

# Frontoparietal Traffic Signals: A Fast Optical Imaging Study of Preparatory Dynamics in Response Mode Switching

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## Abstract

■ Coordination between networks of brain regions is important for optimal cognitive performance, especially in attention demanding tasks. With the event-related optical signal (a measure of changes in optical scattering because of neuronal activity) we can characterize rapidly evolving network processes by examining the millisecond-scale temporal correlation of activity in distinct regions during the preparatory period of a response mode switching task. Participants received a precue indicating whether to respond vocally or manually. They then saw or heard the letter “L” or “R,” indicating a “left” or “right” response

to be implemented with the appropriate response modality. We employed lagged cross-correlations to characterize the dynamic connectivity of preparatory processes. Our results confirmed coupling of frontal and parietal cortices and the trial-dependent relationship of the right frontal cortex with response preparation areas. The frontal-to-modality-specific cortex cross-correlations revealed a pattern in which first irrelevant regions were deactivated, and then relevant regions were activated. These results provide a window into the subsecond scale network interactions that flexibly tune to task demands. ■

## INTRODUCTION

Everyday we encounter the need to respond to the changing demands of our environment by switching our attention between ongoing tasks. Task switching typically results in slower and less accurate performance, although switch costs are reduced when people are given time to prepare (Monsell, 2003; Wylie & Allport, 2000; Allport, Styles, & Hsieh, 1994; Jersild, 1927). Such improvements in switching efficiency have been attributed to greater recruitment of preparatory control processes on switch trials, during which attention is thought to be redirected from previously relevant tasks to focus on new demands (Hopfinger, Buonocore, & Mangun, 2000; Meiran, 2000; Sohn, Ursu, Anderson, Stenger, & Carter, 2000; for a review, see Karayanidis et al., 2010). These effects are associated with increased activity in prefrontal and parietal brain regions (i.e., the “frontoparietal network”; Gilbert & Shallice, 2002; Mesulam, 1990; Posner & Petersen, 1990), but they also typically involve differential activation of task-specific regions (see Kim, Cilles, Johnson, & Gold, 2012, for a meta-analysis). Theories of switching efficiency highlight two mechanisms: general cue-triggered instantiation or directing of attention and a succeeding cascade of task-specific preparatory processes that may involve discarding or inhibiting irrelevant task rules, retrieving trial-appropriate ones and maintaining the relevant task set (Jamadar, Hughes, Fulham, Michie, &

Karayanidis, 2010; Dosenbach et al., 2006; Aron, Monsell, Sahakian, & Robbins, 2004; Perianez et al., 2004; Rushworth, Walton, Kennerley, & Bannerman, 2004; Monsell, 2003; Swainson et al., 2003; Corbetta & Shulman, 2002; Gilbert & Shallice, 2002; Pashler, Johnston, & Ruthruff, 2001). Preparatory control theories assert that prefrontal regions initiate coordination of attention processes and bias brain states toward the relevant stimulus or task (Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005; Corbetta & Shulman, 2002; Miller & Cohen, 2001). However, general knowledge of such dynamics across switching paradigms is limited (Kim, Johnson, Cilles, & Gold, 2011; Monsell, 2003).

Especially little is known about the control processes associated with switching between response modalities and whether this manipulation generates similar brain activation patterns to those observed when switching between two tasks. In this study, we chose response domains with well-characterized and anatomically specific functional profiles: manual and vocal responses. As numerous studies have shown increased activity within sensory cortices because of attentional shifts related to the task stimulus or modality (Weissman, Warner, & Woldorff, 2004; Hopfinger et al., 2000), we predicted modulation of the motor cortex and Broca’s area during the delay period where preparation likely involves “preactivation” of response production areas (Wylie, Javitt, & Foxe, 2006). In a meta-analysis of task-switching experiments that included button press or speech outputs, Dosenbach and colleagues (2006) found activity in parietal and temporal areas, but only in tasks

that required a button press response. Thus, another prediction for task-specific modulation in this study involves activation of distinct networks, with posterior parietal areas for manual preparation and left-lateralized peri-sylvian areas for vocal preparation.

Task-specific reconfiguration may also involve reciprocal inhibition, an idea proposed in some models of attention control (Hasher, Lustig, & Zacks, 2007; Herd, Banich, & O'Reilly, 2006; Miller & Cohen, 2001), where processes required for a particular task may be suppressed when different task demands are imposed. For example, activity in middle frontal gyrus (MFG) to inferior frontal gyrus (IFG) in the left and right hemispheres has been shown to be differentially responsive to verbal or spatial tasks (Gratton, Wee, Rykhlevskaia, Leaver, & Fabiani, 2009; Reuter-Lorenz et al., 2000; Smith, Jonides, & Koeppe, 1996). In a previous EROS study, switching to a verbal task resulted in activation of left pFC while switching to a spatial task involved right pFC (Gratton et al., 2009). Such effects are accompanied by deactivation in the task-irrelevant region (Rykhlevskaia, Fabiani, & Gratton, 2006) and are modulated by the strength of the structural or functional connections between preparatory control areas. Thus, in this experiment, we expect to observe both down- and up-regulation of networks in preparation for response production depending on which aspects of response activation are being primed or suppressed.

Cognitive control processes involved in task switching are likely implemented in networks of regions throughout the brain, with patterns of activation changing with task demands. Functional network connectivity is most often assessed by computing correlations between patterns of activity in distinct areas (for a review, see Rykhlevskaia, Gratton, & Fabiani, 2008). These analyses are typically carried out on fMRI data (Gratton, Nomura, Pérez, & D'Esposito, 2012; Bullmore & Sporns, 2009; Smith et al., 2009; Cohen et al., 2008; Fox et al., 2005) using multivariate or seed-based approaches that reveal regional patterns of synchronization. Although very useful for extracting network components, the slow-evolving hemodynamic signals associated with fMRI limit our ability to identify network dynamics and, in particular, the order of activation of network areas. Electroencephalography-based (EEG and ERP) techniques can better characterize the millisecond-scale unfolding of events within and across trials. Source localization techniques can, in some cases, identify distinct signal generators in the brain and thus provide a way to examine the flow of information between areas, such as the proposed frontal to posterior cascade of attentional control processes. Nonetheless, some details about the areas involved are likely to be lost because of EEG's limited spatial resolution. Increasingly, more studies are conducted with magnetoencephalography (MEG; de Pasquale et al., 2010), which possesses a temporal resolution similar to EEG, but a better spatial resolution. MEG findings and studies that integrate fMRI with ERP results show that the distribution of frontoparietal activity generally proceeds

in an anterior to posterior direction (Brass et al., 2005; Perianez et al., 2004), but other studies using EEG source reconstruction and dynamic causal modeling of fMRI data have observed the opposite flow of activity (Wang et al., 2010; Green & McDonald, 2008). Similar to EEG, MEG has difficulty measuring independently the time course of activity in adjacent cortical regions (i.e., regions located less than a few cm apart); this, as well as its high cost and limited access, constrains functional connectivity research with MEG. In the current study, we employ the event-related optical signal (EROS; see Gratton & Fabiani, 2010, for a review), a technique that combines high spatial and temporal resolution to identify rapidly oscillating and distinct sources of cortical activity.

EROS uses near-infrared light to detect variations in the optical properties of neural tissues caused by neuronal activity (Foust & Rector, 2007; Rector, Carter, Volegov, & George, 2005; Rector, Poe, Kristensen, & Harper, 1997) and is thus capable of localizing activity to the subcentimeter scale and with a temporal resolution of less than 50 msec. We use a frequency domain method, as this technique allows us to measure both the amount of light that diffuses through a brain region and the average time taken by photons to travel between sources and detectors. Despite its high spatiotemporal resolution, the limitations of EROS include its inability to detect activity from deeper subcortical regions and its relatively low signal-to-noise ratio. In addition to increasing the amount of trials and participants, one way to address the signal-to-noise ratio issue while taking advantage of the spatiotemporal properties of EROS is to employ lagged cross-correlation analyses (see Rykhlevskaia et al., 2006). Computations between time series are conducted separately for each participant and thus increase the power to detect rapidly evolving patterns of activity with onsets that may vary across individuals. This approach has been used for time and frequency analyses of EEG and MEG data (Gross et al., 2001; Bressler, 1995; Gevins et al., 1983). The rich spatio-temporal information provided by EROS can help characterize the millisecond progression of activity across regions and thus assess functional connectivity at a high spatiotemporal resolution. We use timing information in the form of lags to model how activity in one area may precede or follow activity in other regions (Rykhlevskaia et al., 2006). To test the predictions of prefrontal-directed disengagement and engagement of task-specific processes, we incorporated the seed-based approach from fMRI with cross-correlations across a range of time lags. From the resulting positive and negative correlations, we can infer relative increases and decreases in brain activity.

To summarize, in this experiment, participants received a precue indicating whether to respond vocally or manually on the upcoming trial. First, to identify distinct preparatory processes, we took advantage of the temporal dynamics and extended cortical coverage offered by EROS. Specifically, we used lagged cross-correlations to characterize the spatiotemporal evolution of preparatory mechanisms. We also concurrently recorded EEG data

to provide an external validation for the time course of the EROS activities. Second, we investigated an understudied area of switching—the switching between response modalities—to test whether in motor output-oriented response preparation we observe frontoparietal activity, similar to when switching between stimulus processing goals. To preview our findings, cross-correlations revealed a robust association between an early parietal switch effect and a subsequent frontal switch effect, confirming the functional connectivity of these two regions. Our results revealed distinct frontoparietal networks based on correlation and propagation of activity from the frontal seed, with network topology differing according to switching modality. These results suggest that flexible network dynamics in frontoparietal networks are critical to switching-related control of attention.

## METHODS

### Participants

Sixteen right-handed adults aged 18–28 years (11 women; mean age = 22 years) participated in the study and received compensation of \$10/hr. One participant was discarded from the analysis because of technical difficulties in data acquisition, resulting in a sample size of 15 for EROS analysis. EEG data were not collected for three participants, leaving 12 participants for EEG analysis. All participants were native English speakers, with normal hearing, normal or corrected-to-normal vision, and normal speech. The study was approved by the University of Illinois Institutional Review Board, and all participants provided informed consent.

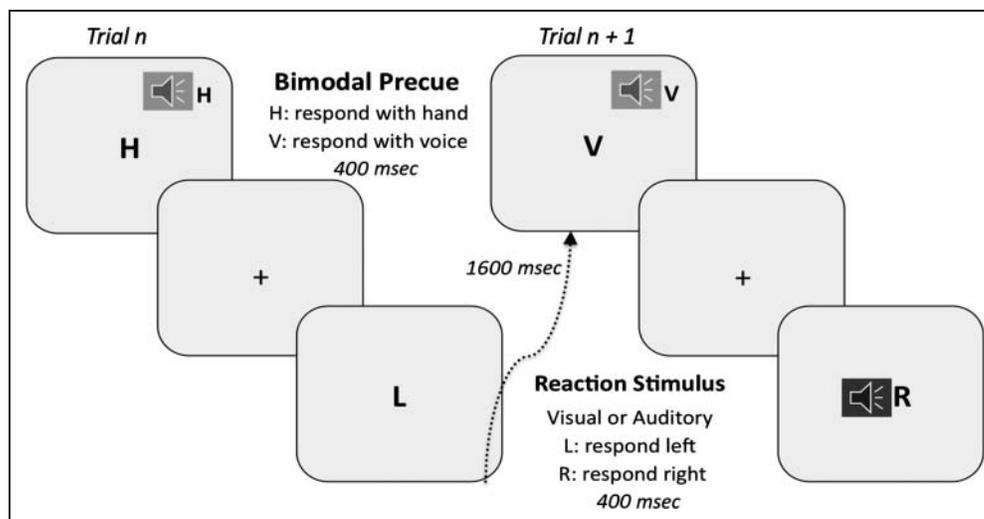
### Behavioral Task

The paradigm is shown in Figure 1. Participants initiated a block of trials by pressing a key on the keyboard. A fixation

cross was presented on a computer screen for 2000 msec, after which bimodal auditory–visual precues consisting of the letters “V” or “H” were simultaneously presented onscreen and via speakers for 400 msec. The precue indicated the relevant response modality for the trial: “V” for a vocal response to be made through a voice key by saying the word “left” or “right” and “H” for a manual (hand) response using either the left or the right hand. Letter precues were presented centrally in white text over a black background and subtended a visual angle of 1.6°. Speakers were positioned on either side of the monitor and auditory precues were presented at 70 dB. The reaction stimulus was presented 2000 msec after the precue and had a duration of 400 msec. For the reaction stimulus, participants saw an “L” or “R” on the screen or heard an “L” or “R” indicating a “left” or “right” response, respectively. For manual trials, participants responded with a key press using either their left or right index finger. For example, if participants received “H” as precue and “L” as reaction stimulus, they should respond by pressing their left index finger. For vocal responses, participants uttered the word “left” or “right” into the voice key. The modality of the reaction stimulus was counterbalanced across response modalities (e.g., the stimulus requiring a vocal response could be either auditory or visual, and the same was true for the stimulus indicating a hand response). Participants were instructed to respond as quickly and accurately as possible. A chin rest was used to establish a fixed distance between mouth and voice key. There were four basic trial types: manual right, manual left, vocal right, and vocal left. At each trial, response modality was either the same as the previous trial (repeat) or different (switch). Switch and repeat trials occurred randomly and equiprobably. The intertrial interval was 2000 msec. Participants completed four runs of 20 blocks with 24 trials each.

To ensure that participants understood the relationship between the precue and reaction stimulus and spoke loudly enough to trigger the microphone key on vocal

**Figure 1.** Response modality switching paradigm. Shown in the figure are two trials depicting a switch sequence. The reaction stimulus’ modality (visual or auditory) was counterbalanced across response modalities.



trials, we administered a training session before the experiment. The first part of training consisted of two task blocks identical to the experiment blocks but presented at a slower pace. During training, the interval between the precue and reaction stimulus was 3200 msec, and the inter-trial interval was 2400 msec. Training continued with five blocks that were administered with the normal experimental timing detailed above.

RT (msec) and accuracy (% correct) were obtained for all trials of the four experimental runs. We discarded the first trial of every block because it could not be defined as a switch or repeat trial and analyzed only RTs for trials with correct responses. If participants emitted both a manual and a vocal response, the trial was counted as incorrect. RTs shorter than 200 msec were discarded from the analysis. Because of technical problems with the voice key, some vocal responses were not recorded during the experiment. For these trials, concurrently obtained video recordings allowed us to code accuracy post hoc, but not RT.<sup>1</sup> Accuracy scores were Fisher-transformed to increase sensitivity in detecting differences among conditions. For conditions with perfect accuracy, scores were converted to 0.999 for the Fisher transformation.

### Electrical Recording and Analysis

EEG activity was recorded concurrently with EROS with a sampling rate of 100 Hz. Electrodes were positioned at five locations based on the 10/20 electrode configuration: Fz, Cz, Pz, Oz, and right mastoid, referenced to the left mastoid, and re-referenced off-line to the average of the two mastoids. To monitor horizontal and vertical eye movements, electrodes were positioned above and below the right eye, and at the outer canthus of each eye. Data were bandpass-filtered on-line at 0.01 to 30 Hz and further processed offline with a fifth order Butterworth high-pass filter set at 0.25 Hz to remove slow drifts. Before analysis, the data were segmented into epochs, time-locked to precue onset, and baseline-corrected using a 200-msec period preceding the precue. Ocular artifact correction was performed (Gratton, Coles, & Donchin, 1983), and epochs with voltage changes greater than 150  $\mu$ V were discarded. Data for correct trials were averaged for each participant, trial condition, and electrode.

Trials were sorted according to the main effects of interest: switch type and response modality. To increase power in detecting differences among the conditions of interest, waveforms were collapsed across reaction stimulus modality and correct response (left/right). Data were then analyzed with a  $2 \times 2$  repeated-measures ANOVA with Switch Condition and Response Modality as factors.

We created consecutive 50-msec windows for the first 1000 msec after the precue, yielding 20 time points for statistical analysis. The electrodes that carried the largest voltage changes (Fz, Cz, and Pz) were used to identify time intervals corresponding to general and modality-specific switching effects. Amplitude measures for the P1

(90–160 msec), N1 (150–230 msec), and P2 (200–250 msec) components were obtained by creating time windows around visually identified peaks in the average waveforms, separately for switch and repeat trials, and for each response modality.

### Optical Recording and Analysis

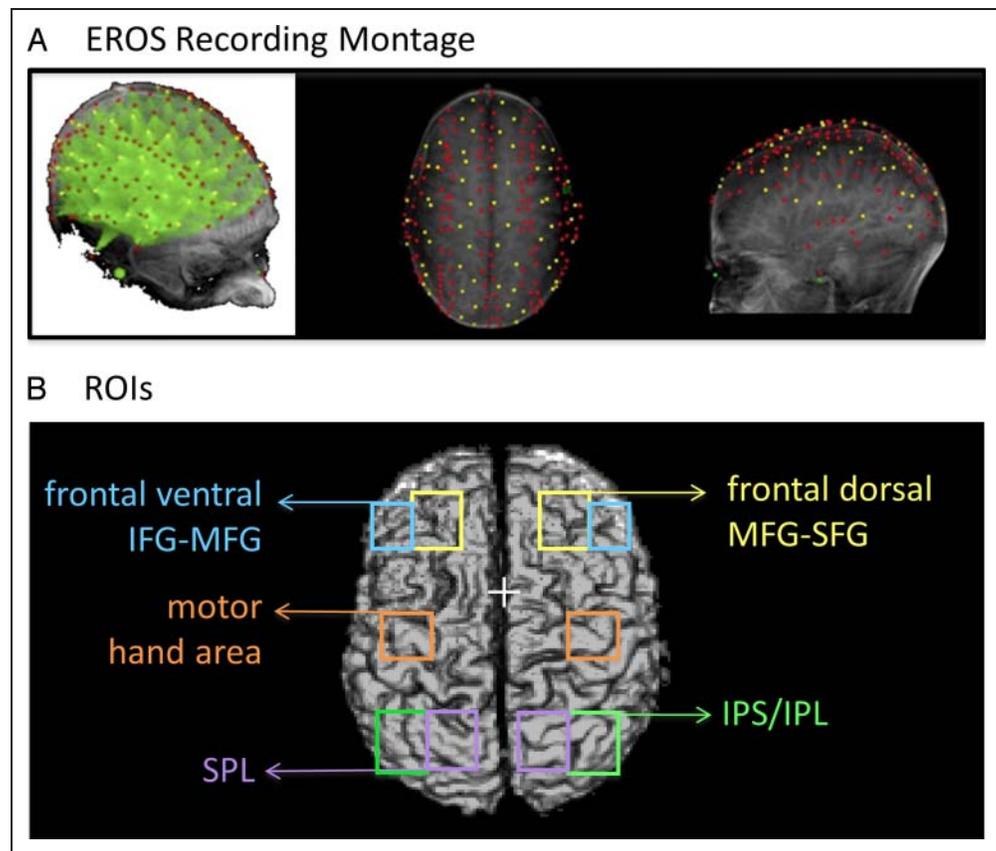
Each participant's optical data were recorded using two independent Imagent frequency domain systems (ISS, Inc.). Laser diodes emitted near infrared light (830 nm) modulated at 110 MHz over frontal and central brain regions and at 300 MHz for parietal and occipital regions. Maclin, Low, Fabiani, and Gratton (2007) showed that these two modulation frequencies yielded relatively similar EROS responses, once the phase delay data are transformed into picoseconds. To avoid cross-talk between the two systems, sources from one system were never closer than 6 cm from any detector on the other system. To achieve this, we recorded from frontal and parietal regions in one set of runs and central and occipital regions in another set of runs, with the order of these runs counterbalanced across participants. Optic fibers 400  $\mu$ m in diameter were used to channel the light onto the scalp surface, and 3-mm fiber-optic bundles connected to photomultiplier tubes detected the output light. Fast Fourier transforms were applied to the output current to compute measures of DC (average) intensity, AC (amplitude), and relative phase delay (in picoseconds). The optical data were continuously recorded over each block and sampled at 39.0625 Hz.

Sources and detector fibers were secured on the participants' heads using modified motorcycle helmets. Four recording montages were used to cover the majority of cortex. Each montage was recorded in a separate run, and the order was counterbalanced across participants. Each montage consisted of 16 detectors and 50–60 time-multiplexed sources, for a total of 256 channels per montage.

The location of each source and detector (Figure 2A) in relation to the nasion and fiducial preauricular points was digitized using a Polhemus "3Space" 3-D digitizer. Volumetric T1-weighted (MPRAGE) MR images were acquired for each participant with vitamin E pills positioned on the nasion and preauricular points. The fiducial markers permitted coregistration of each participant's digitized optical channels with the corresponding anatomical images. The data were submitted to scalp surface-fitting using a Levenberg–Marquardt algorithm (least-squares fit) and standard Talairach transformation (Whalen, Maclin, Fabiani, & Gratton, 2008). Only channels with source detector distances of 15–55 mm were included in the analysis.

Phase delay (time-of-flight) measures from the period of precue onset to 1000 msec following precue onset are included in this article. Phase data were corrected for phase wrapping, pulse artifacts (Gratton & Corballis, 1995), adjusted to a mean of zero for each block, and bandpass-filtered between 0.50 and 10 Hz. The data for correct trials were segmented into epochs time-locked to the onset

**Figure 2.** (A) Estimated projections (in green) of areas investigated by the optical recording montages. Sources (red dots) and detectors (yellow dots) are coregistered onto a 3-D anatomical image. (B) Approximate boundaries of ROIs. See Table 1 for ROI details.



of the precue and averaged separately for each participant, condition (Switch  $\times$  Modality), and channel and baseline-corrected using a 153-msec period preceding the precue, similar to the ERP analysis.

Only channels with phase standard deviation less than 100 psec were included in the analysis (Gratton et al., 2006). In-house software “Opt-3d” (Gratton, 2000) was used to compute statistics and combine data from channels whose diffusion paths intersected a given voxel (Wolf et al., 2000). Data were spatially filtered with an 8-mm Gaussian kernel. To compute statistical maps, group-level  $t$  statistics were derived across participants and then converted to  $z$ -scores, with appropriate correction for multiple comparisons using random field theory (Kiebel, Poline, Friston, Holmes, & Worsley, 1999).  $Z$ -scores were orthogonally projected onto axial, sagittal, and coronal surfaces of a brain in Talairach space.

Trials were sorted according to the main effects of interest: switch type and response modality. To increase power in detecting differences among the conditions of interest, waveforms were collapsed across reaction stimulus modality (auditory/visual) and correct response (left/right). The factors of Switch and Response Modality were entered into a  $2 \times 2$  repeated-measures ANOVA.

ROIs were identified around dorsal and ventral regions of frontal and parietal cortex (Figure 2B), areas hypothesized to show switch-related modulation. ROIs

were created around peak voxel activity of previous studies of task switching (Gratton et al., 2009; Badre & Wagner, 2006; Dosenbach et al., 2006; Brass & von Cramon, 2004; Sohn et al., 2000) and frontoparietal attention networks (Corbetta & Shulman, 2002; Hopfinger et al., 2000). Using the Talairach Daemon software (Lancaster et al., 1997, 2000) as a guide, ROI boundaries were specified to maintain consistency with anatomical structure boundaries and to minimize overlap with other ROIs. The same software was also used to estimate the Brodmann’s areas encompassed by each ROI. Coverage of the EROS montage also limited ROI boundaries, particularly in ventral frontal regions. ROI boundaries are reported in Table 1.

ROIs were also created in response production areas thought to be involved in response preparation. The motor hand area ROI was created around the “omega knob” landmark in the precentral gyrus of both hemispheres (Yousry et al., 1997; see also Maclin, Low, Sable, Fabiani, & Gratton, 2004, for a similar localization approach). The mouth motor area (lips, tongue, larynx) was estimated using previous studies of speech production (Brown, Ngan, & Liotti, 2008; Pulvermuller et al., 2006) and was localized to a ventral section of the motor cortex. Likewise, the Broca’s area ROI was based on previous studies and localized to an area encompassing left posterior inferior frontal gyrus (Tse et al., 2007; Embick, Marantz, Miyashita, O’Neil, & Sakai, 2000).

**Table 1.** ROI Boundaries

<i>Region</i>	<i>Left</i>	<i>Right</i>	<i>Brodmann's Area</i>
Frontal dorsal: MFG–SFG	$x = -40 -20$ $y = 22 45$	$x = 15 35$ $y = 22 45$	8, 9
Frontal ventral: IFG–MFG	$x = -60 -40$ $y = 20 40$ $z = 10 30$	$x = 35 55$ $y = 20 40$ $z = 10 30$	45, 46
Motor hand area	$x = -50 -30$ $y = -30 -10$	$x = 30 50$ $y = -30 -10$	4
IPS/IPL	$x = -55 -33$ $y = -85 -55$ $z = 20 40$	$x = 28 50$ $y = -85 -55$ $z = 20 40$	40
Superior parietal lobule (SPL)	$x = -33 -10$ $y = -80 -55$ $z = 42 52$	$x = 5 28$ $y = -80 -55$ $z = 42 52$	7
Broca's area (not shown)	$y = 0 25$ $z = -5 15$	n/a	44, 45
Motor mouth area (not shown)	$y = -15 5$ $z = 30 45$	$y = -15 5$ $z = 30 45$	4

Coordinates are in Talairach space. Data presented are surface projections. Only two boundary dimensions are reported for ROIs that were analyzed using only axial projections ( $X, Y$ ) and for those analyzed using only sagittal projections ( $Y, Z$ ).

### Cross-correlation Analyses

To elucidate the spatiotemporal dynamics of the brain networks involved in response preparation, lagged cross-correlations (separately for each orientation) were computed for each participant (for more details, see Rykhlevskaia et al., 2006). For each analysis, we selected a seed voxel and correlated the seed's time series with the time series of all other voxels. Because we were interested in preparatory switch activity, analyses were conducted on the time series of the switch effects (i.e., the contrast of switch > repeat). Correlations were conducted at lags separated by 25.6-msec intervals, beginning at a lag of 0 msec and ending at a lag of 256 msec. By characterizing the relative order of activations, lagged cross-correlations allow us to examine events as they unfold and change in response to task demands. Because the cross-correlations are first computed separately for each participant, this analysis has more power to identify complex patterns, which may be obscured in typical analyses that rely on activity occurring at the same time points across individuals. The resulting correlation coefficient maps are based on an average of individual correlation coefficients, computed separately per voxel and statistically evaluated within ROIs as in the initial switch analyses.

The seed region for each analysis was determined by the peak voxel of the switch effects. To characterize the

functional coupling of frontal and parietal switch activity, the seed region was the peak voxel of the general parietal switch effect, which onset at an earlier latency than the frontal effect. To investigate the task-dependent dynamics of the frontal switch effects, the peak voxel was determined separately for each modality. The interval used for the time series correlations was centered around the peak latency of the activation in the seed area.

## RESULTS

### Behavior

Performance data were examined with a  $2 \times 2 \times 2$  (Response Modality [manual, vocal]  $\times$  Stimulus Modality [visual, auditory]  $\times$  Switch [switch, no switch]) repeated-measures ANOVA. Data were collapsed across response sides (left/right) to increase power in detecting differences in our conditions of interest. Separate tests were conducted for RTs and accuracy (% correct).

### RT

Mean RTs are shown in Table 2. There was a marginal effect of switch,  $\Lambda = .82$ ,  $F(1, 14) = 3.06$ ,  $p = .102$ . Although responses tended to be slower on switch trials

for all four trial types, the lack of a robust switch effect indicates that participants may have indeed used the period after the precue to prepare for the switch in response modality.

Although there were no reliable interactions, RTs revealed a main effect of Response Modality,  $\Lambda = .75$ ,  $F(1, 14) = 4.66$ ,  $p < .05$ , and a significant main effect of Stimulus Modality,  $\Lambda = .18$ ,  $F(1, 14) = 64.56$ ,  $p < .001$ . As shown in Table 2, RTs to manual trials and visual stimuli were faster compared with vocal trials and auditory trials, respectively. Performing the task while seated in front of a computer screen may have conferred an advantage for manual and visual trials. Manual response keys may have also been more sensitive than the microphone voice key. It can also be argued that auditory stimuli, compared with visual stimuli, deploy over time and, therefore, may have led to longer RTs.

### Accuracy

Accuracy results are presented in Table 2. There was a significant main effect of Switch,  $\Lambda = .75$ ,  $F(1, 14) = 4.77$ ,  $p < .05$ . Participants were more accurate on repeat trials compared with switch trials. There was no main effect of Response Modality although there was a significant effect of stimulus modality  $\Lambda = .66$ ,  $F(1, 14) = 7.16$ ,  $p = .018$ . Accuracy was higher for auditory than for visual stimuli.

**Table 2.** Mean Performance Metrics for Response  $\times$  Stimulus  $\times$  Switch Trials

Response Modality <sup>a</sup>	Reaction Stimulus			
	Auditory		Visual	
	M	SD	M	SD
<i>Reaction Time (msec)</i>				
Manual				
Repeat	667.19	120.30	528.23	92.39
Switch	679.90	136.17	545.05	103.09
Vocal				
Repeat	727.95	145.89	590.95	115.45
Switch	731.21	155.68	601.47	123.38
<i>Accuracy (% Correct)</i>				
Manual				
Repeat	0.98	0.02	0.96	0.05
Switch	0.97	0.03	0.96	0.04
Vocal				
Repeat	0.98	0.02	0.97	0.02
Switch	0.97	0.03	0.96	0.03

<sup>a</sup> $n = 15$ .

Comparing these results to those obtained with RT indicates a speed–accuracy trade off. Although responses to visual reaction stimuli were faster overall, they were also less accurate than responses to auditory stimuli.

### ERP Effects

The grand-averaged waveforms are presented in Figure 3. Fz, Cz, and Pz carried the largest switch-related voltage changes, with effects emerging as early as 100 msec. To test the significance of these visual impressions, the average waveforms were tested with a  $2 \times 2$  (Switch  $\times$  Response Modality) repeated-measures ANOVA. The analysis was performed separately for each 50 msec time interval and each electrode. Table 3 summarizes the statistical results that were used to identify time intervals of interest for the EROS analysis.

Switch  $\times$  Modality interactions were observed only at Cz between 100 and 250 msec. Pairwise comparisons revealed that for manual precues, switch trials were more positive than repeat trials, whereas for vocal precues, this pattern was reversed. After this initial interaction, there was a main effect of Switch for several intervals between 200 and 400 msec at Fz and Pz, characterized by a negative shift for switch relative to repeat trials. Switch effects were again observed beginning around 600 msec at both electrodes with switch now more positive than repeat. This later effect was more robust and reliable at Pz than at Fz.

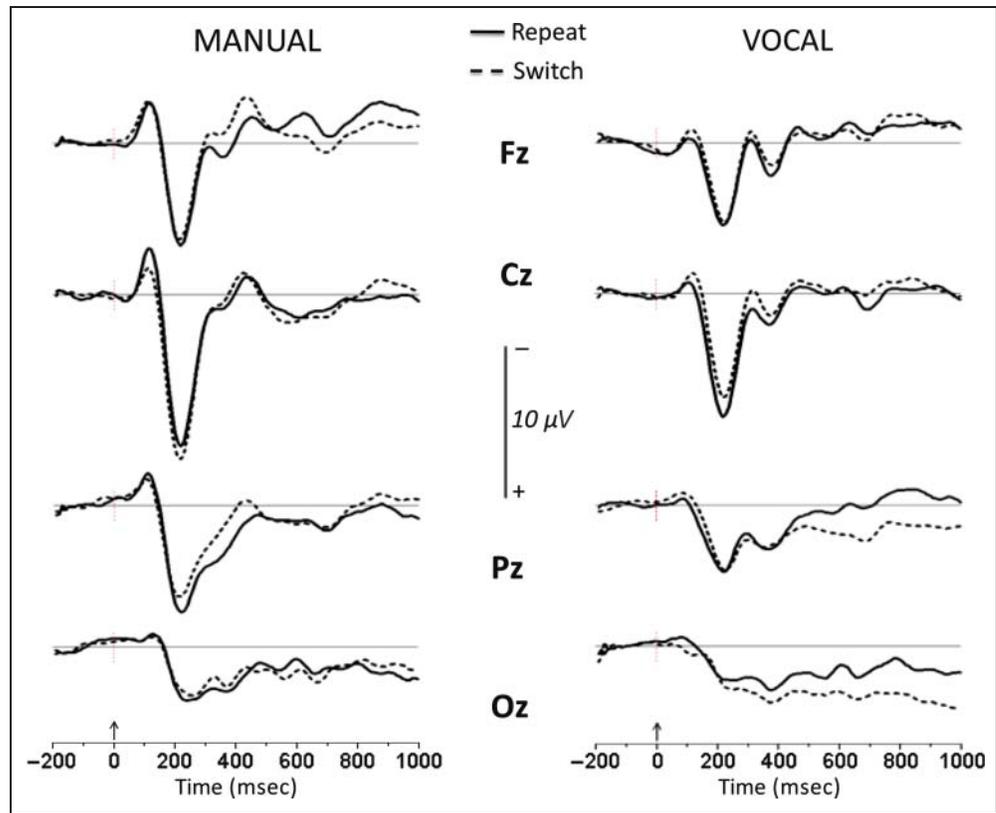
A Response Modality effect was present at all three electrodes from 125 to 275 msec and from 375 to 425 msec after the precue. From 525 to 625 msec, only Cz showed a modality effect. The N1 and P2 components were larger for manual than vocal precues (Figure 3). Although the auditory precues were presented at equal dB (sound pressure level), the specific sounds (“H” vs. “V”) were directly mapped and not counterbalanced across participants. Therefore, it is difficult to determine whether these early differences are a result of exogenous stimulus parameters or reflect endogenous differences in preparation.

In summary, the ERP analysis revealed three intervals of interest in which the experimental manipulations influenced brain activity: one centered around 200 msec after the precue, showing main effects of switch and response modality as well as a switch by modality interaction; one centered around 400 msec after the precue, showing main effects of switch and modality, and one centered around 600 msec again showing switch and modality effects.

### Optical Effects

Average cue-related optical activity was obtained for each participant and condition. To investigate switching-related preparatory activity, the optical data were examined with a  $2 \times 2$  (Switch  $\times$  Response Modality) repeated-measures ANOVA.

**Figure 3.** Grand-averaged ERP waveforms. Repeat trials (solid lines) and switch trials (dashed lines) are shown separately for each response modality, collapsed across stimulus modality. Averages are time-locked to precue presentation. Time zero indicates precue onset.



**Table 3.** Significant ERP Main Effects and Interactions in Electrodes of Interest

Electrode	Time from Precue (msec)																				
	25	75	125	175	225	275	325	375	425	475	525	575	625	675	725	775	825	875	925	975	
<i>Switch</i>																					
Fz							**	***	*				*								
Cz																					
Pz					**			***	*				**	*	*		*				
<i>Modality</i>																					
Fz	**	***	*****		**			**	**												
Cz			***	***	*****	***		*	*		**	**	**								
Pz		*	*****	***	*****	*****		*	***												
<i>Switch × Modality</i>																					
Fz									*												
Cz			**	****	**																
Pz																					

\* $p < .10$ .  
 \*\* $p < .05$ .  
 \*\*\* $p < .01$ .  
 \*\*\*\* $p < .001$ .

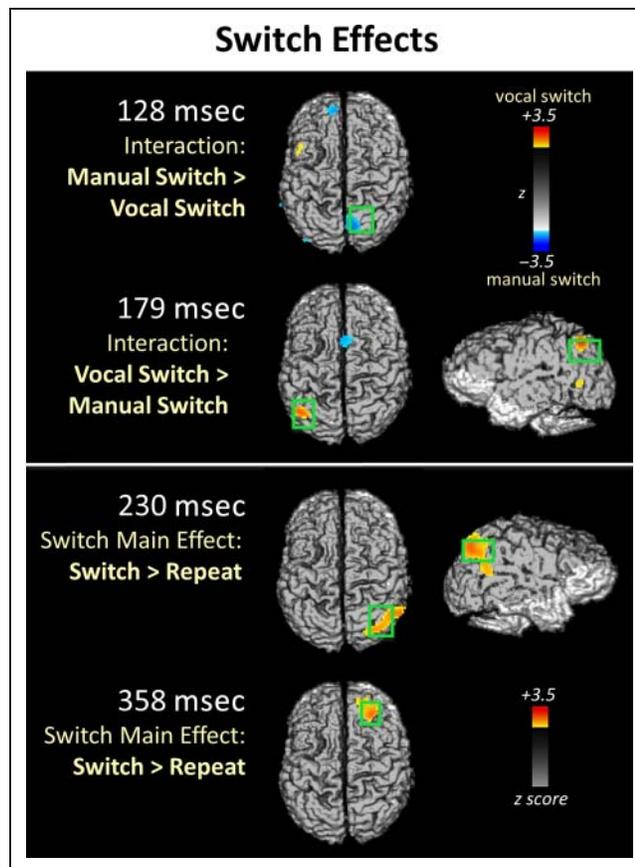
### EROS in Frontal and Parietal Regions

Similar to the ERPs, the first evidence of switch-related preparatory brain activity in EROS data occurred between 100 and 250 msec following the onset of the precue (Figure 4). The EROS data localized this activity to parietal regions. Similar to the ERP data, the earlier activity was modality specific, whereas the later activity was common to all types of switches. Specifically, at 128 msec, there was a reliable Switch  $\times$  Response Modality interaction in right SPL ( $Z = 2.99$ ,  $Z_{\text{crit}(.05)} = 2.88$ ,  $x = 12$ ,  $y = -76$ ), which was characterized by a greater switch effect for manual compared with vocal cues (indicated with blue in the statistical maps in Figure 4). This was followed shortly by an interaction in left intraparietal sulcus (IPS)/inferior parietal lobule (IPL) at 179 msec ( $Z = 3.39$ ,  $Z_{\text{crit}(.05)} = 2.94$ ,  $y = -68$ ,  $z = 39$ ), which showed the opposite pattern, greater switch effect for vocal compared with manual cues (indicated with red in the statistical maps in Figure 4). Then at 230–256 msec, both response modality switches produced activation in right IPS/IPL, indicated by a main effect of Switching ( $Z = 3.08$ ,  $Z_{\text{crit}(.05)} =$

$2.95$ ,  $y = -76$ ,  $z = 34$ ) with no interaction ( $Z = 0.50$ ,  $Z_{\text{crit}(.05)} = 2.81$ ).

After this initial parietal activity, switch effects began to emerge in frontal cortex, with both frontal and parietal effects corresponding to the timing of the Fz and Pz ERP effects. At 358 msec, we found a main effect of Switching in right superior frontal gyrus (SFG)–MFG ( $Z = 3.06$ ,  $Z_{\text{crit}(.05)} = 2.94$ ,  $x = 27$ ,  $y = 34$ ) and a Switch  $\times$  Response Modality interaction ( $Z = 2.98$ ,  $Z_{\text{crit}(.05)} = 2.97$ ,  $x = 27$ ,  $y = 32$ ). The interaction was because of a greater switch effect in manual cue trials compared with vocal cue trials. It should be noted, however, that this right SFG–MFG region also showed slightly more activation overall for vocal than for manual cues. We found a marginal main effect of Response Modality at 435–460 msec ( $Z = 2.94$ ,  $Z_{\text{crit}(.05)} = 3.01$ ), which became significant at a later interval (peak  $Z$  at 563 msec:  $Z = 2.85$ ,  $Z_{\text{crit}(.05)} = 2.80$ ), suggesting that vocal cues recruit right frontal cortex to some extent even on repeat trials.

In summary, the time course of EROS activation of the frontoparietal network reveals, in the present case, a pattern of “first-parietal-then-frontal” activation (consistent with Wang et al., 2010; Green & McDonald, 2008). The timings of EROS activations are temporally consistent with the concurrently recorded ERP data.



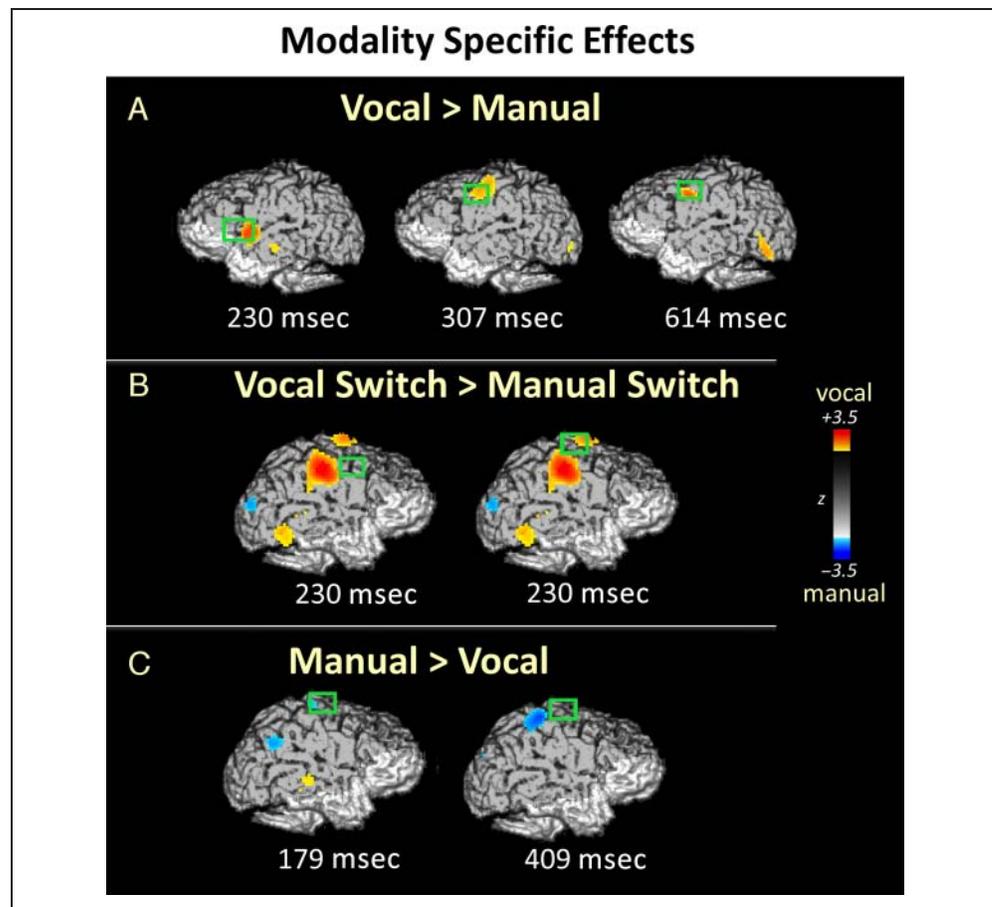
**Figure 4.** Statistical EROS maps corresponding to the peak latencies for the main effect of switching and the switch by response modality interactions. The green rectangles indicate the ROIs. Maps representing the interaction are plotted directionally (i.e., red indicates that the vocal switch effect is greater than the manual switch effect and blue indicates the opposite pattern).

### EROS in Response Production Brain Regions

ROIs for vocal cues included Broca’s area and bilateral mouth and tongue regions of primary motor cortex. Although participants were not performing any response during the cue period, brain regions associated with production could become activated in preparation for later responses. As can be seen in Figure 5A, vocal cues activated Broca’s area and the mouth region of left motor cortex. In Broca’s area, there was a main effect of Response Modality between 204 and 256 msec (peak  $Z = 3.32$ ,  $Z_{\text{crit}(.05)} = 2.98$ ,  $y = 2$ ,  $z = 7$ ). Shortly after this (281–307 msec), the mouth region of left motor cortex showed greater activation for vocal compared with manual cues (peak  $Z = 2.75$ ,  $Z_{\text{crit}(.05)} = 2.54$ ,  $y = -13$ ,  $z = 44$ ), and this area became active again later in the preparatory period (peak at 614 msec:  $Z = 3.17$ ,  $Z_{\text{crit}(.05)} = 2.85$ ,  $y = -3$ ,  $z = 34$ ). Finally, the right mouth region also showed greater activation for vocal compared with manual, but only when switching. At 204–230 msec, there was a switch by response modality interaction in the right mouth ROI (peak  $Z = 3.03$ ,  $Z_{\text{crit}(.05)} = 2.64$ ,  $y = -16$ ,  $z = 32$ ); however, the majority of this activation extended to posterior regions involving somatosensory and inferior parietal cortex (Figure 5B). Surprisingly, there was also greater activation for switching to vocal in the right hemisphere hand region of motor cortex ( $Z = 2.92$ ,  $Z_{\text{crit}(.05)} = 2.75$ ,  $y = -11$ ,  $z = 62$ ).

For manual cues, there was much less task-specific activation. However, manual cues did produce greater activation than vocal cues (indicated by blue in Figure 5C)

**Figure 5.** EROS maps depicting the modality-specific effects. (A) Left-lateralized regions that showed greater activity on vocal than on manual trials. (B) Switch by modality interaction, with red indicating that the vocal switch effect is greater than the manual switch effect. (C) Regions that showed significantly greater activity on manual than on vocal trials.



in the hand region of motor cortex in the right hemisphere at 179 msec ( $Z = -2.52, Z_{\text{crit}(.05)} = 2.34, y = -28, z = 57$ ). A region adjacent but posterior to the hand ROI also showed greater activation for manual cues from 358 to 409 msec, but the activation was outside any of our a priori ROIs (peak at 409 msec:  $Z = 3.13, y = -38, z = 52$ ).

In summary, the EROS data from modality-specific areas shows patterns of activation that are temporally overlapping with those of the frontoparietal regions. The areas activated are for the most part consistent with well-established patterns of cortical specialization.

#### *Right Parietal-seeded Cross-correlations*

Given the importance of frontoparietal networks in preparatory control, we first evaluated the interactions between the parietal and frontal switch effects that were common to both response modalities. We selected the peak voxel in IPS/IPL at 230 msec ( $x = 59, y = -61$ ). We conducted cross-correlation analyses within a time window of 100–640 msec after the precue, the interval corresponding to switch effects in both optical and electrical data. Cross-correlations confirmed the frontoparietal network dynamics, with the parietal effect predicting a positive switch effect in frontal cortex (Figure 6) at a lag of 25 msec ( $Z = 3.68, Z_{\text{crit}(.05)} = 2.90, x = 24, y = 27$ ) and

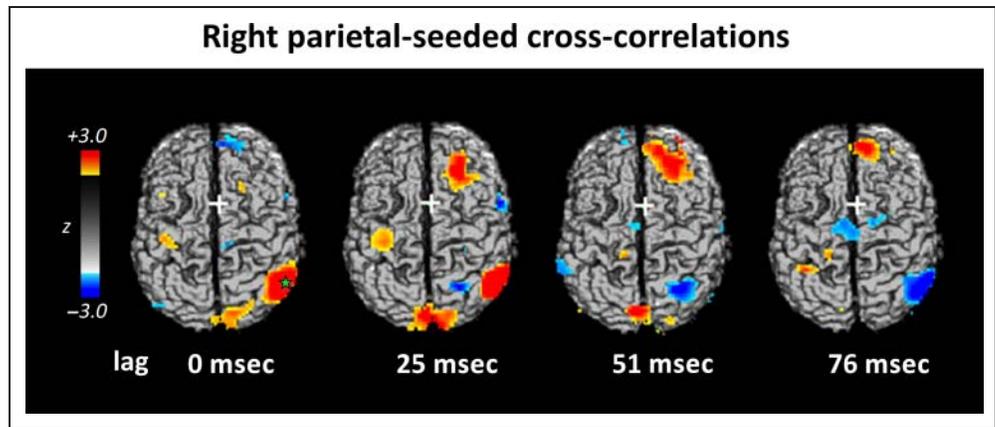
51 msec ( $Z = 3.40, Z_{\text{crit}(.05)} = 2.86, x = 22, y = 39$ ). These lags were consistent with the timing of the frontal switch effects in both vocal and manual conditions, but this analysis emphasizes that, within each participant, the size of the switch effect in parietal cortex predicts the size of the switch effect in frontal cortex.

Correlating the inferior parietal switch effect with the switch effect in manual and vocal conditions separately did not reveal robust effects, suggesting that the parietal activity did not reliably differentiate between modalities and may be related to a general alerting of attention.

#### *Right Frontal-seeded Cross-correlations*

Next, we examined the frontal switch effect to determine its role in response preparation. We used the voxels with the largest right frontal switch effect as seeds because of the region's documented importance for goal-directed behavior (Gratton et al., 2009; Badre & Wagner, 2006; Dosenbach et al., 2006; Brass & von Cramon, 2004; Corbetta & Shulman, 2002; Hopfinger et al., 2000; Sohn et al., 2000), a role confirmed by the general switch effect results found in the current study. Because the manual and vocal switch effects in right frontal cortex differed somewhat in peak location, we chose different peak voxels for each response modality (vocal:  $x = 17, y = 44$ ,

**Figure 6.** EROS statistical maps of the right parietal-seeded cross-correlations revealing functional coupling of right frontal and parietal areas. The green star at 0 msec indicates the approximate location of the seed voxel. The white crosshairs indicate the (0,0) point in Talairach space.



manual:  $x = 27, y = 32$ ) and conducted the analyses on a longer (200–800 msec) interval to account for the delay in activation of frontal, with respect to parietal, regions.

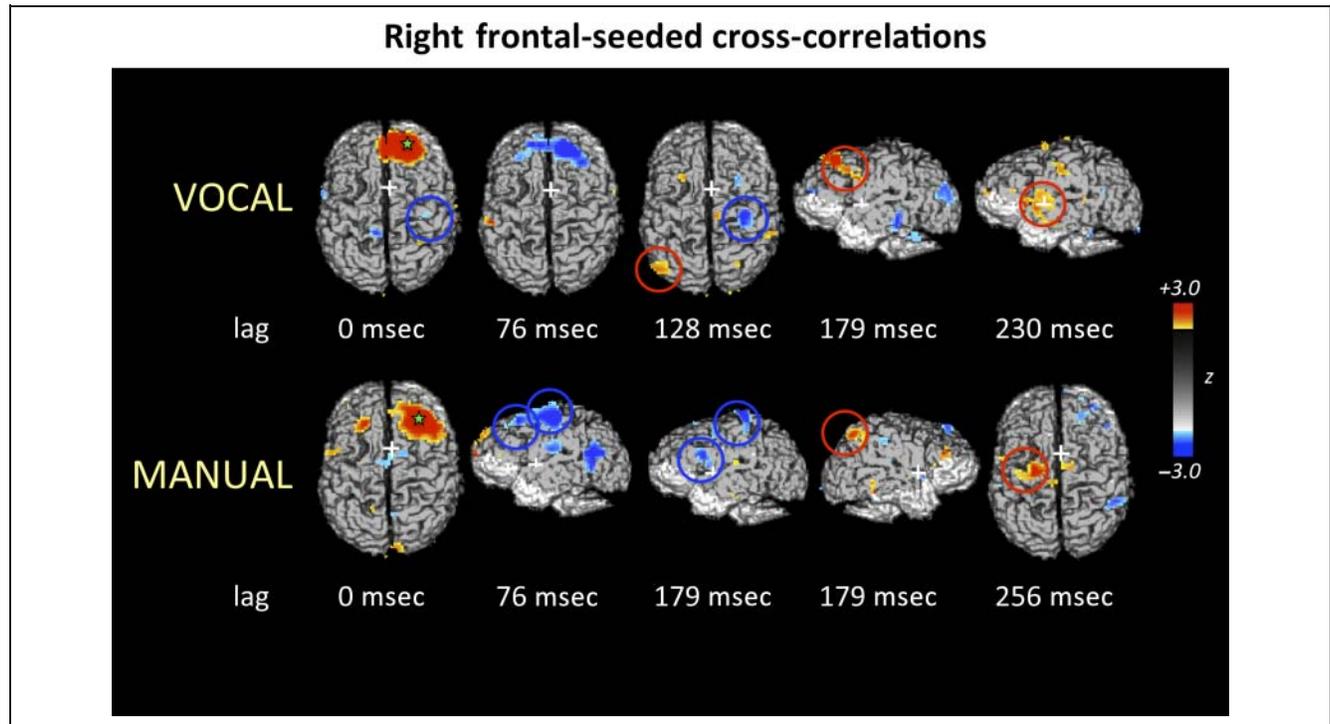
*Cross-correlations related to the vocal switch effect.* In the vocal condition, cross-correlations revealed negative associations with manual preparation areas during the early lags, followed by positive correlations with vocal production regions (Figure 7, top row).

At a lag of 25 msec (not shown in Figure 7), the seed activity was negatively correlated with the switch effect in the hand area of right motor cortex<sup>3</sup> ( $Z = 3.03, Z_{crit(.05)} = 2.80, x = 32, y = -11$ ). This effect was again observed at the 128 msec lag ( $Z = 3.50, Z_{crit(.05)} = 2.79, x = 32, y = -26$ ).

At the 128-msec lag, the frontal seed was marginally and positively associated with a switch effect in left IPS/IPL ( $Z = 2.63, Z_{crit(.10)} = 2.52, x = -53, y = -76$ ). A positive correlation was then found with a left superior frontal area at the 179 msec lag ( $Z = 3.20, Z_{crit(.05)} = 2.79, x = -36, y = 27$ ).

The seed then reliably predicted switch effects in left inferior frontal regions such as the mouth area of left motor cortex at a lag of 179 msec ( $Z = 3.02, Z_{crit(.05)} = 2.51, y = 4, z = 29$ ) and in Broca's area at 230 msec ( $Z = 2.85, Z_{crit(.05)} = 2.74, y = 17, z = -1$ ).

*Cross-correlations related to the manual switch effect.* Similar to the vocal cross-correlations, the right frontal seed was negatively correlated with task-irrelevant regions



**Figure 7.** EROS statistical maps of the right frontal-seeded cross-correlations revealing differential functional coupling of frontal and modality preparation areas.

such as left-lateralized frontal areas, before predicting positive switch effects at the later lags (see Figure 7, bottom row).

The right frontal seed was first positively correlated with the switch effect in left superior frontal cortex at 0 and 25 msec lags (peak at 0 msec:  $Z = 3.05$ ,  $Z_{\text{crit}(.05)} = 2.72$ ,  $x = -26$ ,  $y = 24$ ), indicating bilateral recruitment of frontal regions. We then found several negative correlations. Consistent with deactivation of response-dependent brain regions, the right frontal seed predicted a negative switch effect in the mouth area ROI of left motor cortex at lags of 76 and 204 msec (76 msec:  $Z = 2.78$ ,  $Z_{\text{crit}(.05)} = 2.57$ ,  $y = -16$ ,  $z = 44$ ; 204 msec:  $Z = 2.62$ ,  $Z_{\text{crit}(.05)} = 2.43$ ,  $y = -3$ ,  $z = 44$ ). Surprisingly, though, this negative correlation extended to the left motor hand ROI at lag 76 ( $Z = 3.76$ ,  $Z_{\text{crit}(.05)} = 2.81$ ,  $x = -51$ ,  $y = -28$ ). Also, left MFG–SFG and IPS/IPL were negatively correlated with the frontal seed at this same lag (MFG:  $Z = 3.07$ ,  $Z_{\text{crit}(.05)} = 2.71$ ,  $x = -33$ ,  $y = 22$ ; IPL:  $Z = 2.99$ ,  $Z_{\text{crit}(.05)} = 2.82$ ,  $x = -53$ ,  $y = -71$ ).

At the 179 msec lag, we observed marginal negative correlations with Broca's area ( $Z = 2.55$ ,  $Z_{\text{crit}(.05)} = 2.87$ ,  $y = 4$ ,  $z = 9$ ) and the mouth area of left motor cortex ( $Z = 2.27$ ,  $Z_{\text{crit}(.05)} = 2.43$ ,  $y = -3$ ,  $z = 44$ ). At this same lag, the frontal seed was positively correlated with right IPS/IPL ( $Z = 2.87$ ,  $Z_{\text{crit}(.05)} = 2.93$ ,  $y = -68$ ,  $z = 39$ ). Finally, at lag 256 msec, the frontal switch effect had a marginal positive correlation with a switch effect in the hand area of left motor cortex ( $Z = 2.44$ ,  $Z_{\text{crit}(.05)} = 2.64$ ,  $x = -31$ ,  $y = -21$ ). The small correlation that can be seen in the right motor strip at 256 msec in Figure 7 was outside the right motor cortex ROI and not statistically reliable.

In summary, frontal (but not parietal) activation predicted activation/deactivation in modality-specific areas. The deactivation in regions related to the “to-be-inhibited” modality preceded the activation in regions related to the “to-be-activated” modality.

## DISCUSSION

To our knowledge, this is the first study to characterize the rapid dynamics of preparatory control mechanisms involved in switching between response modalities. Similar to previous studies, we observed a small increase in error rate (3–4%) when switching between response modalities but did not observe switch costs in RTs. The small behavioral switch costs can be attributed to practice before experiment recording and responses involving low processing demands (as switching involved output modalities, and not two different tasks). However, it is also highly likely that participants in fact engaged preparatory processes during the period between precue and response execution. This was supported by frontal and parietal switch effects during the preparatory period in both electrical and optical data, a result that is consistent with previous studies that find smaller switch costs

with increased recruitment of frontoparietal network areas (Wylie et al., 2006; Sohn et al., 2000). More importantly, cross-correlations revealed the dynamic connectivity of regions of the frontoparietal network and the differentiation of network patterns based on current trial demands.

The general parietal switch effect significantly correlated with later switch effects in frontal cortex, confirming the functional connectivity of these two regions. Activations in pFC and parietal cortex have been observed in response to stimuli indicating the nature of an upcoming task, with preferentially greater activation when the cue signals a switch on the next trial (Sohn et al., 2000). Increased engagement of parietal cortex on switch trials is consistent with previous research, highlighting its role in orienting attention and evaluating the behavioral relevance of stimuli (Serences et al., 2005; Corbetta & Shulman, 2002; Hopfinger et al., 2000). The parietal switch effect in the current study, however, did not predict subsequent modality-specific switching effects, suggesting that it was related to a general alerting of attention and may simply relay a signal that a change is needed in the pFC. Indeed, previous studies suggest that prefrontal regions are more involved in memory representations, whereas parietal regions are more important in representing stimulus–response associations (Gratton, Low, & Fabiani, 2008; Corbetta & Shulman, 2002). Previous work also finds that propagation of activity typically proceeds in an anterior to posterior direction, the opposite of what we found. In this experiment, participants cannot appropriately prepare for a particular response because only the modality of the response is known beforehand. Without a stimulus–response representation to guide preparation, participants may have had to rely more on frontal-mediated control mechanisms. Moreover, several recent studies have found that the IPS may play a triggering role in top–down attentional control by relaying information to the pFC that then guides or modulates activity in task-specific areas (Wang et al., 2010; Green & McDonald, 2008).

What processes might the frontal cortex coordinate? The frontal switch effect differentially predicted activity in modality preparation regions, with positive and negative correlations suggesting the presence of excitatory and inhibitory interactions (Banich, 2009; Brass et al., 2005; Braver, Reynolds, & Donaldson, 2003). Relative to frontal activity, irrelevant response processes were first disengaged, followed by activation of regions related to the modality of the current trial. We elucidate the dynamics of frontoparietal regions by showing that the strength of connections between areas is quickly and flexibly tuned to current demands. In this case, connectivity between areas grew during the more demanding switch trials. These results complement the structural findings of Gratton and colleagues (2009), where integrity of the corpus callosum was found to be important for efficient switching between tasks that primarily recruited processes in opposite hemispheres. Together,

these findings underscore the importance of interactions between brain regions, especially as they relate to information being transmitted to relatively distant regions.

Predominantly right frontal activity might be related to the nature of the switching required. Left frontal activity is commonly observed in paradigms that require resolution of interference during response selection or execution (Nelson, Reuter-Lorenz, Persson, Sylvester, & Jonides, 2009; Gratton et al., 2008). As revealed by the small switch costs from switching response modality, there may have been little or even no competition between representations. Alternatively, preparing the hands or mouth may have led to a strategy that encoded the bodily locations of the upcoming responses and thus led to more spatially oriented and thus right-lateralized processing.

Dorsal portions of the frontal gyrus have long been implicated in attention control, particularly in working memory and switching paradigms. A previous EROS study on task switching (Gratton et al., 2009) questioned the criticality of dorsal MFG for task switching, as ventral MFG–IFG task-specific effects were observed even before peak dorsal MFG activity. It was speculated that task switching may be executed not only through a centralized top-down process (using dorsal MFG as a critical node) but also via a distributed process that, with practice, leads to early and task-driven activation in ventral MFG–IFG bypassing the more dorsal region. However, this previous study did not incorporate a practice session to substantiate the theory. In this experiment, we included a practice session and still found a dorsal effect in frontal cortex. We found support for a distributed process in the modality-specific activation of this dorsal frontal region, with a slightly earlier onset for the vocal switch effect compared with the manual switch effect. These results expand on the role of the MFG as a control command center and suggest functional specialization within the MFG that flexibly adopts and triggers task-specific control signals. Indeed, cross-correlations revealed that areas in the MFG differentially correlated with parietal and response production regions depending on the switch and modality demands of the trial. Early modality-specific switch effects were also found in parietal cortex, before the general switch effect. Similar to the differentiation of the frontal effects, the parietal effects were lateralized with a manual switch effect arising in right parietal cortex and a vocal switch effect in left parietal cortex.

We also observed early preparatory effects specific to response modality, regardless of transition (switch/repeat). Manual cues resulted in increased activity in the right hand area of motor cortex and in right parietal regions, and vocal cues resulted in increased activation of left-lateralized speech production areas. We also found activation in an area adjacent and posterior to the right mouth ROI and right hand ROI, indicating the involvement of not only motor, but also somatosensory regions in this type of preparation. Interestingly, these effects were observed even before the frontal effects, providing further support

for a distributed process. Similar patterns have been found in sensory cortices when preparing for an auditory or visual stimulus, where priming or preactivating a respective sensory area was associated with improved performance, particularly in conditions that necessitate more attentional control (Wylie et al., 2006; Weissman et al., 2004). The cross-correlation analyses revealed that these same regions were modulated by switch demands, with greater frontal connectivity during switch trials. Preparatory processes are not necessarily limited to switch trials, and frontal activity may not be essential for switching, but the cross-correlation analysis shows that the interactions between regions were stronger during switch trials, with the frontal cortex as a driving force.

In the frontal-seeded cross-correlations, we obtained lateralized effects with activation in the hand area of left motor cortex for manual preparation but less clear activation in the hand area of the right motor cortex (although a small activation, not reaching the significance criterion, was observed just outside the ROI selected a priori). This apparent lateralization occurs despite the fact that the response hand cannot be known ahead of time. The absence of equivalent activation in both hemispheres may be because of noise in the neural signals, with activity in the other hemisphere not reaching threshold or problems of coregistration. However, a weaker activation in the right hemisphere may also reflect strategic choices that may exist for at least some participants. Namely, whereas the left hemisphere may have to switch between preparation states when getting ready for a manual or vocal response, this type of response “conflict” may not exist for the right hemisphere (as the right hemisphere may be less heavily involved in vocal preparation). Hence, switch-to-manual responses would generate preparatory activity in the left hemisphere compared with no-switch trials, whereas this comparison may not generate differences in the right hemisphere. Because, however, this was not predicted a priori, more research will be needed in support of this explanation.

There was not enough variance in the behavioral data to probe associations between neural switching processes and task performance. Increasing task difficulty by manipulating the interval between cue presentation and task execution, as well as integrating findings from other switching paradigms, can shed light on the importance of such disengagement and engagement processes to performance. Although this is the first EROS study to investigate preparatory activity in parietal regions in addition to anterior areas and one of the first EROS studies to illustrate the time course of activation of a frontoparietal network, EROS’ limited penetration within the brain prevents us from interrogating subcortical effects that may contribute to network preparatory activity, particularly in a task performed after extensive practice.

Despite these limitations, we gained a better understanding of preparatory processes by illustrating the

extended dynamics of preparatory activity in frontoparietal network and response preparation regions. Using lagged cross-correlations, we developed an integrative account of the general and modality-specific effects in demonstrating that interactions between frontal cortex, parietal cortex, and motor cortices were dynamic and changed with trial demands. We found support for the frontal region as a hub or control center that coordinates activity in networked regions to support performance. Functional MRI paradigms have found changes in brain network connectivity as a function of cognitive state or condition (Moussa et al., 2011), but this is one of the first studies to investigate connectivity at this finer spatiotemporal scale (see also Gratton et al., 2009). Monitoring these preparatory processes has the potential to inform closed loop systems that can augment cognition, such as brain machine interfaces. Applications of this kind of rapid on-line information include providing feedback to prevent errors in complex tasks and utilizing neural indices of performance or attention to optimize the presentation of information to a user to support performance.

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### Notes

1. Seven participants had zero to five vocal trials requiring recoding, whereas the number of trials recoded for the rest of the participants was 13, 21, 30, 44, 79, 95, 127, and 231, respectively.
2. All *Z* scores represent peak *Z* scores in the ROI.
3. We lowered the *z*-score threshold to examine later lags to determine the laterality of the effect and found it to be unilateral. It is possible that a left hemisphere effect was lost as signal travelled from the opposite hemisphere. Alternatively, preparatory mechanisms in the right hemisphere may be unique and related to the handedness (right) of the participants.

### REFERENCES

Allport, A., Styles, E. A., & Hsieh, S. (1994). Shifting intentional set: Exploring the dynamic control of tasks. In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 421–452). Cambridge, MA: MIT Press.

Aron, A. R., Monsell, S., Sahakian, B. J., & Robbins, T. W. (2004). A componential analysis of task-switching deficits associated with lesions of left and right frontal cortex. *Brain: A Journal of Neurology*, *127*, 1561–1573.

Badre, D., & Wagner, A. D. (2006). Computational and neurobiological mechanisms underlying cognitive flexibility.

*Proceedings of the National Academy of Sciences, U.S.A.*, *103*, 7186–7191.

Banich, M. T. (2009). Executive function. *Current Directions in Psychological Science*, *18*, 89–94.

Brass, M., Ullsperger, M., Knoesche, T. R., von Cramon, D. Y., & Phillips, N. A. (2005). Who comes first? The role of the prefrontal and parietal cortex in cognitive control. *Journal of Cognitive Neuroscience*, *17*, 1367–1375.

Brass, M., & von Cramon, D. Y. (2004). Decomposing components of task preparation with functional magnetic resonance imaging. *Journal of Cognitive Neuroscience*, *16*, 609–620.

Braver, T. S., Reynolds, J. R., & Donaldson, D. I. (2003). Neural mechanisms of transient and sustained cognitive control during task switching. *Neuron*, *39*, 713–726.

Bressler, S. L. (1995). Large-scale cortical networks and cognition. *Brain Research, Brain Research Reviews*, *20*, 288–304.

Brown, S., Ngan, E., & Liotti, M. (2008). A larynx area in the human motor cortex. *Cerebral Cortex (New York, N.Y.: 1991)*, *18*, 837–845.

Bullmore, E., & Sporns, O. (2009). Complex brain networks: Graph theoretical analysis of structural and functional systems. *Nature Reviews Neuroscience*, *10*, 186–198.

Cohen, A. L., Fair, D. A., Dosenbach, N. U., Miezin, F. M., Dierker, D., Van Essen, D. C., et al. (2008). Defining functional areas in individual human brains using resting functional connectivity MRI. *Neuroimage*, *41*, 45–57.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.

de Pasquale, F., Della Penna, S., Snyder, A. Z., Lewis, C., Mantini, D., Marzetti, L., et al. (2010). Temporal dynamics of spontaneous MEG activity in brain networks. *Proceedings of the National Academy of Sciences, U.S.A.*, *107*, 6040–6045.

Dosenbach, N. U., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., et al. (2006). A core system for the implementation of task sets. *Neuron*, *50*, 799–812.

Embick, D., Marantz, A., Miyashita, Y., O’Neil, W., & Sakai, K. L. (2000). A syntactic specialization for Broca’s area. *Proceedings of the National Academy of Sciences, U.S.A.*, *97*, 6150–6154.

Foust, A. J., & Rector, D. M. (2007). Optically teasing apart neural swelling and depolarization. *Neuroscience*, *145*, 887–899.

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences, U.S.A.*, *102*, 9673–9678.

Gevins, A. S., Schaffer, R. E., Doyle, J. C., Cuttillo, B. A., Tannehill, R. S., & Bressler, S. L. (1983). Shadows of thought: Shifting lateralization of human brain electrical patterns during brief visuomotor task. *Science (New York, N.Y.)*, *220*, 97–99.

Gilbert, S. J., & Shallice, T. (2002). Task switching: A PDP model. *Cognitive Psychology*, *44*, 297–337.

Gratton, C., Nomura, E. M., Pérez, F., & D’Esposito, M. (2012). Focal brain lesions to critical locations cause widespread disruption of the modular organization of the brain. *Journal of Cognitive Neuroscience*, *24*, 1275–1285.

Gratton, G. (2000). “Opt-cont” and “Opt-3D”: A software suite for the analysis and 3D reconstruction of the event-related optical signal (EROS). *Psychophysiology*, *37*, S44.

Gratton, G., Brumback, C. R., Gordon, B. A., Pearson, M. A., Low, K. A., & Fabiani, M. (2006). Effects of measurement method, wavelength, and source-detector distance on the fast optical signal. *Neuroimage*, *32*, 1576–1590.

Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, *55*, 468–484.

- Gratton, G., & Corballis, P. M. (1995). Removing the heart from the brain: Compensation for the pulse artifact in the photon migration signal. *Psychophysiology*, *32*, 292–299.
- Gratton, G., & Fabiani, M. (2010). Fast optical imaging of human brain function. *Frontiers in Human Neuroscience*, *4*, 52.
- Gratton, G., Low, K. A., & Fabiani, M. (2008). Time course of executive processes: Data from the event-related optical signal (EROS). In S. A. Bunge & J. D. Wallis (Eds.), *Perspectives on rule-guided behavior* (pp. 197–223). New York: Oxford University Press.
- Gratton, G., Wee, E., Rykhlevskaia, E. I., Leaver, E. E., & Fabiani, M. (2009). Does white matter matter? Spatio-temporal dynamics of task switching in aging. *Journal of Cognitive Neuroscience*, *21*, 1380–1395.
- Green, J. J., & McDonald, J. J. (2008). Electrical neuroimaging reveals timing of attentional control activity in human brain. *PLoS Biology*, *6*, 730–738.
- Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., & Salmelin, R. (2001). Dynamic imaging of coherent sources: Studying neural interactions in the human brain. *Proceedings of the National Academy of Sciences, U.S.A.*, *98*, 694–699.
- Hasher, L., Lustig, C., & Zacks, R. T. (2007). Inhibitory mechanisms and the control of attention. In A. Conway, C. Jarrold, M. Kane, A. Miyake, & J. Towse (Eds.), *Variation in working memory* (pp. 227–249). New York: Oxford University Press.
- Herd, S. A., Banich, M. T., & O'Reilly, R. C. (2006). Neural mechanisms of cognitive control: An integrative model of stroop task performance and fMRI data. *Journal of Cognitive Neuroscience*, *18*, 22–32.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*, 284–291.
- Jamadar, S., Hughes, M., Fulham, W. R., Michie, P. T., & Karayanidis, F. (2010). The spatial and temporal dynamics of anticipatory preparation and response inhibition in task-switching. *Neuroimage*, *51*, 432–449.
- Jersild, A. T. (1927). Mental set and shift. *Archives of Psychology, Whole No. 89*, 5–82.
- Karayanidis, F., Jamadar, S., Ruge, H., Phillips, N., Heathcote, A., & Forstmann, B. U. (2010). Advance preparation in task-switching: Converging evidence from behavioral, brain activation, and model-based approaches. *Frontiers in Psychology*, *1*, 25.
- Kiebel, S. J., Poline, J. B., Friston, K. J., Holmes, A. P., & Worsley, K. J. (1999). Robust smoothness estimation in statistical parametric maps using standardized residuals from the general linear model. *Neuroimage*, *10*, 756–766.
- Kim, C., Cilles, S. E., Johnson, N. F., & Gold, B. T. (2012). Domain general and domain preferential brain regions associated with different types of task switching: A meta-analysis. *Human Brain Mapping*, *33*, 130–142.
- Kim, C., Johnson, N. F., Cilles, S. E., & Gold, B. T. (2011). Common and distinct mechanisms of cognitive flexibility in prefrontal cortex. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *31*, 4771–4779.
- Lancaster, J. L., Rainey, L. H., Summerlin, J. L., Freitas, C. S., Fox, P. T., Evans, A. C., et al. (1997). Automated labeling of the human brain: A preliminary report on the development and evaluation of a forward-transform method. *Human Brain Mapping*, *5*, 238–242.
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., et al. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping*, *10*, 120–131.
- Maclin, E. L., Low, K. A., Fabiani, M., & Gratton, G. (2007). Improving the signal-to-noise ratio of event-related optical signals. *IEEE Engineering in Medicine and Biology Magazine: The Quarterly Magazine of the Engineering in Medicine & Biology Society*, *26*, 47–51.
- Maclin, E. L., Low, K. A., Sable, J. J., Fabiani, M., & Gratton, G. (2004). The event-related optical signal to electrical stimulation of the median nerve. *Neuroimage*, *21*, 1798–1804.
- Meiran, N. (2000). Modeling cognitive control in task-switching. *Psychological Research*, *63*, 234–249.
- Mesulam, M. M. (1990). Large-scale neurocognitive networks and distributed processing for attention, language, and memory. *Annals of Neurology*, *28*, 597–613.
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202.
- Monsell, S. (2003). Task switching. *Trends in Cognitive Sciences*, *7*, 134–140.
- Moussa, M. N., Vechlekar, C. D., Burdette, J. H., Steen, M. R., Hugenschmidt, C. E., & Laurienti, P. J. (2011). Changes in cognitive state alter human functional brain networks. *Frontiers in Human Neuroscience*, *5*, 83.
- Nelson, J. K., Reuter-Lorenz, P. A., Persson, J., Sylvester, C. Y., & Jonides, J. (2009). Mapping interference resolution across task domains: A shared control process in left inferior frontal gyrus. *Brain Research*, *1256*, 92–100.
- Pashler, H., Johnston, J. C., & Ruthruff, E. (2001). Attention and performance. *Annual Review of Psychology*, *52*, 629–651.
- Perianez, J. A., Maestu, F., Barcelo, F., Fernandez, A., Amo, C., & Ortiz Alonso, T. (2004). Spatiotemporal brain dynamics during preparatory set shifting: MEG evidence. *Neuroimage*, *21*, 687–695.
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.
- Pulvermuller, F., Huss, M., Kherif, F., Moscoso del Prado Martin, F., Hauk, O., & Shtyrov, Y. (2006). Motor cortex maps articulatory features of speech sounds. *Proceedings of the National Academy of Sciences, U.S.A.*, *103*, 7865–7870.
- Rector, D. M., Carter, K. M., Volegov, P. L., & George, J. S. (2005). Spatio-temporal mapping of rat whisker barrels with fast scattered light signals. *Neuroimage*, *26*, 619–627.
- Rector, D. M., Poe, G. R., Kristensen, M. P., & Harper, R. M. (1997). Light scattering changes follow evoked potentials from hippocampal schaeffer collateral stimulation. *Journal of Neurophysiology*, *78*, 1707–1713.
- Reuter-Lorenz, P. A., Jonides, J., Smith, E. E., Hartley, A., Miller, A., Marshuetz, C., et al. (2000). Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. *Journal of Cognitive Neuroscience*, *12*, 174–187.
- Rushworth, M. F., Walton, M. E., Kennerley, S. W., & Bannerman, D. M. (2004). Action sets and decisions in the medial frontal cortex. *Trends in Cognitive Sciences*, *8*, 410–417.
- Rykhlevskaia, E., Fabiani, M., & Gratton, G. (2006). Lagged covariance structure models for studying functional connectivity in the brain. *Neuroimage*, *30*, 1203–1218.
- Rykhlevskaia, E., Gratton, G., & Fabiani, M. (2008). Combining structural and functional neuroimaging data for studying brain connectivity: A review. *Psychophysiology*, *45*, 173–187.
- Serences, J. T., Shomstein, S., Leber, A. B., Gohay, X., Egeth, H. E., & Yantis, S. (2005). Coordination of voluntary and stimulus-driven attentional control in human cortex. *Psychological Science*, *16*, 114–122.
- Smith, E. E., Jonides, J., & Koeppel, R. A. (1996). Dissociating verbal and spatial working memory using PET. *Cerebral Cortex (New York, N.Y.: 1991)*, *6*, 11–20.
- Smith, S. M., Fox, P. T., Miller, K. L., Glahn, D. C., Fox, P. M., Mackay, C. E., et al. (2009). Correspondence of the brain's functional architecture during activation and rest. *Proceedings of the National Academy of Sciences, U.S.A.*, *106*, 13040–13045.
- Sohn, M. H., Ursu, S., Anderson, J. R., Stenger, V. A., & Carter, C. S. (2000). The role of prefrontal cortex and posterior

- parietal cortex in task switching. *Proceedings of the National Academy of Sciences, U.S.A.*, *97*, 13448–13453.
- Swainson, R., Cunnington, R., Jackson, G. M., Rorden, C., Peters, A. M., Morris, P. G., et al. (2003). Cognitive control mechanisms revealed by ERP and fMRI: Evidence from repeated task-switching. *Journal of Cognitive Neuroscience*, *15*, 785–799.
- Tse, C. Y., Lee, C. L., Sullivan, J., Garnsey, S. M., Dell, G. S., Fabiani, M., et al. (2007). Imaging cortical dynamics of language processing with the event-related optical signal. *Proceedings of the National Academy of Sciences, U.S.A.*, *104*, 17157–17162.
- Wang, L., Liu, X., Guise, K. G., Knight, R. T., Ghajar, J., & Fan, J. (2010). Effective connectivity of the frontoparietal network during attentional control. *Journal of Cognitive Neuroscience*, *22*, 543–553.
- Weissman, D. H., Warner, L. M., & Woldorff, M. G. (2004). The neural mechanisms for minimizing cross-modal distraction. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *24*, 10941–10949.
- Whalen, C., Maclin, E. L., Fabiani, M., & Gratton, G. (2008). Validation of a method for coregistering scalp recording locations with 3D structural MR images. *Human Brain Mapping*, *29*, 1288–1301.
- Wolf, U., Wolf, M., Toronov, V., Michalos, A., Paunescu, L. A., & Gratton, E. (2000). *Detecting cerebral functional slow and fast signals by frequency-domain near-infrared spectroscopy using two different sensors*. Paper presented at OSA Meeting in Optical Spectroscopy and Imaging and Photon Migration (Miami, April 2–5, 2000).
- Wylie, G., & Allport, A. (2000). Task switching and the measurement of “switch costs”. *Psychological Research*, *63*, 212–233.
- Wylie, G. R., Javitt, D. C., & Foxe, J. J. (2006). Jumping the gun: Is effective preparation contingent upon anticipatory activation in task-relevant neural circuitry? *Cerebral Cortex (New York, N.Y.: 1991)*, *16*, 394–404.
- Yousry, T. A., Schmid, U. D., Alkadhi, H., Schmidt, D., Peraud, A., Buettner, A., et al. (1997). Localization of the motor hand area to a knob on the precentral gyrus. A new landmark. *Brain: A Journal of Neurology*, *120*, 141–157.