Published in final edited form as:

Psychophysiology. 2009 September ; 46(5): 1069–1079. doi:10.1111/j.1469-8986.2009.00854.x.

Share or compete? Load-dependent recruitment of prefrontal cortex during dual-task performance

Kathy A. Low, Echo E. Leaver, Arthur F. Kramer, Monica Fabiani, and Gabriele Gratton
University of Illinois at Urbana-Champaign

Abstract

Dual-task performance requires flexible attention allocation to two or more streams of information. Dorsolateral prefrontal cortex (DLPFC) is considered important for executive function and recent modeling work proposes that attention control may arise from selective activation and inhibition of different processing units within this region. Here we used a tone discrimination task and a visual letter memory task to examine whether this type of competition could be measurable using a neuroimaging technique, the event-related optical signal, with high spatial and temporal resolution. Left and right DLPFC structures were differentially affected by task priority and load, with the left middle frontal gyrus (MFG) being preferentially recruited by the visual memory task, whereas the two tasks competed for recruitment, in a spatially segregated manner, in right MFG. The data provide support for a competition view of dual-task processing.

Keywords

Event-related optical signal (EROS); event-related brain potentials (ERPs); attention; executive control; prefrontal cortex; dual task

We often find ourselves having to actively maintain multiple streams of information at the same time, especially when performing two or more tasks concurrently (Kramer & Madden, 2008). This “mental juggling” has been investigated by postulating the existence of a limited pool of “mental resources,” to explain how different tasks conflict with each other for the control of attention (e.g., Band et al., 2006; Wickens, 1980; Pashler & Johnston, 1998). More recently, researchers have focused on the frontal cortex as a key element for the deployment of attention to different processing streams (Miller & Cohen, 2001). An influential model by Cohen and his collaborators (Braver & Cohen, 2001) proposes that the dorsolateral prefrontal cortex (DLPFC) exerts a critical role in attention control (see also Bunge & Wallis, 2008 for a comprehensive overview of the role of frontal cortex in executive function). Specifically, it postulates that different processing streams are represented in different processing units within this region, with attention control being implemented through the differential activation of the units associated with each processing stream. According to this view, therefore, dual task conditions involve the selective activation and inhibition of different units within DLPFC. In this paper we present data supporting this view of attention control during dual task conditions.

The brain regions involved in attention control and task coordination during dual task processing have been investigated using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET). Several studies have reported recruitment of brain

regions during dual task blocks that were *not* engaged during either of the single tasks (Collette et al., 2005; D'Esposito et al., 1995; Dreher and Grafman, 2003; Szameitat et al., 2002). This additional activation is typically found in frontal and/or parietal regions and is generally interpreted as evidence of a neural correlate of central executive function. In contrast, there are also a number of studies that report no new areas of activation under dual task demands; rather, dual task brain activation could be explained as an additive effect of the brain activity arising in each of the component tasks (Adcock et al., 2000) or by increased activity in the regions involved in each single task (Bunge et al., 2000; Erickson et al., 2005, 2007). These data suggest that the additional executive processing demanded by dual task paradigms (e.g., task coordination, divided attention, minimization of task interference) may not require specialized neuronal activity, contrary to what has been suggested by the studies that report recruitment of unique brain regions under dual task requirements. Finally, there is a third set of results that are more consistent with the notion of *competition* for resources across tasks, as predicted by resource allocation models of dual task performance (which assume that two tasks may tap into common pools of resources; e.g., Navon & Gopher, 1979; Wickens, 1980). These studies report *reduced* activity in specific brain regions under dual compared to single task demands (Goldberg et al., 1998; Just et al., 2008).

In addition to fMRI studies, ERPs have also been used extensively in the investigation of dual task processing. In particular, the P300 or P3 component of the ERP has been used as an index of the allocation of attention across tasks. In a typical experiment, the difficulty of a primary task (or the priority given to that task) is manipulated while participants are asked to simultaneously perform a secondary task, such as an oddball task (count or respond to rare tones among a series of standard, frequent tones). Across a variety of primary tasks, the amplitude of the P3 component to the secondary oddball task is reduced as primary task difficulty increases (Allison & Polich, 2008; Isreal et al., 1980b; Kramer et al., 1983; Kramer et al., 1987; Kok, 1997), provided that the increased difficulty affects perceptual and/or central processing as opposed to strictly motor processing (Isreal et al., 1980a). These findings are generally interpreted within a resource theory framework of attentional allocation in which the primary and secondary tasks both tap into a common pool of resources (Navon & Gopher, 1979; Wickens, 1980; 2002). As more resources are allocated to the primary task, fewer are available to support the secondary task, and this diminished availability of resources is reflected in the diminished P3 amplitude to the secondary task. Wickens and colleagues (1983) reasoned that if both tasks are accessing a common resource, then as the P3 to the secondary task decreases, the P3 to the primary task should increase with increasing difficulty or increasing task priority. In fact, this type of reciprocal relationship during dual task processing has been reported by several investigators (Hoffman et al., 1985; Sirevaag et al., 1989; Strayer & Kramer, 1990; Wickens et al., 1983).

A reciprocal relationship of an ERP component across tasks suggests that the two tasks may share processing “real estate” in the brain (Duncan & Owen, 2000; Just et al., 2001). One could conceptualize this sharing in two ways. One possibility is that the processing units involved in allocating attention across two tasks might be undifferentiated, but flexibly engaged to promote one task or another depending on the immediate task demands. Alternatively, the processing units involved in attention allocation might be organized. One possible organization principle is spatial segregation, with elements at particular locations being more readily attributed to one task or another. If the processing units are distributed spatially (at least at a scale resolvable by non-invasive neuroimaging methods), then one might expect differentiated brain areas being recruited selectively for each of the two tasks, depending on instructions/demands. In line with this discussion, Uncapher and Rugg (2005) investigated the effects of secondary task difficulty on visual word list encoding. The secondary task required monitoring an auditory stream of spoken digits to determine the

gender of the voice (“easy” task) or whether the digit differed from the previous digit in odd/even category (“hard” task). By using an event-related fMRI design, they were able to analyze the brain activity separately for the two tasks and found a trade-off in processing between the two tasks in both DLPFC and lateral parietal cortex. As auditory task difficulty increased, activity in these regions decreased during word list encoding, but increased following the auditory task presentation. This latter finding is consistent with the dual task ERP studies reviewed above. In this work Uncapher and Rugg focused on the regions of overlap across the two tasks, to isolate “general purpose” rather than task-specific regions. In the current study, we start from the same premise that regions of DLPFC are in fact “task-general” at the macro level (see Gratton et al., 2008; Bunge & Wallis, 2008; Corbetta & Shulman, 2002), in that they are likely to be engaged in attention control and deployment across a variety of tasks and modalities. In addition, however, we ask the question of whether there is also evidence of spatial¹ and/or temporal organization within these areas.

For this reason we turned to another measure, the event-related optical signal (EROS; Gratton et al., 1995; Gratton & Fabiani, 2001), which, while possessing temporal properties similar to ERP responses, also provides detailed spatial information about the brain areas involved in processing. Specifically, we asked whether EROS would be sensitive to graded changes in cortical activity, similarly to ERPs, while also providing more precise spatial information about the overlapping regions of involvement. Similar to Uncapher and Rugg (2005), we chose to investigate two tasks that varied in modality and that are known to activate DLPFC, presumably due to their common reliance on working memory (Kiehl et al., 2001; Linden, et al., 1999; Low et al., 2006; Monoach et al., 1997; Narayanan et al., 2005; Rypma et al., 2006; Stevens et al., 2005). One task was an auditory oddball task, similar to that used in the dual task ERP studies reported above, which required mentally updating a count of rare tones among a series of standard tones and reporting the final count at the end of each block. The other task used in the present study was a visual Sternberg letter recognition task that involved the encoding of a memory set of two or four letters and shortly thereafter making a decision regarding whether a single probe letter was part of that memory set (Sternberg, 1966). The stimuli for these two tasks were alternated during each block (memory set - tone - probe letter - tone) but the priority given to each task was varied across blocks by instructing participants to attend only to the auditory oddball task, attend only to the visual Sternberg task, or to attend to both tasks equally. Thus, both task priority (block instructions) and task difficulty (memory load) were varied. Based on previous research using the oddball task, we predicted that the frontal cortex would show greater activity following rare target tones during blocks when they were attended compared to when these tones were ignored (Kiehl et al., 2001; Linden et al., 1999; Low et al., 2006). We further predicted, based on the ERP research reported above, that under dual task instructions the tone-related brain activity would be conditional on the memory load imposed by the Sternberg task (see also Strayer & Kramer, 1990), with greater activity following tones presented while holding only two letters and less activity following tones presented while holding four letters. Assuming that the two tasks tap into a common pool of limited resources, as the Sternberg task becomes more difficult, more of the limited supply of central resources will be allocated to remembering the letters and less will be available for updating the tone count when a target tone is presented and, therefore, less tone-related brain activation will occur on high memory load trials.

For the Sternberg task, we expected that target letters, similarly to target tones, would also produce greater activity in frontal cortex when they were attended compared to when they were ignored (Monoach et al., 1997; Narayanan et al., 2005). However, during dual task

¹Of course, if the spatial organization principle is microscopic (e.g. cortical columns), then non-invasive imaging techniques would likely not have the spatial resolution necessary to distinguish between undifferentiated and spatially organized processing units.

performance we predicted an opposite pattern to that of the tones based on memory load. Identifying the target letter on high load trials should require more resources than low load trials. Therefore we expected to see greater brain activation for target letters on high compared to low load trials. Thus, the present study was designed to investigate whether EROS recordings of brain activation would show a reciprocal relationship in frontal cortex across two working memory tasks as we varied task priority and difficulty. Finally, we also investigated whether the overlapping DLPFC areas were contributing to attention control in both tasks, or whether there was evidence of spatial organization (and perhaps reciprocal inhibition) within this cortical region across tasks.

Methods

Subjects

Eighteen young adults (12 women; mean age = 22.5 years) participated in this study. The participants indicated they had normal hearing and normal or corrected-to-normal vision and were not taking medications that would directly affect the central nervous system. The electrophysiological data from one subject were excluded due to errors in data collection. Prior to participation, all subjects signed informed consent. All procedures described in this report were approved by the University of Illinois Institutional Review Board.

Stimuli and Procedures

The paradigm included two interleaved tasks, a visual Sternberg memory task and an auditory oddball task. In the Sternberg task a memory set of two or four letters was presented followed 3200 ms later by a single probe letter. Subjects were asked to remember the letters and determine whether the probe letter was a member of the immediately preceding set and register that decision with a button press response with the right or left hand, counterbalanced across subjects. The visual stimuli consisted of white capital letters on a black background. Each letter subtended 0.5° of visual angle. Memory items were presented in sets of two (one on each side of a fixation cross) or four (two on each side of fixation) and single probe letters were presented centrally. The probe letters were displayed immediately above the fixation and persisted for 400 ms.

In the oddball task, a tone was presented every 3200 ms. The tone could be frequent (80%) or rare (20%) and subjects were instructed to keep a silent mental count of the number of rare tones presented during the block and report this count at the end of the block. The auditory stimuli were delivered via earphones at approximately 70 dB SPL. The tones were either 500 or 1000 Hz and were presented for 400 ms. The assignment of tone (500/1000 Hz) to probability condition (rare/frequent) was counterbalanced across subjects.

The stimuli from these two tasks were interleaved within a block of trials such that a stimulus was presented every 1600 ms and followed the pattern: letter set - tone - single/probe letter - tone, alternating for a total of 24 of these sequences per block. The instructions, however, varied across blocks. In different blocks subjects were instructed to do one of the following: 1) perform only the Sternberg task and ignore the tones (Stern); 2) perform only the oddball task and ignore the letters (Odd); or 3) perform both tasks (Dual). The instructions changed on every block and the order of instructions was counterbalanced across subjects. In total, subjects completed 8 blocks of each instruction condition.

Optical recording and analysis

Complete details of the optical recording procedures are reported in a previous report of a subset of these data (Low et al., 2006) referring only to the auditory oddball condition and will be described here in brief form.² Optical data were recorded over two sessions using

four modified ISS model 96208 frequency domain oximeters (Imagent ®; ISS, Inc., Champaign, IL). Within a session, the montage consisted of 8 detectors and 28 sources (combined to allow for 80 recording channels) covering the superior and middle frontal gyri and the posterior portion of the inferior frontal gyrus. The area sampled by this montage is shown by the dark gray coloring on the frontal cortex in the figures (e.g., Figure 1). The light sources were laser diodes emitting light at a wavelength of 690 nm, modulated at 220 MHz. The final sampling rate for the optical data was 62.5 Hz.

The locations of the sources and detectors were digitized with a Polhemus “3Space”™ 3D digitizer and co-registered with a volumetric T1-weighted MR image for each subject. The co-registered data were then Talairach-transformed to permit registration across subjects. The phase data were corrected off-line for phase wrapping, pulse artifacts were removed (Gratton & Corballis, 1995), and the data were low-pass filtered to 5 Hz (Maclin et al., 2003). Channels with standard deviations of the phase greater than 6 degrees were excluded from further analysis (for further details on these analytic steps see Gratton & Fabiani, 2007).

Finally, the phase data were divided into epochs around stimulus events of interest with 160 ms pre-stimulus baseline and 1000 ms post-stimulus recording. The time-locking events of interest were the onset of rare tones (Tones) in the auditory oddball task and the target (or probe) letters (Letters) in the visual memory search task. Although rare tones could occur either during the memory interval or between trials, we restricted analyses to only those tones occurring during the memory interval. This was done to equate, as much as possible, the dual task processing requirements of target tones and letters, each having to be evaluated while holding a memory load from the other task.

In-house software “OPT-3D” (Gratton, 2000) was used to combine channels whose mean diffusion paths intersected for a given brain volume (voxel) and to compute group-level statistics. A 4-mm Gaussian filter (based on 2 cm kernel) was used to spatially filter the data. The group-level statistics were then converted to Z-scores and orthogonally projected onto images of the superior surface of a brain in Talairach space (Talairach & Tournoux, 1988).

Statistical analysis of the EROS data primarily focused on two *a priori* regions of interest (ROIs) that encompassed portions of middle frontal gyrus (MFG) and superior frontal gyrus (SFG) in each hemisphere. The boundaries of these ROIs were defined in Talairach space as $x = (+/-) 7$ to $(+/-) 42$ and $y = 10$ to 55 . These boundaries were used in our initial analysis of these data (Low et al., 2006) and were based on the range of reported peak fMRI activations in MFG for similar target detection tasks (Casey et al., 2001; Kiehl et al., 2001; Linden, et al., 1999; Narayanan et al., 2005; Rypma et al., 2002). Correction for multiple comparisons was then applied based on the number of independent resolution elements (resels) within this region (Gratton et al., 2006; see also Kiebel et al., 1999).

Electrical recording and analysis

Prior to fitting the optical recording helmet, electrodes were applied for simultaneous recording of electrophysiological (EEG) signals. Using a Grass Model 12 amplifier with a bandpass setting of .01 to 30 Hz, EEG data were recorded from electrodes placed at Fp1, Fp2, F7, F8, C5, C6, and Pz and were referenced (off-line) to the average of electrodes at right and left mastoid locations. Eye movements and blinks were monitored with bipolar

²In our initial publication of this data we focused on the single task conditions only, presenting data related to rare versus frequent tone processing under active (count tones) versus passive (ignore tones) task instructions. The present paper concentrates on the processing trade-offs accompanying dual task demands.

recordings from the left and right outer canthi and above and below the left eye. Eye movements and blinks were corrected using the procedure developed by Gratton and colleagues (Gratton et al., 1983). Trials with voltage changes greater than 150 μ V across the 1400-ms recording window were rejected. This resulted in the rejection of ~10% of the trials. The data were then signal-averaged for each subject, channel, and trial type with time-locking to the onset of the rare tones and to the onset of the target letters. The averaged waveforms were baseline-corrected using a 160 ms window immediately preceding the target stimuli. For the analysis, we focused on Fp1, Fp2, and Pz as these electrodes carried the largest voltage changes. Mean amplitude measurements were computed for 100 ms intervals from 50-150 ms, 150-250 ms, and for 5 consecutive intervals starting at 300 ms. The first positive and negative peaks at Pz were shifted slightly later in time for the grand average waveforms time-locked to the letters (see Figure 2) so we measured two additional windows (100-200 and 200-300 ms) to better capture these first two components.

Results

Behavioral Performance

Table 1 provides the mean accuracy and reaction time data for the two tasks. Participants were less accurate counting the rare oddball tones in the dual task compared to the single task condition ($F(1,17) = 5.62, p < .05$). Accuracy for the end of block count (out of 8 blocks total) under single task instructions was 85.5% and this dropped to 75.8% when performing under dual task conditions. An alternative method for measuring accuracy is to compute the absolute difference between the reported tone count and the true count. Accuracy computed in this way was also greater for single (98.3%) compared to dual (95.8%) instructions. In contrast, performance on the Sternberg memory task did not differ between dual and single task instructions ($F < 1$ for both reaction time and accuracy). One interpretation of this pattern might be that subjects were prioritizing the Sternberg task over the oddball task when asked to perform both simultaneously. Alternatively, these results may indicate that the longer term memory requirements of the tone-counting task may be more prone to interference than the shorter term memory requirements in the Sternberg task.

Increasing the memory set size from 2 to 4 had the expected effects of slowing reaction time ($F(1,17) = 133.83, p < .001$, means: 668 vs. 764 ms, respectively) and reducing accuracy ($F(1,17) = 16.17, p < .001$, means: 92% vs. 88%, respectively). These effects did not interact with dual versus single task instructions (p 's $> .10$).

Optical and Electrical Brain Activity

The analysis of the EROS and ERP data focused first on comparing target processing when the target is task-relevant versus task-irrelevant, separately for time-locking to tones and letters. We then explored how this brain activity changes under the low and high memory load requirements that accompany the dual task condition. To more specifically investigate graded changes across task priority and memory load, we present linear trend analyses with opposite directional predictions for target tones (Odd $>$ Dual 2 $>$ Dual 4 $>$ Stern) versus target letters (Stern $>$ Dual 4 $>$ Dual 2 $>$ Odd). Finally, because some previous fMRI studies investigating dual-task coordination have reported recruitment of additional brain regions (Collette et al., 2005; D'Esposito et al., 1995; Dreher and Grafman, 2003; Szameitat et al., 2002) or increased activation for dual- compared to single-task requirements (Bunge et al., 2000; Erickson et al., 2005, 2007), we tested whether any region showed greater EROS activity under dual- compared to single-task instructions for each of the target types.

Effect of Task Relevance on Target Tone Processing—The statistical maps of the EROS data in Figure 1A indicate that both SFG and MFG showed greater activation during

tone-relevant blocks (oddball) compared to tone-irrelevant (Sternberg) blocks. The time courses of mean phase activity associated with the peak voxel for each of these regions are shown in the lower panel (Figure 1C). The effect of tone relevance was reliable in SFG from 96 to 176 ms following tone onset (peak Z at 128 ms = 3.46, $Z_{\text{crit}} = 3.02$; Talairach coordinates: $x = 7$, $y = 54$) and later in right MFG from 336 to 448 ms (peak Z at 368 ms = 3.44, $Z_{\text{crit}} = 3.04$; Talairach coordinates: $x = 22$, $y = 44$). This region of MFG was also the site for the peak difference between the rare (counted) and frequent (ignored) tones, as presented in the initial report of a subset of this data (Low, et al., 2006).

The ERP waveforms following the target tones can be seen in Figure 2A. Differences due to task relevance begin to emerge at Pz as early as 100 ms, with a slight positive shift overlying the N1 component for task-relevant tones compared to task-irrelevant ones ($F(1,16) = 5.55$, $p = .032$). As expected, the P3 response to the rare tones was greater when the tones were task-relevant (oddball instructions) compared to blocks when they were irrelevant (Sternberg instructions) [all 100 ms windows 300-700 ms were $p < .001$]. At frontal electrodes a reliable difference between instruction conditions did not emerge until later, with greater frontal negativity starting around 400 ms following rare tones when they were task-relevant [400-500: $F(1,16) = 6.02$, $p = .026$; 500-600: $F(1,16) = 6.97$, $p = .018$].

Effect of Task Relevance on Target Letter Processing—The presentation of target letters when they were task-relevant (Sternberg instructions) as opposed to task-irrelevant (Oddball instructions) also produced EROS activation in right MFG (Figure 1B) with a locus that was slightly more lateral and posterior to that produced following target tones. As can be seen in the mean phase waveforms (Figure 1D), sub-threshold differences started to emerge around 200 ms, but these differences only reached statistical criterion from 528 to 544 ms (peak $Z = 3.23$, $Z_{\text{crit}} = 3.17$; Talairach coordinates: $x = 37$, $y = 32$).

The ERP waveforms following the target letters (Figure 2B) also show differences as a result of task-relevancy. The first difference emerged at Pz with greater positivity from 100-200 ms ($F(1,16) = 8.17$, $p = .011$). As with target tone processing, there was greater P3 activity for task-relevant target letters compared to task-irrelevant and this increase in positivity persisted through much of the epoch [all 100 ms windows 300-700 ms were $p < .001$]. At frontal electrodes, the positivity around 200 ms and the negativity around 450 ms were both greater when the target letters were task-relevant compared to task-irrelevant ($F(1,16) = 12.78$, $p = .003$ and $F(1,16) = 4.74$, $p = .045$, respectively).

Dual Task Effects on Target Tone Processing—To investigate whether the right MFG activation was sensitive to graded changes in cognitive load, we compared target tone processing during the dual task instructions for tones that occurred while holding a memory set size of 2 versus 4 (Dual 2 > Dual 4) and tested the linear trend across all four conditions (Oddball > Dual 2 > Dual 4 > Sternberg). These analyses were directional to investigate the possibility that fewer resources may be available for processing the tones as difficulty increases on the Sternberg task and, in turn, lead to less tone-related brain activation.

Figure 3A (top) shows greater tone-related activation for Dual 2 compared to Dual 4. The peak of differential activity within the right ROI occurred at 320 ms (not shown in the figure), but this peak was on the boundary of the box and therefore localized to superior frontal gyrus (peak $Z = 3.09$, $Z_{\text{crit}} = 2.98$; $x = 7$, $y = 54$). There were, however, sub-threshold differences in MFG from 320 to 416 ms ($p < .05$ before correction for multiple comparisons). Furthermore, the linear trend analysis (Figure 3A, bottom) revealed robust activation in both SFG (peak at 128 ms: $Z = 3.64$, $Z_{\text{crit}} = 2.99$; $x = 7$, $y = 54$) and MFG (peak at 368 ms: $Z = 3.68$, $Z_{\text{crit}} = 3.03$; $x = 22$, $y = 42$). The mean phase values associated with each of the conditions going into the linear trends are provided in Figure 4A (solid lines).

We also conducted an exploratory analysis of the tone-locked averages to see if any areas showed greater overall activation for dual compared to the single task condition. As shown in Figure 6A, greater activation was found in the posterior portion of medial superior frontal cortex between 100 and 250 ms following target tones under dual task instructions compared to oddball instructions (160 ms: peak $Z = 3.16$, $p = .0008$ for a one-tailed test before correction for multiple comparisons; $x = 2$, $y = 19$).

The ERP data time-locked to the tones were also investigated for changes under dual-task instructions. Both the parietal P3 and frontal negativity were reduced during dual task blocks. As the dual task memory load increased from 2 to 4 letters, the P3 following the target tone diminished (300-400 ms: $F(1,16) = 5.94$, $p = .027$). The linear trend across all four conditions was significant from 300-500 ms (p 's $< .001$). These findings are consistent with a number of other dual task ERP studies showing a reduction in P3 activity to a secondary task as primary task difficulty increases (for reviews see Donchin et al., 1986 and Kok, 2001). In the present study, frontal electrodes Fp1 and Fp2 also showed sensitivity to load, with less negativity as memory load increased. At 300-400 ms, load interacted with side of recording ($F(1,16) = 5.12$, $p = .038$) and follow-up comparisons showed that the difference between dual 2 and dual 4 was only significant on the left during this time interval (Fp1: $F(1,16) = 6.96$, $p = .018$; Fp2: $F(1,16) = 1.34$, $p > .05$). However, the remaining 100 ms windows from 400-800 ms all showed a main effect of load (p 's $< .05$) with no interaction with side of recording. The trend analysis (performed separately for Fp1 and Fp2) showed a reliable linear trend (O > D2 > D4 > S) for intervals from 300-600 ms (p 's $< .05$, except Fp2 at 300-400 ms, $F(1,16) = 3.95$, $p = .06$). The mean amplitude measurements contributing to the linear trend at the frontal electrodes are shown in Figure 4B.

Dual Task Effects on Target Letter Processing—Figures 3 and 4 show that the pattern of EROS activity across conditions for target letters was opposite to that produced by target tones in the right hemisphere. Letters presented during dual task blocks produced greater activation in right MFG on Dual 4 trials compared to Dual 2 (peak at 608 ms: $Z = 3.24$, $Z_{\text{crit}} = 3.14$; $x = 32$, $y = 39$). Not only was the direction of the effect opposite, but also the latency was later for the letters (528-608 ms, $p < .05$) compared to the tones (304-336 ms, $p < .05$). The linear trend across the four conditions (Sternberg > Dual 4 > Dual 2 > Oddball) was also reliable in right MFG (peak at 544 ms: $Z = 3.21$, $Z_{\text{crit}} = 3.16$; $x = 34$, $y = 34$). It should also be noted that there was no effect of memory load (4 > 2) in the Sternberg only task; high and low load conditions showed equivalent activation in right MFG during single task requirements. This suggests that the decrease in activation from single to dual was due to the dual task demands and not simply a lack of MFG involvement in low load conditions (i.e., set size 2 trials during Sternberg only blocks produced activation in right MFG but set size 2 during dual blocks did not). The peak location for the linear trend for target letters was more lateral and slightly more posterior than that produced by the tones. A jackknife and multivariate analysis of variance procedure using the Wilks' Lambda criteria for significance was used to test whether the location corresponding to the peak linear trend for auditory tones (368 ms) differed from the location for the peak linear trend following visual letters (528 ms). The locations were indeed different ($F(2,13) = 6.63$, $p < .01$). Follow-up analysis of each dimension separately revealed that the peak locations differed only in laterality (left-right d: $F(1,14) = 12.06$, $p = .004$; anterior-posterior: $F(1,14) = 1.65$, $p = 0.22$).

Interestingly, a homologous area in the left hemisphere showed a markedly similar pattern of activity, but during the epoch immediately following the rare tones. Closer inspection of the maps for “target tones” at 128 ms (Figure 3A) reveals an area in the left hemisphere that showed a graded linear pattern across conditions, but in a direction opposite our prediction

for tone-locked activity. This pattern is indicated by blue coding for negative Z-scores (peak at 144 ms: $Z = -3.39$, $p = .0007$ for a 2-tailed test uncorrected for multiple comparisons; $x = -30$, $y = 27$). The pattern of means accompanying the activity in each hemisphere is overlaid in Figure 5. The data clearly indicate that the left MFG became active shortly following the onset of a rare tone when instructions were to *ignore* the tones and concentrate on the Sternberg memory task. One possible interpretation of these findings is that the left hemisphere may be important in dealing with the distraction caused by rare events that could disrupt rehearsal of the memory set. We will address this argument further in the discussion.

In the exploratory analysis (Figure 6B), two regions of left frontal cortex showed greater activation following target letters under dual task instructions compared to single task Sternberg instructions (L-IFG at 336 ms: peak $Z = 3.18$, $p = .0007$, $x = -55$, $y = 29$; L-SFG at 400 ms: peak $Z = 3.08$, $x = -20$, $y = 22$; $p = .001$, one-tailed test before correction for multiple comparisons). Both regions preceded the right MFG activity and, unlike the right hemisphere effects, were independent of memory load during dual task blocks.

Finally, the ERP waveforms following the target letters (Figure 2B) showed effects at both Pz and Fp1 and Fp2. In the latency range of the P3 complex, the Dual 2 condition produced greater positivity than the Dual 4 condition (100 ms intervals from 300-600ms: $F(1,16) = 26.94$, 19.81 , 13.38 , p 's $< .002$). This finding, though not consistent with a trade-off between the oddball and Sternberg tasks, is consistent with previous ERP studies and will be discussed in more detail in the discussion. Figure 4 shows that in contrast to the pattern at Pz, frontal electrodes showed a graded response producing a linear trend during the 400-500 ms measurement window ($F(1,16) = 3.80$ and 4.80 , $p < .07$ and $.05$ for Fp1 and Fp2, respectively).

Discussion

This is the first report of EROS recorded during a dual task paradigm and the results clearly indicate graded reciprocal effects in prefrontal cortex related to changing task demands. For both the auditory oddball task and the visual Sternberg task, activation in right DLPFC was greatest when target items were task relevant (100% priority), intermediate when performing both working memory tasks (50/50 priority), and smallest when target items were ignored (0% priority). Thus, imposing dual task instructions lead to a decrease in activation for both target letters and target tones. Moreover, while the peak location of these changes only differed by about a centimeter for the two types of targets, the effect of memory load on activation had opposite effects. For Sternberg letters, the intermediate dual task activity was greater on high load trials compared to low load trials. In contrast, for oddball tones presented during the memory interval, activity was greater during low load trials compared to high load trials. This trade-off in activation as task priority and memory load changes suggests a role of DLPFC in flexibly allocating limited cognitive resources. This interpretation is consistent with that of Uncapher and Rugg (2005) outlined in the introduction and is also supported by Erickson et al.'s (2007) finding, in an event-related fMRI study, of high and significant correlations (r 's $> .70$) between activity in the dorsal prefrontal cortex and performance in a psychological refractory period dual-task.

The reciprocal graded changes in right MFG are similar in nature to the effects of task priority and task difficulty on P3 amplitude in many dual task studies (Hoffman et al., 1985; Sirevaag et al., 1989; Strayer & Kramer, 1990; Wickens et al., 1983). Yet, in the present study, P3 amplitude for target tones and target letters did not show reciprocal effects. While the P3 to target tones got smaller with increasing load from the Sternberg task, as expected, the P3 to target letters also got smaller with increasing load. In fact, a decrease in P3 amplitude with increasing load is often found in Sternberg paradigms (Kok, 2001; Kramer

and Strayer, 1988; Mecklinger et al., 1992; Wijers et al., 1989), and the present data indicate that this pattern does not change under dual task demands. Several ideas have been put forth to explain the reduction in P3 amplitude with increasing memory load. For example, it may reflect a trade-off between memory rehearsal (an on-going process) and probe comparison/target identification processes³ (Kramer and Strayer, 1988) and/or it may reflect the increasing amount of equivocation or uncertainty about the classification of the target (Ruchkin & Sutton, 1978; Johnson, 1986; Kok, 1997). This latter interpretation could also explain the P3 effects to the oddball task; holding the tone count might be more disrupted by large memory sets and therefore there would be more uncertainty when updating the count on high load compared to low load trials.

In contrast to the P3 results, however, the frontal negativity recorded at Fp1 and Fp2 showed a markedly similar pattern, both in timing and in the directions of graded effects, to that of the EROS recording over MFG (see Figure 4). Both the frontal negativity and the EROS response occurred earlier following tones compared to letters and both showed reciprocal graded changes across task demands and task priority. Although both the optical and the electrical activity show patterns consistent with flexible allocation of attention, the exact relationship of the two measures is unclear. Graded effects in the EROS data were found at different latencies in the right and left frontal cortex whereas the electrical activity did not show any obvious lateralization pattern as a function of latency. With so few electrodes, it is impossible to isolate potential overlapping components that might act together to produce the observed patterns of electrical activity, and at the same time, the optical montage was not extensive enough to cover frontopolar cortical areas. Of course, even if we had ample optical and electrical coverage of the brain, the two methods may not necessarily measure the same neural activity. For example, ERPs are sensitive only to open field arrangements whereas EROS does not have this limitation. In contrast, EROS is only sensitive to relatively superficial neural changes. Therefore, the two neuroimaging methods should be considered complimentary in terms of understanding dynamic changes in brain activity.

The EROS data clearly indicate that different (although adjacent) locations of the right MFG are associated with processing of the auditory (tones) and visual stimuli (letters). The distance between these two regions (about 1 cm or so) makes it unlikely that differential effects between modalities could be observed with ERPs, especially since we did not use a high-density recording array. In this situation, the localization power of EROS was particularly useful. This finding has important implications: It means that the pool of resources allocated to the two tasks depending on task instructions is not really undifferentiated, but possesses a spatial organization related to the stimulation modality. A more medial region appears to be related to auditory information, and a more lateral region to visual information. Further studies will be necessary to determine whether this organization is specific to modality or whether some level of spatial organization would be present even within a given modality.

The data also suggest that activation (indicated by increase in phase delay) of one of these two regions of MFG is often associated with an opposite sign response (decrease in phase delay) in the other of these two regions. Because increases in phase delay are usually considered to be related to scattering changes associated with neuronal post-synaptic depolarization in a large number of neurons in a particular region (Gratton & Fabiani, 2007), it may be hypothesized that a reduction in phase delay may be associated with the opposite type of response (hyper-polarization of these neurons). The hyper-polarization, in turn, may

³In fact, the P3 following the memory set in this study did show greater amplitude for set size 4 compared to set size 2 in the dual task blocks, consistent with an interpretation of a trade-off in resources between memory rehearsal and probe comparison. The present study, however, was not designed to rule out other possible explanations.

be taken as an index of inhibition of a particular cortical region. Although at present quite hypothetical, this interpretation, if confirmed, would lead to conclude that activation of one of these MFG regions is associated with inhibition of the other. Although these brain activities were observed at different times, they can be understood as relative activations or deactivations occurring over a background of tonic activation, due to the sustained memory load imposed by both tasks, which would encompass both baseline and post-stimulation effects. This would translate into a mechanism of competition between these two cortical regions - or at least between the processing streams associated with each of them (Duncan et al, 1997).

The picture that would then emerge is one in which different modalities would compete with each other for “real estate” (i.e., neuronal activation) within the right MFG. This competition is influenced both by instructions as well as computational load (i.e., memory set size). Although preliminary and speculative in nature, this interpretation is consistent with current computational models of attention control, such as that proposed by Braver and Cohen (2001), as well as current views of the role of prefrontal cortex, and in particular the MFG, in attention and executive function (e.g., Bunge & Wallis, 2008; Corbetta & Shulman, 2002; Gratton, Low, & Fabiani, 2008). It is important to keep in mind that the paradigm used in this study not only interleaved stimuli from the two tasks (even when the instructions were to ignore one of the stimuli), but it also alternated the instructions from one block to another. This alternation may have encouraged the trade-off pattern of brain activation. In the single task conditions, it would seem beneficial to “turn off” a brain area that was responsible for allocating attention to the modality that should now be ignored. The fact that in previous blocks (i.e., dual task and the opposite single task) these stimuli were attended probably heightened the need for this type of control.

Interestingly, this interplay between different modalities is present in the right MFG only. At the same time the left MFG shows differential activation for dual vs. single task conditions for the visual letter-matching condition (which could be considered a difficult verbal task), but no activation for the tone oddball task (an easier task). Instead, when tone counting is all that is required (oddball only blocks) or when tones occur during low memory loads, the tones elicited a negative response in the left MFG (which, as proposed earlier, might be interpreted as inhibitory activity). Previous data suggest that the left hemisphere may play a role when information must be maintained in working memory in the presence of interference (Jonides et al., 1998). Our findings appear consistent with this interpretation, though it should be noted that we found these effects in a more dorsal region of prefrontal cortex. The lack of a similar effect for the auditory oddball task may be related to the fact that the right hemisphere is more specialized for oddball tone processing than the left one (Stevens et al., 2005), and/or to the relatively lesser difficulty of this task with respect to the Sternberg task. The asymmetry between the effects observed for the two tasks may then be summarized in the following fashion: whereas left MFG structures are actively recruited only by the Sternberg task (and excluded from access by the tone oddball task), right MFG structures can be recruited by both tasks, although in a spatially-organized and competitive fashion, in which instructions and task demands play a significant role. Thus, the Sternberg task has exclusive access to the left MFG, and competes with the oddball task for access to the right MFG.

This interpretation is consistent with the behavioral results, which indicate dual task costs for the oddball task but not for the Sternberg task. Also, this interpretation is consistent with the P3 results, which indicate reductions in the amplitude of the P3 elicited by the oddball tones in the dual task condition with respect to the single task condition, a reduction which is visible only in the high memory load in the Sternberg task. Finally, it is consistent with the presence of large differences between single- and dual-task conditions for the frontal ERPs

elicited by the oddball tones but, to a much smaller degree, for those elicited by the probe letters. The frontal ERPs elicited by the oddball tones also show some form of task-related asymmetry (see Figure 2), which may be consistent with the different roles of the two hemispheres in the two tasks. However, the specific relationship between the frontal ERP and EROS effects is difficult to ascertain in the current data set, mainly because the small number of electrodes used prevents a spatial analysis of the ERP data.

In conclusion, the data of the current study indicate that dual task manipulations involving visual/verbal and auditory/tonal working memory tasks lead to differential recruitment of prefrontal cortex regions, mostly in the MFG. Left and right prefrontal structures are differentially affected by instructions and task demands, with the left MFG being preferentially recruited by the visual/verbal task, whereas the two tasks compete for the recruitment of right MFG structures. The right MFG appears to be spatially organized, with a medial region more specialized for auditory/tonal information and a more lateral region more specialized for the visual/verbal information. Task demands may however partially overrule this basic organization. Consistent with the Braver and Cohen's (2002) model, the data provide support for a competition view of dual task processing. They also demonstrate the advantages provided by the use of an imaging technique (EROS) combining spatial and temporal resolution.

Acknowledgments

This work was supported by, NIMH Grant # MH080182 to G. Gratton, and ONR-MURI grant #N00014-07-1-0903 to A. Kramer, G. Gratton & M. Fabiani. We thank Charles L. Brown III for computer programming and technical assistance on the ERP waveform display program, and Dr. David Friedman for ERP software developed in his laboratory. Echo Leaver is now at Skidmore College, Saratoga Springs, NY.

References

- Adcock RA, Constable RT, Gore JC, Goldman-Rakic PS. Functional neuroanatomy of executive processes involved in dual-task performance. *Proceedings of the National Academy of Sciences*. 2000; 97(7):3567–3572.
- Allison BZ, Polich J. Workload assessment of computer gaming using a single-stimulus event-related potential paradigm. *Biological Psychology*. 2008; 77(3):277–283. [PubMed: 18093717]
- Band GPH, Jolicoeur P, Akyürek EG, Memelink J. Integrative views on dual-task costs. *European Journal of Cognitive Psychology*. 2006; 18(4):481–492.
- Bunge SA, Klingberg T, Jacobsen RB, Gabrieli JDE. A resource model of the neural basis of executive working memory. *Proceedings of the National Academy of Sciences*. 2000; 97(7):3573–3578.
- Bunge, SA.; Wallis, JD., editors. *Neuroscience of rule-guided behavior*. Oxford University Press; Oxford: 2008.
- Braver TS, Cohen JD. Working memory, cognitive control, and the prefrontal cortex: Computational and empirical studies. *Cognitive Processing*. 2001; 2:25–55.
- Casey BJ, Forman SD, Franzen P, Berkowitz A, Braver TS, Nystrom LE, Thomas KM, Noll DC. Sensitivity of prefrontal cortex to changes in target probability: A functional MRI study. *Human Brain Mapping*. 2001; 13(1):26–33. [PubMed: 11284044]
- Collette F, Olivier L, Van der Linden M, Laureys S, Delfiore G, Luxen A, Salmon E. Involvement of both prefrontal and inferior parietal cortex in dual-task performance. *Cognitive Brain Research*. 2005; 24(2):237–251. [PubMed: 15993762]
- Corbetta M, Shulman GL. Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*. 2002; 3:201–215.
- D'Esposito M, Detre JA, Alsop DC, Shin RK, Atlas S, Grossman M. The neural basis of the central executive system of working memory. *Nature*. 1995; 378:279–281. [PubMed: 7477346]

- Donchin, E.; Kramer, AF.; Wickens, C. Applications of brain event-related potentials to problems in engineering psychology. In: Coles, MGH.; Donchin, E.; Porges, S., editors. *Psychophysiology: Systems, processes, and applications*. Guilford Press; New York: 1986. p. 702-718.
- Dreher J-C, Grafman J. Dissociating the roles of the rostral anterior cingulate and the lateral prefrontal cortices in performing two tasks simultaneously or successively. *Cerebral Cortex*. 2003; 13(4): 329–339. [PubMed: 12631562]
- Duncan J, Humphreys G, Ward R. Competitive brain activity in visual attention. *Current Opinion in Neurobiology*. 1997; 7(2):255–261. [PubMed: 9142748]
- Duncan J, Owen AM. Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurological Sciences*. 2000; 23(10):475–483.
- Erickson KI, Colcombe SJ, Wadhwa R, Bherer L, Peterson MS, Scalf PE, Kramer AF. Neural correlates of dual-task performance after minimizing task-preparation. *Neuroimage*. 2005; 28:967–979. [PubMed: 16109493]
- Erickson KI, Colcombe SJ, Wadhwa R, Bherer L, Peterson MS, Scalf PE, Kim JS, Alvarado M, Kramer AF. Training induced functional activation changes in dual-task processing: An fMRI study. *Cerebral Cortex*. 2007; 17:192–204. [PubMed: 16467562]
- Goldberg TE, Berman KF, Fleming K, Ostrem J, Van Horn JD, Esposito G, Mattay VS, Gold JM, Weinberger DR. Uncoupling cognitive workload and prefrontal cortical physiology: A PET rCBF study. *NeuroImage*. 1998; 7(4):296–303. [PubMed: 9626670]
- Gratton G. "Opt-cont" and "Opt-3D": a software suite for the analysis and 3D reconstruction of the event-related optical signal (EROS). *Psychophysiology*. 2000; 37:S44.
- Gratton G, Brumback CR, Gordon BA, Pearson MA, Low KA, Fabiani M. Effects of measurement method, wavelength, and source-detector distance on the fast optical signal. *Neuroimage*. 2006; 32:1576–1590. [PubMed: 16872842]
- Gratton G, Coles MGH, Donchin E. A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*. 1983; 55:468–484. [PubMed: 6187540]
- Gratton G, Corballis PM. Removing the heart from the brain: Compensation for the pulse artifact in the photon migration signal. *Psychophysiology*. 1995; 32:292–299. [PubMed: 7784538]
- Gratton G, Corballis PM, Cho E, Fabiani M, Hood D. Shades of gray matter: Noninvasive optical images of human brain responses during visual stimulation. *Psychophysiology*. 1995; 32:505–509. [PubMed: 7568645]
- Gratton G, Fabiani M. Shedding light on brain function: the event-related optical signal. *Trends in Cognitive Sciences*. 2001; 5(8):357–363. [PubMed: 11477005]
- Gratton, G.; Fabiani, M. Optical Imaging. In: Parasuraman, R.; Rizzo, M., editors. *Neuroergonomics: The Brain at Work*. Oxford University Press; Cambridge, MA: 2007. p. 65-81.
- Gratton, G.; Low, KA.; Fabiani, M. Time course of executive processes: Data from the event-related optical signal. In: Bunge, SA.; Wallis, JD., editors. *Neuroscience of rule-guided behavior*. Oxford University Press; New York, NY: 2008. p. 197-223.
- Hoffman JE, Houck MR, MacMillan FW, Simons RF, Oatman LC. Event-related potentials elicited by automatic targets: A dual-task analysis. *Journal of Experimental Psychology: Human Perception & Performance*. 1985; 11(1):50–61. [PubMed: 3156958]
- Isreal JB, Chesney GL, Wickens C, Donchin E. P300 and tracking difficulty: Evidence for multiple resources in dual-task performance. *Psychophysiology*. 1980a; 17:259–273. [PubMed: 7384376]
- Isreal JB, Wickens CD, Chesney GL, Donchin E. The event related brain potential as an index of display monitoring workload. *Human Factors*. 1980b; 22:211–224. [PubMed: 7390505]
- Johnson R Jr. A triarchic model of P300 amplitude. *Psychophysiology*. 1986; 23:367–384. [PubMed: 3774922]
- Jonides J, Smith EE, Marshuetz C, Koeppel RA, Reuter-Lorenz PA. Inhibition in verbal working memory revealed by brain activation. *Proceedings of the National Academy of Sciences*. 1998; 95(14):8410–8413.
- Just MA, Carpenter PA, Keller TA, Emery L, Zajac H, Thulborn KR. Interdependence of nonoverlapping cortical systems in dual cognitive tasks. *NeuroImage*. 2001; 14(2):417–426. [PubMed: 11467915]

- Just MA, Keller TA, Cynkar J. A decrease in brain activation associated with driving when listening to someone speak. *Brain Research*. 2008; 1205:70–80. [PubMed: 18353285]
- Kiebel SJ, Poline J-B, Friston KJ, Holmes AP, Worsley KJ. Robust smoothness estimation in statistical parametric maps using standardized residuals from the general linear model. *NeuroImage*. 1999; 10(6):756–766. [PubMed: 10600421]
- Kiehl KA, Laurens KR, Duty TL, Forster BB, Liddle PF. Neural sources involved in auditory target detection and novelty processing: An event-related fMRI study. *Psychophysiology*. 2001; 38(1): 133–142. [PubMed: 11321614]
- Kok A. Event-related-potential (ERP) reflections of mental resources: a review and synthesis. *Biological Psychology*. 1997; 45:19–56. [PubMed: 9083643]
- Kok A. On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*. 2001; 38:557–577. [PubMed: 11352145]
- Kramer, AF.; Madden, D. Attention. In: Craik, FIM.; Salthouse, TA., editors. *The handbook of aging and cognition*. 3rd edition. Psychology Press; New York: 2008. p. XX-XX.
- Kramer AF, Sirevaag EJ, Braune R. A psychophysiological assessment of operator workload during simulated flight missions. *Human Factors*. 1987; 29(2):145–160. [PubMed: 3610180]
- Kramer AF, Strayer DL. Assessing the development of automatic processing: An application of dual-task and event-related brain potential methodologies. *Biological Psychology*. 1988; 26:231–267. [PubMed: 3207785]
- Kramer AF, Wickens CD, Donchin E. An analysis of the processing requirements of a complex perceptual-motor task. *Human Factors*. 1983; 25(6):597–621. [PubMed: 6671646]
- Linden DEJ, Prvulovic D, Formisano E, Völlinger M, Friedhelm EZ, Goebel R, Dierks T. The functional neuroanatomy of target detection: An fMRI study of visual and auditory oddball tasks. *Cerebral Cortex*. 1999; 9:815–823. [PubMed: 10601000]
- Low KA, Leaver E, Kramer AF, Fabiani M, Gratton G. Fast optical imaging of frontal cortex during active and passive oddball tasks. *Psychophysiology*. 2006; 43:127–136. [PubMed: 16712583]
- Maclin EL, Gratton G, Fabiani M. Optimum filtering for EROS measurements. *Psychophysiology*. 2003; 40(4):542–547. [PubMed: 14570162]
- Manoach DS, Schlag G, Bly BM, Benfield A, Edelman RR, Warach S. Prefrontal cortex fMRI signal changes are correlated with working memory load. *NeuroReport*. 1997; 8:545–549. [PubMed: 9080445]
- Mecklinger A, Kramer AF, Strayer DL. Event related potentials and EEG components in a semantic memory search task. *Psychophysiology*. 1992; 29(1):104–119. [PubMed: 1609022]
- Miller EK, Cohen JD. An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*. 2001; 24:167–202.
- Narayanan NS, Prabhakaran V, Bunge SA, Christoff K, Fine EM, Gabrieli JDE. The role of the prefrontal cortex in the maintenance of verbal working memory: An event-related fMRI analysis. *Neuropsychology*. 2005; 19(2):223–232. [PubMed: 15769206]
- Navon D, Gopher D. On the economy of the human processing system. *Psychological Review*. 1979; 86:214–255.
- Pashler, H.; Johnston, JC. Attentional limitations in dual-task performance. In: Pashler, H., editor. *Attention*. Psychology Press/Erlbaum (UK) Taylor & Francis; Hove, England: 1998. p. 155-189.
- Ruchkin, DS.; Sutton, S. Equivocation and P300 amplitude. In: Otto, D., editor. *Multidisciplinary perspectives in event-related potential research*. U.S. Government Printing Office/EPA; Washington, DC: 1978.
- Rypma B. Factors controlling neural activity during delayed-response task performance: Testing a memory organization hypothesis of prefrontal function. *Neuroscience*. 2006; 139(1):223–235. [PubMed: 16343777]
- Rypma B, Berger JS, D'Esposito M. The influence of working-memory demand and subject performance on prefrontal cortical activity. *Journal of Cognitive Neuroscience*. 2002; 14(5):721–731. [PubMed: 12167257]
- Sirevaag EJ, Kramer AF, Coles MGH, Donchin E. Resource reciprocity: An event-related brain potentials analysis. *Acta Psychologica*. 1989; 70:77–97. [PubMed: 2728903]

- Sternberg S. High-speed scanning in human memory. *Science*. 1966; 153:652–654. [PubMed: 5939936]
- Strayer DL, Kramer AF. Attentional requirements of automatic and controlled processing. *Journal of Experimental Psychology: Learning, Memory, & Cognition*. 1990; 16(1):67–82.
- Stevens MC, Calhoun VD, Kiehl KA. Hemispheric differences in hemodynamics elicited by auditory oddball stimuli. *NeuroImage*. 2005; 26(3):782–792. [PubMed: 15955488]
- Szameitat AJ, Schubert T, Muller K, von Cramon DY. Localization of executive functions in dual-task performance with fMRI. *Journal of Cognitive Neuroscience*. 2002; 14(8):1184–1199. [PubMed: 12495525]
- Talairach, J.; Tournoux, P. Co-planar stereotaxic atlas of the human brain. Georg Thieme Verlag; Stuttgart: 1988.
- Uncapher MR, Rugg MD. Effects of divided attention on fMRI correlates of memory encoding. *Journal of Cognitive Neuroscience*. 2005; 17(12):1923–1935. [PubMed: 16356329]
- Wickens, CD. The structure of processing resources. In: Nickerson, RS., editor. *Attention and performance VIII*. Lawrence Erlbaum; Hillsdale, NJ: 1980. p. 239-258.
- Wickens CD. Multiple resources and performance prediction. *Theoretical Issues in Ergonomics Science*. 2002; 3(2):159–177.
- Wickens CD, Kramer AF, Vanasse L, Donchin E. Performance of concurrent tasks: A psychophysiological analysis of reciprocity of information-processing resources. *Science*. 1983; 221:1080–1082. [PubMed: 6879207]
- Wijers AA, Mulder G, Okita T, Mulder LJM. Event-related potentials during memory search and selective attention to letter size and conjunctions of letter size and color. *Psychophysiology*. 1989; 26(5):529–547. [PubMed: 2616701]

Figure 1.

Task-relevant versus task-irrelevant EROS data. The top panels are spatial maps based on group level Z-statistics of the EROS data projected to the axial surface (LF = Left Front). The area in darker gray represents the brain area sampled by the recording montage and the light green rectangle indicates the region of interest (ROI). The bottom panels contain the time course of mean phase delay corresponding to the locations of the peak differences (white cross within the ROI). **A.** Target Tones: Task-relevant (oddball blocks) versus task-irrelevant (Sternberg blocks) at 128 ms and 368 ms following the onset of the target tones. **B.** Target Letters: Task-relevant (Sternberg) versus task-irrelevant (Oddball) at 528 ms following the onset of target letters. **C.** Grand average waveforms time-locked to target tones under oddball instructions (blue line) compared to Sternberg instructions (red line). **D.** Grand averages time-locked to target letters under oddball instructions (now task-irrelevant, blue line) compared to Sternberg instructions (red line). The light gray vertical bars represent the time windows for which task-relevant differed from task-irrelevant phase changes.

Figure 2.

Grand average ERP waveforms for blocks with oddball (blue line), Sternberg (red line) and dual-task (black lines) instructions. The dual task condition is further subdivided into trials with a memory load of two letters (solid black line) or four letters (dashed black line). **A.** Averages time-locked to the onset of the rare target tones. Zero indicates tone onset. **B.** Averages time-locked to the onset of single target letters. Zero indicates single letter onset.

Figure 3.

EROS effects of memory load during dual task blocks and linear trend analyses. **A.** Activity time-locked to the onset of target tones. The top panel shows that right SFG and MFG were more active on dual task trials with low (dual 2) compared to high (dual 4) load conditions. The bottom panel indicates a linear trend for these same regions (Oddball > Dual 2 > Dual 4 > Sternberg). **B.** Activity time-locked to the onset of target letters (the same time point is presented for both contrasts even though the peak occurred slightly later—608 ms—for the dual 4 vs. 2 comparison). The top panel shows that a lateral region of right MFG was more active on dual 4 compared to dual 2 trials and the bottom panel indicates this region was also characterized by linear trend reciprocal to that produced by tones (Sternberg > Dual 4 > Dual 2 > Oddball).

Figure 4.

A. Mean phase EROS values contributing to the reciprocal linear trends across conditions. The solid line represents activity time-locked to the target tones (peak location: $x = 22$, $y = 44$) and the dashed line represents activity time-locked to the target letters (peak location $x = 37$, $y = 32$). **B.** Mean amplitude ERP measures contributing to the linear trends across conditions. The solid lines represent activity time-locked to the target tones and the dashed lines represent activity time-locked to the target letters.

Figure 5.

Comparison of mean phase EROS activity of homologous left and right frontal cortical regions, but time-locked to different events. The solid line represents activity in the right hemisphere 544 ms after letter onset. The dashed line represents activity in the left hemisphere 128 ms after the onset of rare tones.

Figure 6. Dual- versus single-task EROS maps. **A.** Activity in medial SFG following target tones was greater during dual-task blocks compared to single-task oddball blocks. **B.** Activity in left IFG and left lateral SFG following target letters was greater during dual-task blocks compared to single-task Sternberg blocks. Activity in left IFG and left lateral SFG following target letters was greater during dual-task blocks compared to single-task Sternberg blocks.

Table 1

Accuracy and Reaction Time

Task Instructions	Accuracy (%)		RT (ms)
	Oddball Task	Sternberg Task	Sternberg Task
Oddball Only	85.5 (3.1)	--	--
Dual 2	75.8 (4.6)	91.8 (2.2)	668.8 (31.9)
Dual 4		88.5 (2.4)	764.0 (31.8)
Sternberg Only			
Load 2	--	93.8 (1.9)	666.5 (33.6)
Load 4	--	87.9 (2.4)	764.7 (33.1)

Note: Values are mean (SE).