggests that irrelevant peripheral

visual distractors compete for representation with the RSVP task and is consistent with competitive interactions within extrastriate cortex (Desimone & Duncan, 1995). But why would neural-competitive interaction also manifest at frontocentral electrodes? Duncan (1996) proposed that competition should be integrated across neural systems (see also Beck & Kastner, 2009; Desimone, 1998). That is, competition should not only occur within sensory cortex but should carry through to higher level association areas in parietal and frontal cortices as well. The precise cortical sources contributing to the frontocentral distribution of the 2.5-Hz steady-state signal in our experiment are unknown. However, this anterior distribution most likely reflects task-related processing beyond the sensory level. To the extent that these frontocentral effects can be considered to reflect higher level cortical processing, results are further consistent with this integrated competition proposal (Duncan, 1996, 2006).

In addition to neural competition between visual distractors and task stimuli, we also found that competitive effects were influenced by the level of perceptual load at a subset of electrodes. The suppressive effects of neural competition were apparent between task stimuli and visual distractors under low load but were diminished under high load. These interactions between perceptual load and visual competition were apparent at a posterior occipital-temporal electrode and broadly over frontocentral electrode positions. Findings are consistent with the biased competition model of selective attention (Desimone & Duncan, 1995) and indicate that increased perceptual load resolved neural competition in favor of the task stimulus over that of the peripheral distractors.

Why would interactions with perceptual load only occur at a subset of those electrodes exhibiting task-distractor competition? Neural-competitive interactions occur throughout the visual system, but the effect of attention and top-down biasing is greatest within higher order cortical visual areas (Kastner et al., 1998; for a review, see Beck & Kastner, 2009). Attentional effects may have been apparent at only a subset of electrodes simply because the activity at those leads reflected the contribution of higher order visual areas more so than others.

The presence of irrelevant peripheral visual distractors also had a clear effect on behavioral performance in the central RSVP task and interacted with the level of perceptual load. RSVP task performance under low load was unaffected by visual distractors. However, visual distractors had a detrimental effect on task performance under high load, significantly reducing accuracy in their presence relative to their absence (Figure 2). Peripheral distractors had a negative impact on central RSVP accuracy despite the fact that their presence in no way changed the contingencies of the task at hand. We suggest that these findings indicate that peripheral visual stimulation increases perceptual load under high load due to increased competition between peripheral distractors and target items in the central RSVP stream. Steady-state data revealed

competition between peripheral distractors and RSVP stimuli in both low- and high-load conditions. Because steady-state signals reflect the activity over the entire trial, this result is indicative of distractors competing with the *entire* RSVP stream. However, behavioral results reflect the detection of *individual* target stimuli among the RSVP stream and the nature of target stimuli must be considered. Low-load targets were discriminable from other items in the RVSP stream by the single feature of color (i.e., red). Such a difference in bottom-up salience biases neural competition in favor of a salient item (Beck & Kastner, 2007). Thus, peripheral distractors would be expected to have little effect on the detection of low-load targets, consistent with the ceiling-level performance in our behavioral data. In contrast to low-load targets, high-load targets were a conjunction of two features (i.e., color and orientation) and were not discriminable from nontarget items by any particular feature. We propose that the features shared with nontarget items in the RSVP stream render high-load targets more susceptible to competition from peripheral distractors and impair task performance because of interference with the cortical representation of target items.

Visual distractor SSEP data suggested that peripheral distractors were filtered under high perceptual load, yet the presence of these distractors led to a reduction in task performance under the same conditions. If distractors were filtered out, then why would they still have an effect on task performance? Although SSEP visual distractor signals were significantly reduced under high load, it is clear that visual distractors were not perfectly filtered. Robust visual distractor signals were still apparent under high perceptual load (albeit reduced relative to low load). Furthermore, although some electrodes showed evidence of resolved task-distractor competition in RSVP task SSEP signals under high load, others continued to exhibit competitive effects under high perceptual load. Thus, although we find evidence of distractor filtering and resolved visual competition, such effects are imperfect and distractors do not appear to ever be completely filtered out.

The interactions between perceptual load and neural competition present in our experiment are consistent with a recent proposal by Torralbo and Beck (2008). They suggest that perceptual load and associated distractor filtering is a result of increased neural competition between distractor and target items and that such competition necessitates a stronger top-down bias signal to resolve competition in favor of the target item. In turn, a stronger top-down attentional bias signal results in increased distractor filtering. This competition account of perceptual load was proposed to explain situations where load is manipulated by an increased number of surrounding nontarget items. However, a more general formulation of this idea can be extended to our results. We manipulated perceptual load at fixation by requiring the identification of single feature (low-load) or conjunction (high-load) targets in a central RSVP stream. We manipulated visual competition and evaluated distractor filtering through the introduction of flickering

peripheral checkerboards. Steady-state cortical potentials revealed several effects consistent with the general proposal of Torralbo and Beck. First, irrelevant visual distractors competed for representation with task-relevant stimuli. Neural competition was evidenced by signal suppression of 2.5-Hz RSVP SSEPs. In the absence of bottom-up salience cues (i.e., high load), this task-distractor competition also increased the perceptual load of the central RSVP task such that the identification of conjunction targets became more difficult in the presence of irrelevant peripheral distractors. Second, high perceptual load resolved this task-distractor competition in favor of the task-relevant stimulus. Distractor-induced signal suppression of 2.5 Hz task signals was reduced under high load, suggesting a reduction of task-distractor competition. Third, high perceptual load resulted in filtering of irrelevant visual distractors. Irrelevant visual distractor signals (8.5 Hz) were significantly reduced in the high-load condition, suggesting reduced cortical processing of these stimuli. Together these findings suggest that increased perceptual load resolved task-distractor neural competition (at least partially) in favor of a central task-relevant stimulus over peripheral distractors, improving the visual cortical representation of task stimuli and impoverishing that of the visual distractors (distractor filtering).

Conclusions

In this study, we used a frequency-tagging SSEP paradigm to address two important questions regarding the neural mechanisms of perceptual load. The first was concerned with whether sensory-level distractor filtering is modality specific or modality general. Measurement of irrelevant visual and irrelevant auditory cortical signals suggests that visual load had a significant effect on the amplitude of within-modality visual distractor signals but had no effect on between-modality auditory distractor signals. We interpret this finding as evidence that sensory-level distractor filtering is modality specific. However, it remains possible that perceptual load affects between-modality distractor processing at a later stage than that reflected in our electrophysiological measures. A second question focused on how the presence of irrelevant distractors impacted the processing of task-relevant stimuli. Consistent with a neural competition account, the presence of within-modality visual distractors attenuated the amplitude of task-related cortical signals. This effect further interacted with perceptual load such that competition between task and distractor stimuli was reduced under high load at a subset of electrode sites. We propose that this result is due to a strengthened top-down bias signal that resolves target-distractor competition.

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