

# Where and When the Anterior Cingulate Cortex Modulates Attentional Response: Combined fMRI and ERP Evidence

S. Crottaz-Herbette and V. Menon

## Abstract

■ Attentional control provides top-down influences that allow task-relevant stimuli and responses to be processed preferentially. The anterior cingulate cortex (ACC) plays an important role in attentional control, but the spatiotemporal dynamics underlying this process is poorly understood. We examined the activation and connectivity of the ACC using functional magnetic resonance imaging (fMRI) along with fMRI-constrained dipole modeling of event-related potentials (ERPs) obtained from subjects who performed auditory and visual oddball attention tasks. Although attention-related responses in the ACC were similar in the two modalities, effective connectivity analyses showed modality-specific effects with increased ACC influences on the Heschl and superior

temporal gyri during auditory task and on the striate cortex during visual task. Dipole modeling of ERPs based on source locations determined from fMRI activations showed that the ACC was the major generator of N2b-P3a attention-related components in both modalities, and that primary sensory regions generated a small mismatch signal about 50 msec prior to feedback from the ACC and a large signal 60 msec after feedback from the ACC. Taken together, these results provide converging neuroimaging and electrophysiological evidence for top-down attentional modulation of sensory processing by the ACC. Our findings suggest a model of attentional control based on dynamic bottom-up and top-down interactions between the ACC and primary sensory regions. ■

## INTRODUCTION

Attention enables an organism to sift through many different incoming sensory stimuli and to focus on task-relevant stimuli. Attentional control involves the modulation of neural activity in specific regions according to task demands. Single-cell recording studies in animals (McAdams & Maunsell, 2000; Connor, Preddie, Gallant, & Van Essen, 1997) and neuroimaging studies in humans (Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999; Martinez et al., 1999; Watanabe et al., 1998) have shown that attention enhances neural activity in many brain regions. The anterior cingulate cortex (ACC), located in the medial surface of frontal gyrus, is thought to play an important role in attentional control (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Milham, Banich, Webb, et al., 2001; Paus, 2001; Bush, Luu, & Posner, 2000; Davis, Hutchison, Lozano, Tasker, & Dostrovsky, 2000; Gehring & Knight, 2000; Carter, Botvinick, & Cohen, 1999; Devinsky, Morrell, & Vogt, 1995). Thus, increased activation of the ACC has been observed during performance of tasks that require subjects to selectively attend to a stimulus or an inhibiting response to a particular stimulus, and to orient attention to an unexpected or novel stimulus

(Bush, Luu, et al., 2000; Peterson et al., 1999; Bush, Whalen, et al., 1998; Posner & Dehaene, 1994). In addition, several studies have shown that patients with cingulotomy or lesions in the ACC have executive and attention deficits (Swick & Turken, 2002; Ochsner et al., 2001; Cohen, Kaplan, Moser, Jenkins, & Wilkinson, 1999; Cohen, Kaplan, Zuffante, et al., 1999). To perform such control functions, it has been proposed that the ACC may influence widely distributed regions of the brain that are engaged in various aspects of task performance (Posner & Raichle, 1994). Here, we examine the role of the ACC in modulating sensory responses in both auditory and visual modalities, using a novel approach that incorporates both connectivity and timing of neural processes.

Several human neuroimaging studies have suggested that the ACC has a modulatory effect on higher order cortical regions, which were reviewed in Koski and Paus (2000). Attentional modulation has also been reported in primary sensory cortices in human (Petkov et al., 2004; Chawla, Rees, & Friston, 1999; Jancke, Mirzazade, & Shah, 1999a, 1999b; Somers, Dale, Seiffert, & Tootell, 1999; Woodruff et al., 1996; Alho, Woods, Algazi, & Näätänen, 1992; Woods, Alho, & Algazi, 1992) and animal studies (Mehta, Ulbert, & Schroeder, 2000; Luck, Chelazzi, Hillyard, & Desimone, 1997; Treue & Maunsell, 1996; Ferrera, Rudolph, & Maunsell, 1994). Although it

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Stanford University School of Medicine

is generally assumed that these changes result from top-down influences (Giesbrecht, Woldorff, Song, & Mangun, 2003; Kanwisher & Wojciulik, 2000; Kastner & Ungerleider, 2000; Desimone & Duncan, 1995; Posner & Petersen, 1990), the precise functional neuroanatomy and neural mechanisms underlying such modulations are poorly understood. An important question here is whether the ACC influences activation in sensory processing areas.

To more directly investigate this question, we used a simple oddball task involving the detection of infrequent stimuli embedded in a sequence of frequent stimuli (Desmedt, Debecker, & Manil, 1965; Sutton, Braren, Zubin, & John, 1965). This simple task has the advantages of involving strong top-down attentional process and minimizing confounding factors such as working memory and language, which allowed us to examine the role of the ACC in attentional modulation. Brain responses to oddball tasks have been extensively studied using functional brain imaging (Horn, Syed, Lanfermann, Maurer, & Dierks, 2003; Ardekani et al., 2002; Horovitz, Skudlarski, & Gore, 2002; Kiehl, Laurens, Duty, Forster, & Liddle, 2001; Kiehl & Liddle, 2001; Clark, Fannon, Lai, Benson, & Bauer, 2000; Stevens, Skudlarski, Gatenby, & Gore, 2000; Linden et al., 1999; Yoshiura et al., 1999; McCarthy, Luby, Gore, & Goldman-Rakic, 1997; Menon, Ford, Lim, Glover, & Pfefferbaum, 1997; Ebmeier et al., 1995). These studies clearly show that, in addition to the ACC and the lateral prefrontal cortex, infrequent auditory stimuli elicit significantly greater responses in early sensory regions, including the Heschl gyrus (Kiehl & Liddle, 2003; Horovitz et al., 2002; Kiehl et al., 2001; Stevens et al., 2000; Linden et al., 1999; Opitz, Mecklinger, Friederici, & von Cramon, 1999; Yoshiura et al., 1999; Menon et al., 1997; Ebmeier et al., 1995). Similarly, infrequent visual stimuli elicit greater activation in striate and extrastriate cortices (Madden, Whiting, Provenzale, & Huettel, 2004; Moores et al., 2003; Ardekani et al., 2002; Clark et al., 2000; Yoshiura et al., 1999). These activations index attentional effects because purely sensory aspects of the tasks have been controlled for. What is currently not known is whether these early attentional effects are results of top-down modulatory signals from the ACC.

The timing of brain responses to oddball stimuli has been examined extensively using event-related potentials (ERPs; for reviews, see Soltani & Knight, 2000; Näätänen, 1992). These studies have shown that a comparison between ERPs evoked by infrequent and by frequent stimuli reveal two main components: the N2b and P3 components (Näätänen, 1992; Sutton et al., 1965). Poor spatial resolution of scalp-recorded ERPs, however, precludes accurate determination of the relative location of specific neural sources. Although several studies on oddball tasks have used functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) together with ERPs (Bledowski, Prvulovic, Goebel, Zanella, & Linden, 2004; Huettel & McCarthy,

2004; Mulert et al., 2004; Horovitz et al., 2002; Linden et al., 1999; Woldorff, Matzke, Zamarripa, & Fox, 1999; Menon et al., 1997; Ebmeier et al., 1995), these studies have not effectively integrated the two types of data using appropriate biophysical models. As a result, both the magnitude and the temporal profile of ACC responses in and of itself, and in relation to responses in the sensory areas, remain poorly understood.

We acquired event-related fMRI and ERP data during identical auditory and visual oddball tasks. We used effective connectivity analysis (Friston, Buechel, et al., 1997) of fMRI data, along with fMRI-constrained dipole modeling of ERP data, to more directly examine the role of the ACC in attentional control. The combined use of these techniques allowed us to take advantage of the relative strengths of fMRI and ERPs (Menon et al., 1997). We hypothesized that, if the ACC plays an important role in attentional control, it will show significantly greater stimulus-dependent modality-specific connectivity with sensory processing regions. In other words, the ACC will show increased connectivity with the auditory cortex during auditory tasks and increased connectivity in the visual cortex during visual tasks—even if ACC responses do not differ between the two tasks. We further hypothesized that, if the ACC has a modulatory role, it would be a strong and early neural generator of the N2b-P3 components of the ERP. The combined event-related fMRI and ERP analysis provides valuable insights into dynamic interactions between the ACC and primary sensory areas.

## METHODS

### Subjects

Fifteen subjects participated in the fMRI study (8 women, 7 men; age,  $24.0 \pm 4.5$  years). A different group of 12 subjects participated in the ERP study (6 men, 6 women; age,  $28.0 \pm 5.3$  years). For technical reasons, we were not able to use the same group of subjects for fMRI and ERP studies. Subjects were all right-handed, as assessed using a modified Edinburgh test (Oldfield, 1971). All subjects participated in this study after giving written informed consent. The human subjects committee at the Stanford University School of Medicine approved all protocols used in this study. The subjects were recruited from the surrounding community.

### Stimuli and Task Design

For both fMRI and ERP studies, subjects were presented with auditory and visual stimuli in two separate experiments. Each stimulus was presented for 150 msec, with an interstimuli interval of 1850 msec (2 sec between stimuli onsets). Two hundred stimuli were presented in each experiment. Each experiment contained two types of stimuli; 80% of trials consisted of frequent standard stimuli and 20% of trials consisted of infrequent

stimuli. Therefore, each sequence contained 40 infrequent stimuli and 160 frequent stimuli. Half of the subjects were asked to press a button on a handheld response box with the right index finger in response to all frequent stimuli, and to press another button with the right middle finger in response to infrequent stimuli. The other half of the subjects pressed the first button in response to infrequent stimuli and the second button in response to frequent stimuli. Instructions were presented for 4 sec at the beginning of each sequence. There was a 30-sec rest at the beginning (before the instruction) and at the end of each experiment. Each experiment lasted 7 min 48 sec. In the auditory experiment, pure tones of 1000 and 2000 Hz were presented. For half of the subjects, the infrequent stimulus was the 1000-Hz tone, whereas for the other half, the infrequent stimulus was the 2000-Hz tone. In the visual experiment, the stimuli consisted of blue and green circles presented in the center of the screen against a black background. For half of the subjects, the blue circle was the infrequent stimulus, whereas for the other half, the green circle was the infrequent stimulus. The order of the tasks was randomized between subjects. For technical reasons, these tasks were programmed using PsyScope 1.2.5 (Cohen, MacWhinney, Flatt, & Provost, 1993) for the fMRI session and using E-Prime 1.1 (Psychology Software Tools, Inc.) for the ERP session. Stimuli were presented using a fast stochastic event-related design (Chawla et al., 1999; Burock, Buckner, Woldorff, Rosen, & Dale, 1998; Menon et al., 1997). A jittered stimulus presentation was used, with a mean interdeviant interval of 10 sec and a standard deviation of 8 sec. The jittered stimulus presentation was optimized for estimating differential brain responses to the two types of stimuli by iterating several thousand times over finite random sequences to detect the most efficient design (Chawla et al., 1999; Somers et al., 1999).

### **Behavioral Data Analysis**

For both fMRI and ERP studies, accuracy was computed as the percentage of trials (infrequent and frequent stimuli) in which the subject responded correctly with an appropriate button push. A trial was considered incorrect if the subject did not respond within the 2 sec following stimulus onset. Reaction time was measured from the time of stimulus onset. Accuracy and reaction time for correct responses were analyzed using a  $2 \times 2$  analysis of variance (ANOVA), with factors Task (infrequent vs. frequent) and Modality (auditory vs. visual) for both fMRI and ERP studies.

### **fMRI Acquisition**

Images were acquired on a 3-T GE Signa scanner. Twenty-eight axial slices (4.0 mm thick, 1 mm skip) parallel to the anterior and posterior commissures cov-

ering the whole brain were imaged with a temporal resolution of 2 sec using a T2\*-weighted gradient spiral-in and spiral-out pulse sequence ( $T_R = 2000$  msec,  $T_E = 30$  msec, flip angle =  $90^\circ$ , interleave = 1; Glover & Law, 2001; Glover & Lai, 1998). The field of view was 200 mm, and the effective in-plane spatial resolution was 3.125 mm. To aid in the localization of functional data, a high-resolution T1-weighted spoiled grass gradient recalled 3-D MRI sequence was used with the following parameters:  $T_R = 35$  msec,  $T_E = 6$  msec, flip angle =  $45^\circ$ , field of view = 24 cm, slices in coronal plane = 124, matrix =  $256 \times 192$ . Initiation of scan and task was synchronized using a TTL pulse delivered to the scanner timing microprocessor board from a "CMU Button Box" microprocessor (<http://psyscope.psy.cmu.edu>) connected to the computer running PsyScope 1.2.5.

### **Image Preprocessing**

Spiral-in and spiral-out data were combined by using a weighted average of the two images, slice by slice. Weighting between the images for spiral-in and spiral-out acquisitions was determined by the intensities of the average image so that, in regions where the spiral-out average image had a lower intensity, the resultant image was weighted toward the spiral-in image and vice versa. In uniform regions, the combination reverts to a simple average of spiral-in and spiral-out images (for more details, see Glover & Law, 2001). Images were reconstructed, by inverse Fourier transforms, for each of the 120 time points into  $64 \times 64 \times 28$  image matrices (raw data voxel size,  $3.125 \times 3.125 \times 5$  mm). fMRI data were preprocessed using SPM99 (<http://www.fil.ion.ucl.ac.uk/spm>). Images were corrected for movement using least squares minimization without higher order corrections for spin history and were normalized to stereotaxic Talairach coordinates (Talairach & Tournoux, 1988). Images were then resampled every 2 mm (processed data voxel size,  $2 \times 2 \times 2$  mm) using sinc interpolation and smoothed with a 4-mm Gaussian kernel to decrease spatial noise.

### **fMRI Statistical Analysis**

Statistical analysis was performed on individual and group data using the general linear model and the theory of Gaussian random fields, as implemented in SPM99. This method takes advantage of multivariate regression analysis and corrects for temporal and spatial autocorrelations in fMRI data (Friston, Holmes, et al., 1995). Activation foci were superimposed on high-resolution T1-weighted images, and their locations were interpreted using known neuroanatomical landmarks (Duvernoy, Bourgouin, Cabanis, & Cattin, 1999; Mai, Assheuer, & Paxinos, 1997). Montreal Neurological Institute (MNI) coordinates were transformed to Talairach coordinates using nonlinear transformation (Brett, Johnsrude, & Owen, 2002).

A within-subjects procedure was used to model all the effects of interest for each subject. Individual subject models were identical across subjects (i.e., a balanced design was used). Confounding effects of fluctuations in global mean were removed by proportional scaling where, for each time point, each voxel was scaled by the global mean at that time point. Low-frequency noise was removed with a high-pass filter (0.5 cycles/min) applied to the fMRI time series at each voxel. A temporal smoothing function, corresponding to a canonical hemodynamic response function, was applied to the fMRI time series to enhance the temporal signal-to-noise ratio. We then defined the effects of interest for each subject with relevant contrasts of parameter estimates.

Group analysis was performed using a random-effects model that incorporated a two-stage hierarchical procedure. This model estimated the error variance for each condition of interest across subjects, rather than across scans, and therefore provided a stronger generalization to the population from which data were acquired (Holmes & Friston, 1998). In the first stage, contrast images for each subject and each effect of interest were generated as described above. In the second stage, these contrast images were analyzed using a general linear model to determine voxelwise  $t$  statistics. One contrast image was generated per subject for each effect of interest. A one-way two-tailed  $t$  test was then used to determine group activation for each effect.  $t$  Statistics were normalized to  $Z$  scores, and significant clusters of activation were determined using the joint expected probability distribution of the height and extent of  $Z$  scores (Poline, Worsley, Evans, & Friston, 1997), with height ( $Z > 1.67$ ,  $p < .05$ ) corrected at the cluster level ( $p < .05$ ) for whole brain comparisons. Contrast images were calculated using a within-subjects design for comparisons of infrequent–frequent conditions. All frequent and infrequent trials were included in the analysis because error rates were exceedingly small.

### Effective Connectivity

Effective connectivity analysis (Friston, Buechel, et al., 1997) was used to examine the interaction of the ACC with other brain regions during auditory and visual tasks. Effective connectivity is defined here as the influence of one region upon another, after discounting the influence of task-related effects and the effects of a common driving input.

Individual time series data points were first extracted for both auditory and visual tasks from voxels in a volume of interest (VOI), which consisted of a 4-mm-radius sphere centered on local activation maxima of overlapping auditory and visual activation in the ACC in group activation maps. For each subject, fMRI data points were averaged across voxels within this ROI after mean correction and high-pass filtering ( $F < 1/120$ ) to remove low-frequency signal drifts and then averaged

across sessions. No other transforms were performed on the time series. After obtaining time series data, a regressor, corresponding to the task-dependent physiological interaction (PI) of the ACC, was computed as scalar (dot) product of the ACC time series with task waveform. The task waveform was a time series of the same length as the ACC time series and consisted of +1 for time points corresponding to the presentation of infrequent stimuli, -1 for frequent stimuli, and 0 elsewhere. In addition to a PI regressor, the general linear model used in effective connectivity analysis included the main effects of task and time series from the VOI. Our analysis of effective connectivity was thus specific for ACC-modulated influences that occurred over and above any task and context-independent effects. Brain regions that showed significant PI effects were determined by testing for positive slopes of the PI regressor by applying a  $t$  contrast, which was 1 for the PI regressor and 0 for all other effects. Subject-specific contrast images were determined and then entered into random-effects group analyses. This second-level connectivity analysis allowed us to extend the inference to the population from which the data were acquired. The significance of the results was assessed at the cluster level ( $p < .05$ ), with whole brain corrections ( $p < .05$ ) for multiple comparisons.

### ERP Acquisition

Electroencephalogram (EEG) and vertical electro-oculogram (VEOG) signals were recorded continuously from 36 electrodes using the Quickcap (Compumedics Neuroscan Inc., El Paso, TX) and the Nuamps system (Compumedics Neuroscan, Inc.). VEOG was recorded from two electrodes placed on the infraorbital and supraorbital ridges of the left eye. The signals were bandpass-filtered (0.1–70 Hz) and digitized at a rate of 1000 Hz. All leads were referenced to the right mastoid. Electrode impedance was kept below 5 k $\Omega$ . EEG acquisition was performed on a PC running the Acquire 4.3 acquisition software (Compumedics Neuroscan, Inc.). To accurately indicate the timing of stimuli presentation, each stimulus was associated with a trigger sent from the parallel port of the PC running the stimulation software E-Prime 1.1 (Psychology Software Tools, Inc., Pittsburgh, PA) to the Nuamps and then to the PC running the EEG Acquire 4.3 software.

### ERP Analysis

EEG data were processed using the Edit 4.3 software (Compumedics Neuroscan, Inc.). The data were bandpass-filtered (0.1–50 Hz, 96 dB/oct, zero-phase shift) and baseline-corrected using the entire epoch. The next step was the correction of blink artifacts using the regular artifact reduction algorithm implemented in the Edit 4.3 software. Finally, portions of signals containing artifacts

larger than 80  $\mu\text{V}$  were removed. The EEG data were then epoched offline from  $-200$  to  $1000$  msec relative to the stimuli. Finally, epochs were averaged together to obtain even-related responses. The N2, P3a, and P3b components were analyzed on infrequent–frequent subtraction.

### Dipole Modeling

Dipole source modeling was used to examine the relationship between ERP and fMRI activation using Brain Electrical Source Analysis (BESA) 5.0 (MEGIS Software GmbH, Grafelfing, Germany). Dipole locations were determined using task-specific peak fMRI activations (local maxima). The standard method implemented in BESA allows Talairach coordinates to be entered into a three-shell model of cortex, skull, and scalp (Fuchs, Ford, Sands, & Lew, 2004; Woldorff, Liotti, et al., 2002; Liotti, Woldorff, Perez, & Mayberg, 2000; Pouthas, Garnero, Ferrandez, & Renault, 2000; Opitz et al., 1999; Wang et al., 1999; Menon et al., 1997; Tarkka, Stokic, Basile, & Papanicolaou, 1995). We created a dipole model for the auditory task and another dipole model for the visual task. When fMRI activations were similar in both tasks, the dipole was placed at the same coordinates in both tasks. Brain areas that do not have layered organization needed to generate far fields that can be recorded on the scalp (Nunez, 1999; Pedley & Traub, 1990), such as the thalamus and basal ganglia, were not used to model scalp potentials.

The orientation and strength of equivalent dipoles were determined by the least squares fitting procedure, minimizing the difference between measured and model-predicted waveforms for all electrodes simultaneously, as implemented in BESA 5.0 ([www.besa.de](http://www.besa.de)). The orientation and strength of the dipoles were fitted on the whole ERP window, from  $-200$  to  $1000$  msec poststimulus, for both auditory and visual models separately. The locations of the dipoles are displayed on the MRI template available with BESA 5.0. To compare the amplitude of the responses observed in different dipoles, we computed the average of the standard deviation for prestimulus points over all dipoles of each model. We then divided the amplitude of each point by this average standard deviation for each model separately.

## RESULTS

### Behavioral Performance

Subjects performed auditory and visual oddball tasks in two separate experiments. In each experiment, subjects were asked to detect infrequent stimuli embedded in a stream of frequent stimuli. Subjects were asked to respond to both infrequent and frequent stimuli. Accuracy was high during auditory and visual tasks for both ERP and fMRI sessions. In the fMRI session, the average

and standard error for the accuracy were  $94.57 \pm 1.4\%$  for infrequent auditory stimuli,  $95.28 \pm 2.11\%$  for frequent auditory stimuli,  $90.46 \pm 2.44$  for infrequent visual stimuli, and  $99.02 \pm 0.29\%$  for frequent visual stimuli. The average reaction times for the four conditions were  $494.31 \pm 24.26$ ,  $434.64 \pm 21.28$ ,  $453.52 \pm 12.93$ , and  $387.41 \pm 15.64$  msec, respectively. Accuracy was higher,  $F(1,12) = 6.96$ ,  $p = .022$ , and reaction time was shorter,  $F(1,12) = 59.30$ ,  $p < .0001$ , for frequent stimuli than for infrequent stimuli. The interaction between Modalities (visual, auditory) and Stimuli (frequent, infrequent) was significant for accuracy,  $F(1,12) = 14.00$ ,  $p = .003$ .

In the ERP session, subjects performed auditory and visual oddball tasks identical to those performed in the fMRI session. The average and standard error for the accuracy were  $94.58 \pm 1.89\%$  for infrequent auditory stimuli,  $99.53 \pm 0.22\%$  for frequent auditory stimuli,  $88.75 \pm 3.23\%$  for infrequent visual stimuli, and  $99.32 \pm 0.24$  for frequent visual stimuli. The average reaction times for the four conditions were  $453.26 \pm 26.46$ ,  $375.14 \pm 31.10$ ,  $486.49 \pm 17.32$ , and  $364.91 \pm 22.21$  msec, respectively. Similar to the results observed in the fMRI session, accuracy in the ERP session was higher,  $F(1,11) = 13.85$ ,  $p = .003$ , and reaction time was shorter,  $F(1,11) = 403.30$ ,  $p < .0001$ , for frequent stimuli than for infrequent stimuli. The reaction time was shorter during the auditory task than during the visual task,  $F(1,11) = 56.10$ ,  $p < .01$ . The interaction between Modalities (visual, auditory) and Stimuli (frequent, infrequent) was also significant for reaction time,  $F(1,11) = 229.20$ ,  $p < .0001$ .

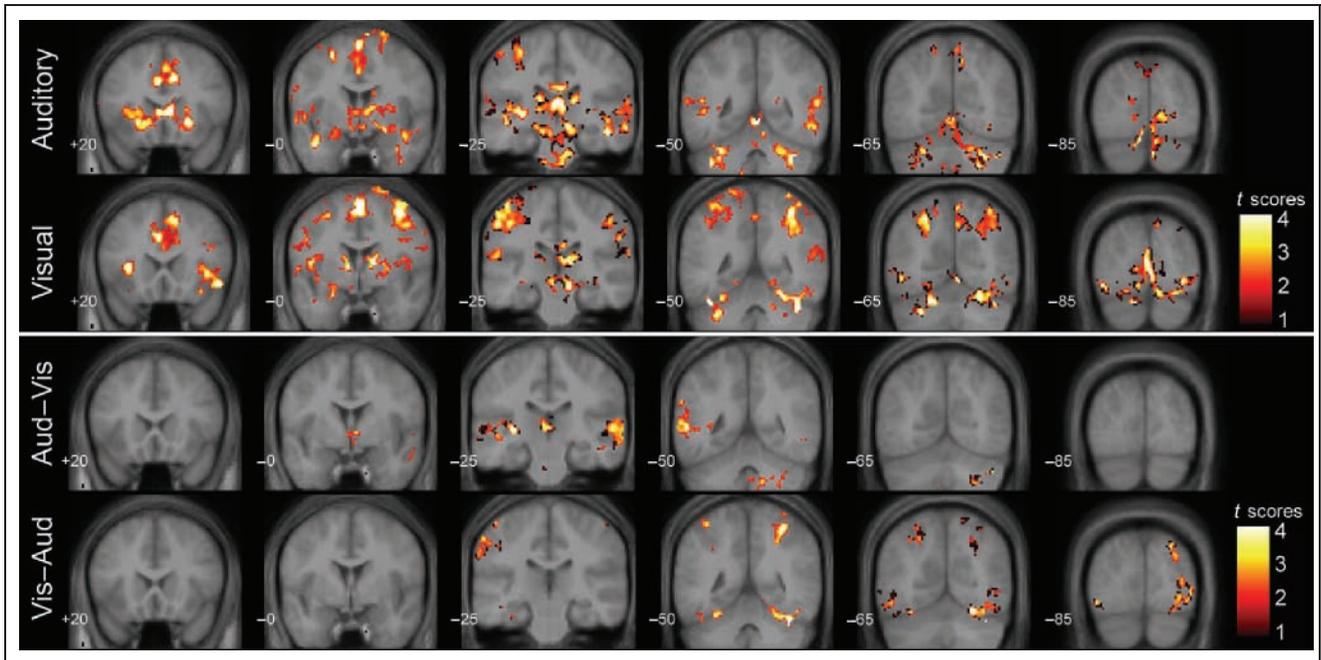
### Brain Activation

We first examined brain areas that showed greater fMRI activation to infrequent, compared to frequent, stimuli in the auditory and visual oddball tasks. Each task was first analyzed separately. Both tasks showed overlapping activation in the ACC, as well as in the SMA, inferior parietal cortex (IPC), basal ganglia, cerebellum, and left premotor cortex (Figure 1, top).

Modality differences in processing the infrequent, compared to frequent, stimuli were examined using paired  $t$  tests. No modality differences were observed in the ACC (Figure 1, bottom). Compared to the visual oddball task, activation during the auditory oddball task was observed in the left and right Heschl gyrus, middle and superior temporal gyri, supramarginal gyrus (SMG), cerebellum, and thalamus. Compared to the auditory oddball task, the visual oddball task had greater activation bilaterally in the lingual and fusiform gyri, middle and inferior occipital gyri, superior and inferior parietal gyri, inferior temporal gyri, and cerebellum.

### Effective Connectivity

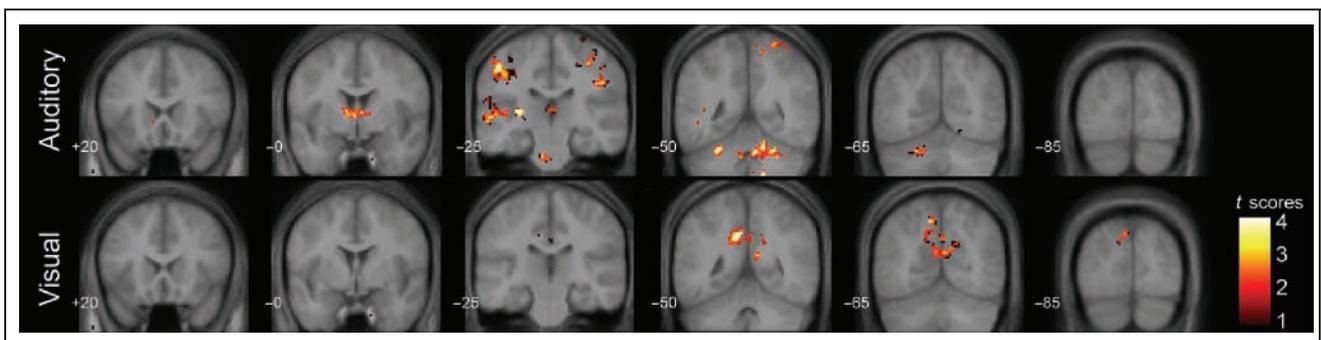
We examined the stimulus-dependent effective connectivity of the ACC using fMRI time series data. We



**Figure 1.** Brain areas that showed significantly greater activation during the detection of infrequent stimuli compared to frequent stimuli in the auditory and visual oddball tasks (top). Brain areas showing modality-related differences (bottom) with greater activation during the auditory task when compared to the visual task (Aud-Vis), and during the visual task when compared to the auditory task (Vis-Aud). Attention-related activation of the ACC is observed in both tasks; however, no modality differences are observed in the ACC. Each cluster is significant after correction for multiple spatial comparisons ( $p < .05$ ). Activations are shown superposed on group-averaged, spatially normalized, T1-weighted structural images.

first identified a subregion that showed overlapping activation in the ACC during the auditory and visual oddball tasks. A VOI was extracted using a 4-mm-radius sphere centered at the peak in this subregion of the ACC (Talairach coordinates:  $x = -4$ ,  $y = 20$ ,  $z = 26$ ), as shown in Figure 1. Average  $t$  scores were computed for each subject using a voxelwise threshold of  $t > 0$ . Consistent with the analysis of Brain activation, a paired  $t$  test showed no difference between the two modalities,  $t(12) = 1.00$ ,  $p = .33$ , in the ACC VOI.

During the auditory oddball task, the ACC showed greater stimulus-dependent effective connectivity,  $p < .05$ , corrected for multiple spatial comparisons, with the left Heschl gyrus, left middle and superior temporal gyri, left and right precentral and postcentral gyri, SMG, caudate, thalamus, and cerebellum (Figure 2 and Table 1). Activation was also detected in the right Heschl gyrus,  $p < .01$ , uncorrected. During the visual oddball task, this same ACC VOI showed greater stimulus-dependent effective connectivity with the striate cortex,



**Figure 2.** Brain regions that showed increased stimulus-dependent connectivity with the ACC (Talairach coordinates:  $x = -4$ ,  $y = 20$ ,  $z = 26$ ) during the auditory (top) and visual (bottom) oddball tasks. Modality-specific effects are observed in both tasks, with increased ACC influences on the Heschl and superior temporal gyri during the auditory task and on the striate cortex during the visual task. Each cluster is significant after correction for multiple spatial comparisons ( $p < .05$ ). Activations are shown superposed on group-averaged, spatially normalized, T1-weighted structural images.

**Table 1.** Brain Regions that Showed Increased Stimulus-dependent Connectivity with the ACC (Talairach Coordinates:  $x = -4, y = 20, z = 26$ ) during the Auditory (Top) and Visual (Bottom) Oddball Tasks

	Corrected $p$ Value	No. of Voxels	Z Score	Peak Talairach Coordinates
<i>(a) Effective connectivity with the ACC, auditory (infrequent–frequent)</i>				
L/R cerebellum 6, 4, 5, brainstem	.001	1153	3.87	24 -44 -22
L superior and middle temporal gyrus, L SMG, L Heschl gyrus,	.001	766	3.84	-30 -22 8
R postcentral and precentral gyri, R superior parietal gyrus, R SMG	.001	1057	3.74	46 -26 32
L postcentral gyrus, L inferior and superior parietal gyrus, L SMG	.001	598	3.32	-40 -38 56
L/R caudate, L/R thalamus	.001	508	2.93	-10 -2 6
<i>(b) Effective connectivity with the ACC, visual (infrequent–frequent)</i>				
L/R precuneus, L/R cuneus, L/R middle and posterior cingulate gyrus, L/R calcarine sulcus	.001	1255	3.85	-6 -46 36

For each significant cluster, region of activation, significance level, number of activated voxels, maximum Z score, and location of peak in Talairach coordinates are shown. Each cluster was significant after height and extent correction ( $p < .05$ ).

L = left; R = right.

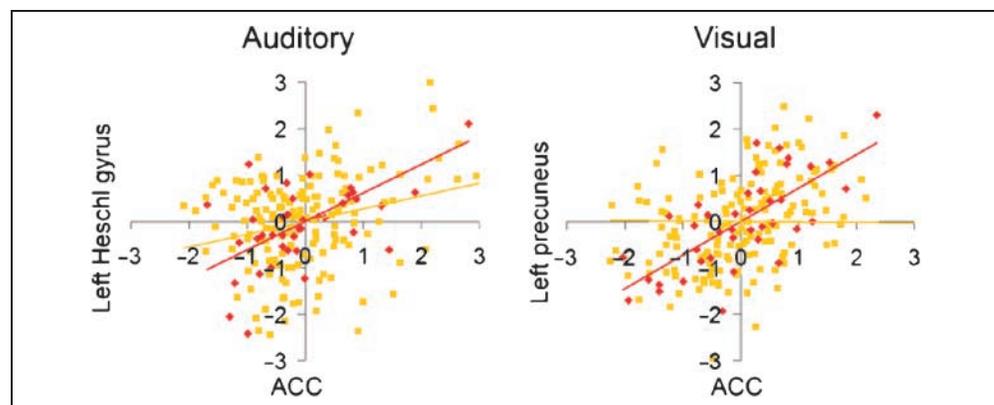
precuneus, cuneus, and posterior cingulate gyrus (Figure 2). Figure 3 shows single-subject data and demonstrates in a more explicit manner our finding of increased stimulus-dependent connectivity; responses in the ACC and early sensory regions were more tightly linked during the processing of infrequent, compared to, frequent stimuli.

### Scalp-recorded N2b and P3 ERP Components

Group-averaged ERPs confirmed that the oddball task used in the fMRI study evokes large N2 (or N2b)

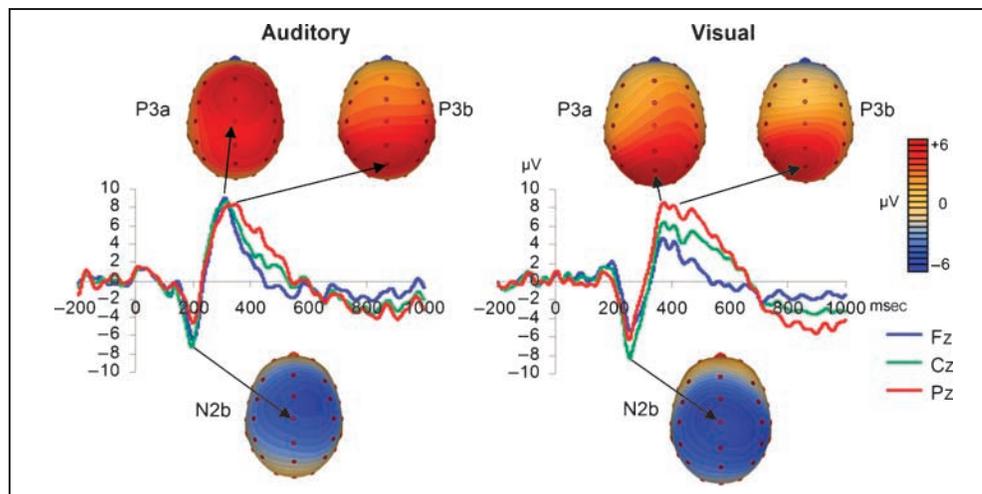
followed by P3 components on the scalp. Figure 4 shows these components with ERPs to the frequent stimuli subtracted from ERPs to the infrequent stimuli, separately for the auditory and visual oddball tasks. For both tasks, the N2b component had a scalp topography that was maximal over central electrodes, 194 msec poststimulus for the auditory ERP and 256 msec poststimulus for the visual ERP. For both auditory and visual tasks, the topography of the P3 components showed two different peaks. For the auditory task, the first peak was maximal over central electrodes at 310 msec poststimulus, and the second peak was maximal over centroparietal elec-

**Figure 3.** Modality-specific connectivity of the ACC. Plot of the fMRI time series showing the relation between the ACC (Talairach coordinates:  $x = -4, y = 20, z = 26$ ) and the left Heschl gyrus (Talairach coordinates:  $x = -50, y = -20, z = 8$ ) during the auditory oddball task (top) and between the ACC (Talairach coordinates:  $x = -4, y = 20, z = 26$ ) and the left precuneus (Talairach coordinates:  $x = -8, y = -60, z = 48$ ) during the visual oddball task



(bottom) from representative subjects. Data in red correspond to infrequent stimuli, and data in yellow correspond to frequent stimuli. A regression line is presented for each set of data. Data were mean-corrected and normalized. For the auditory task, there is a tighter connectivity between the ACC and the Heschl gyrus during infrequent, rather than frequent, stimuli. Similarly, for the visual task, there is a tighter connectivity between the ACC and the precuneus during infrequent, rather than frequent, stimuli. Note that, for the visual task, the regression line for frequent stimuli (yellow line) overlaps with the  $x$ -axis of the graph.

**Figure 4.** Difference in ERP waveforms (ERPs to infrequent – ERPs to frequent stimuli) at electrodes Fz, Cz, and Pz for the auditory (left) and visual (right) oddball tasks. Topographical maps are shown for the N2b, P3a, and P3b components.  $\mu\text{V}$  = microvolts.



trodes at 351 msec poststimulus. Similar results were found for the visual task, with a first peak at 370 msec poststimulus and a second peak at 451 msec poststimulus, even if the difference between the topographies of each peak is less obvious for the visual task than for the auditory task (Figure 4). For both tasks, the topography and latency of these peaks suggest that the first peak corresponds to the P3a component and the second peak corresponds to the P3b component (Näätänen, 1992).

### Dipole Modeling

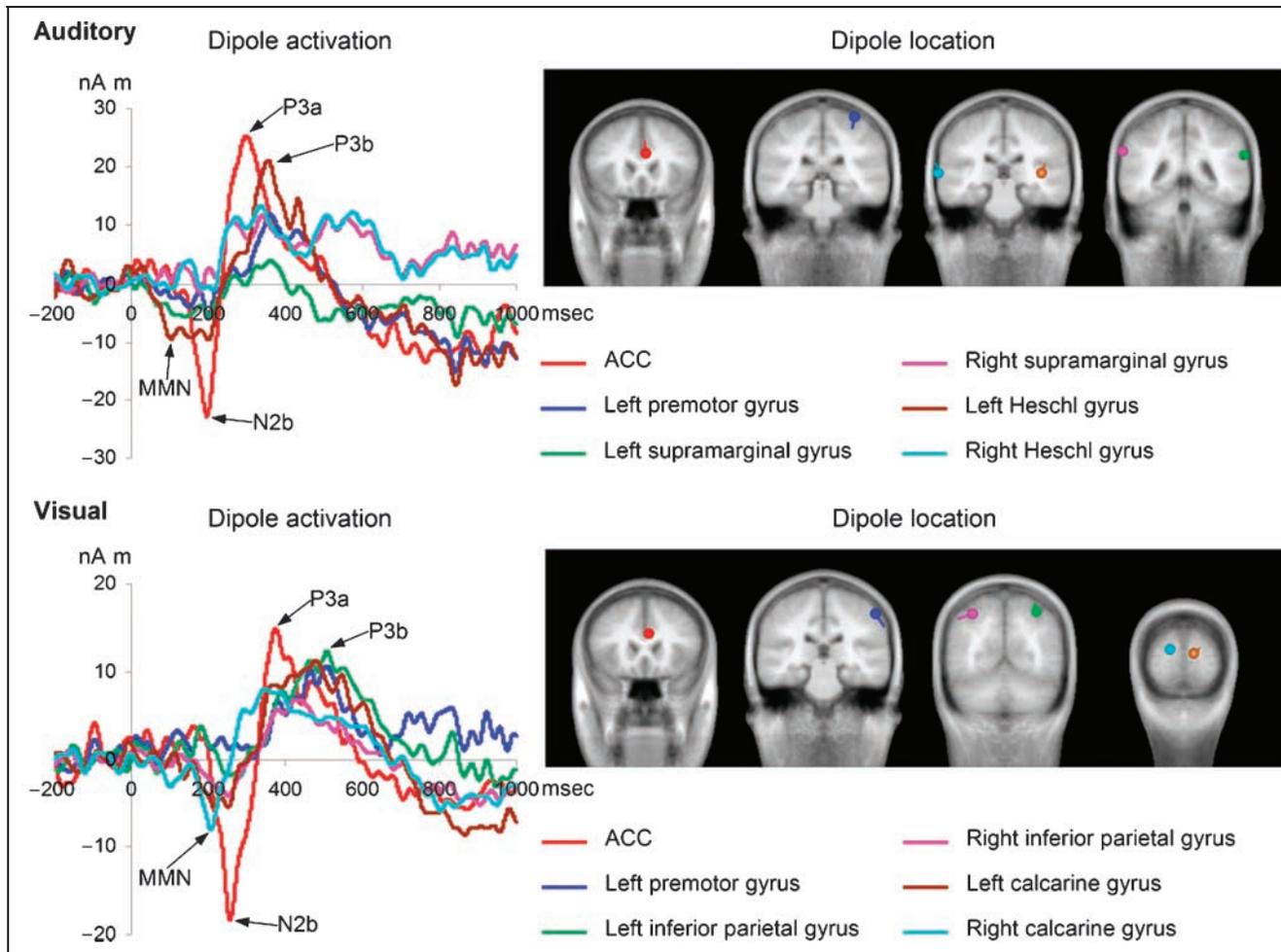
Dipole modeling on group-averaged ERPs was conducted using brain activations derived from fMRI analysis to seed dipole locations; this analysis provided an estimate of the time course of ERP responses in each location. Six dipole locations were chosen for each task (Figure 5). Dipole locations were based on the local maxima of fMRI activation clusters obtained by comparing infrequent and frequent stimuli (Figure 1). For the auditory oddball task, dipoles were placed in the ACC (Talairach coordinates:  $x = -4, y = 20, z = 26$ ), left Heschl gyrus (Talairach coordinates:  $x = -38, y = -22, z = 6$ ), right Heschl gyrus (Talairach coordinates:  $x = 66, y = -22, z = 6$ ), left SMG (Talairach coordinates:  $x = -60, y = -40, z = 24$ ), right SMG (Talairach coordinates:  $x = 62, y = -36, z = 28$ ), and left premotor cortex (Talairach coordinates:  $x = -32, y = -16, z = 64$ ). For the visual oddball task, dipoles were placed in the ACC (Talairach coordinates:  $x = -4, y = 20, z = 26$ ), left IPC (Talairach coordinates:  $x = -32, y = -56, z = 48$ ), right IPC (Talairach coordinates:  $x = 32, y = -54, z = 46$ ), left calcarine sulcus (Talairach coordinates:  $x = -10, y = -88, z = 6$ ), right calcarine sulcus (Talairach coordinates:  $x = 14, y = -84, z = 10$ ), and left premotor cortex (Talairach coordinates:  $x = -52, y = -24, z = 46$ ). Each dipole was fixed in location but was allowed to vary in orientation to reach

the best fit during the whole window of the ERP (200 msec prestimulus to 1000 msec poststimulus). The time course of each dipole derived from this analysis is shown in Figure 5.

The auditory dipole model accounted for 81% of the variance in the whole auditory ERP (from –200 to 1000 msec poststimulus), and the visual dipole model accounted for 88% of the variance in the whole visual ERPs for the same window. For both modalities, the respective models provided very good fits at the latencies of the N2b and P3 (P3a and P3b) components. The auditory model accounted for 94% of the variance in the auditory N2b peak (at 194 msec poststimulus), and the visual model accounted for 95% of the variance in the visual N2b peak (256 msec poststimulus). For both auditory and visual oddball tasks, the largest and most reliable peak at the N2b latency was observed in the ACC. All other dipoles either had lower amplitudes or were delayed with respect to the ACC response. For this dipole placed in the ACC, a later peak was observed in both modalities between 300 and 400 msec poststimulus, corresponding to the P3a peak described on the ERP (Figure 4). For this peak, the auditory model accounted for 95% of the variance in the auditory P3a (297 msec poststimulus), and the visual model accounted for 93% of the variance in the visual P3a (at 375 msec poststimulus). Finally, a late slow wave was observed on all dipoles, except on the ACC dipole. This activity peaked at 345 msec poststimulus in the auditory modality (accounting for 93% of the variance) and at 471 msec poststimulus in the visual modality (accounting for 95% of the variance). This late activity corresponded to the P3b component in the scalp-recorded ERP (Figure 5).

### DISCUSSION

We combined event-related fMRI and ERPs to investigate the spatiotemporal dynamics of attention-related ACC



**Figure 5.** Dipole model of ERP waveforms for the auditory (top) and visual (bottom) oddball tasks. Dipole locations were based on observed fMRI activations. Left: Time courses of dipole responses from  $-200$  to  $1000$  msec poststimulus show a large contribution of the ACC dipole to the N2b and P3a ERP components. Early responses corresponding to mismatch negativity (MMN) ERP component are observed in the Heschl gyrus for the auditory task and in the calcarine gyrus for the visual task. All dipoles, except the dipoles placed in the ACC, show late response in both auditory and visual tasks corresponding to the P3b ERP component. Right: Dipole locations are shown on a template MRI image. nA m = nanoampere meters.

responses during auditory and visual oddball tasks. Compared to frequent stimuli, infrequent stimuli showed significantly greater responses in the ACC as well as primary modality-specific sensory cortex. Although attention-related activation of the ACC was similar in both modalities, its connectivity was remarkably modality-specific. We found that the effective connectivity of the ACC was significantly greater with the Heschl gyrus for the infrequent, compared to frequent, auditory stimuli; similarly, the ACC connectivity was significantly greater with the striate cortex and the precuneus to infrequent, compared to frequent, visual stimuli. ERP recordings confirmed that oddball tasks elicit prominent frontocentral and central N2b and P3 signals—ERP components that are well-known to index attentional processing (Näätänen & Picton, 1986; Näätänen, Simpson, & Loveless, 1982; Renault & Lesevre, 1979). fMRI-constrained dipole modeling showed that the

ACC is the major generator of the N2b–P3a components of the ERP. Taken together, these results provide converging event-related fMRI and ERP evidence for top–down attentional modulation by the ACC on sensory processing areas.

### Attentional Modulation of Sensory Processing Regions by the ACC

Our findings of significant fMRI activation in the primary auditory and visual cortices to infrequent, compared with frequent, stimuli are consistent with previous studies, which have found that early sensory processing regions can be modulated by attention (e.g., Woldorff, Hazlett, et al., 2004; Hopfinger, Buonocore, & Mangun, 2000; Chawla et al., 1999). Similar attention-related activations in the visual cortex have been reported in tasks involving high-level visual representation (Buckner

et al., 1995; Fletcher et al., 1995), visual attention in spatial discrimination (Faillenot, Decety, & Jeannerod, 1999), object features detection (Nagahama et al., 1999), and attentive tracking of moving objects (Culham et al., 1998). Similarly, in the auditory modality, attention-related changes have been reported in the primary and association auditory cortex to numbers (Woodruff et al., 1996) and spoken syllables (Pugh et al., 1996). Most of these studies have tended to focus on either the visual or the auditory modalities, often with entirely different and complex experimental paradigms in the two modalities. The within-subjects design used in our study confirms modality-specific changes in sensory regions in response to the detection of infrequent stimuli.

More importantly, our findings go beyond existing studies in showing not only that early sensory processing regions are more active during attention-demanding tasks, but also that these regions show greater modality-specific effective connectivity with the ACC. In the visual oddball task, we found increased connectivity between the ACC and the precuneus and striate cortex. A few studies have examined the interaction of the ACC with other brain regions, within the context of attentional or cognitive control. Mazoyer, Wicker, and Fonlupt (2002) reported a positive correlation between the ACC and the precuneus during an attentional goal-directed visual task. However, ACC activation was far more posterior in their study (Talairach  $y$  coordinate =  $-16$  mm) than in our study (Talairach  $y$  coordinate =  $+20$  mm) and corresponded to the middle cingulate gyrus rather than to the ACC. Furthermore, the correlational analysis used in their study did not remove the effects of a common driving input, as was accomplished with our effective connectivity analysis. Using methods similar to those used in our study, Stephan et al. (2003) reported an increased effective connectivity of the ACC with the left inferior frontal gyrus during letter decisions, whereas the right ACC showed enhanced coupling with right parietal areas during visuospatial decisions. However, this study did not report increased connectivity with the visual cortex. Our finding of attentional modulation of sensory regions by the ACC is reinforced by parallel results in both the auditory and the visual modalities. Methodologically, it is important to note that the effective connectivity analyses used exactly the same VOI in both auditory and visual oddball tasks. Thus, the same area of the dorsal ACC is involved in distinct attentional networks, depending on the modality of the stimulus.

### **Role of the ACC**

The ACC VOI used in the connectivity analysis was centered in the area with the greatest overlap in task-related activation during auditory and visual tasks. This region corresponds to the dorsal aspect of the ACC (Brodmann's area 32) and is part of the cognitive

and executive area of the anterior cingulate gyrus (Bush, Luu, et al., 2000; Vogt, Finch, & Olson, 1992). This dorsal ACC region is thought to play an important role in cognitive control, but the manner in which attentional control is implemented is under intense debate. According to the "anterior attentional system" hypothesis (Bush, Luu, et al., 2000; Posner & Dehaene, 1994; Posner & Petersen, 1990), the dorsal ACC implements cognitive control by directly allocating attentional resources in response to changing task demands. On the other hand, the "conflict monitoring" hypothesis (Botvinick, Cohen, & Carter, 2004; Kerns et al., 2004; Botvinick, Braver, et al., 2001; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999) suggests that the dorsal ACC primarily monitors and detects conflicts in information processing. In this model, the dorsal ACC is thought to have a less direct role in attentional control; once the ACC detects a conflict, it signals the dorsolateral prefrontal cortex, which then executes necessary cognitive control (Kerns et al., 2004). In either case, either directly or indirectly, the dorsal ACC is hypothesized to play a critical role in cognitive control.

The oddball task does involve response conflict because subjects develop a dominant response tendency with standard stimuli that (on the remaining 20% of trials) they need to inhibit, and they should make a different response associated with a deviant stimulus. Consistent with this, dorsal ACC activations observed in our study overlap with those reported during classical response conflict tasks, such as the Stroop (Kerns et al., 2004; Milham, Banich, Webb, et al., 2001). In contrast, the dorsolateral prefrontal cortex did not show significant activation in the two tasks used in our study. Furthermore, the ACC did not show significantly greater interaction with the dorsolateral prefrontal cortex during either the auditory or the visual task. It is possible that the dorsolateral prefrontal cortex is not critically involved in the oddball task where the level of conflict and interference is low compared to, for example, that in the Stroop task. A further possibility is that the ACC may mediate attentional control via the posterior inferior frontal cortex—another region implicated in cognitive control (Brass, Derrfuss, Forstmann, & Cramon, 2005). However, the lateral inferior frontal cortex also did not show greater effective connectivity with the ACC during either the auditory or the visual tasks. Our findings are consistent with the results of Milham, Banich, Webb, et al., who have shown that the involvement of the anterior cingulate in attentional control is primarily limited to situations of response conflict, whereas the involvement of left prefrontal cortex extends to the occurrence of conflict at nonresponse levels (Milham, Banich, Webb, et al., 2001). Taken together, these results suggest that, within the context of the oddball task, the ACC may play a more direct role in modulating attentional response. In tasks such as the Stroop, which require a relatively higher level

of cognitive control, the dorsolateral prefrontal cortex and other lateral prefrontal cortex regions may play a more important role in modulating attentional response (Milham, Banich, Claus, & Cohen, 2003). This view is consistent with the notion that cognitive control may not be a unitary phenomenon and that there may be multiple neural routes to attentional control (Milham & Banich, 2005).

A completely different perspective regarding the role of the ACC in attentional control was presented recently by Fellows and Farah (2005). They assessed cognitive control in four human subjects with damage to the dorsal ACC, all of whom showed normal adjustments in performance following manipulation of response conflict in both Stroop and Go/No-go tasks. Furthermore, damage to the dorsal ACC neither impaired the phenomenon of posterior slowing nor altered the ability to adjust performance in response to explicit speed or accuracy instructions. Therefore, they argue that the dorsal ACC is not necessary for cognitive control. The limited number of subjects studied and the unilateral nature of lesion in three of four subjects preclude a definitive assessment of this statement at this stage. It should, however, be noted that a previous study of the same Stroop task in two subjects with unilateral dorsal ACC damage showed somewhat different findings (Swick & Jovanovic, 2002). One individual with right dorsal ACC damage failed to modulate performance between high and low conflict blocks, and a left dorsal ACC-damaged subject showed less modulation than six control subjects. It is nevertheless possible that ACC responses observed in our study reflect both attentional and psychophysiological changes in response to salient events in the environment (Critchley, Tang, Glaser, Butterworth, & Dolan, 2005; Critchley, Mathias, et al., 2003). This is an important topic that warrants further investigation.

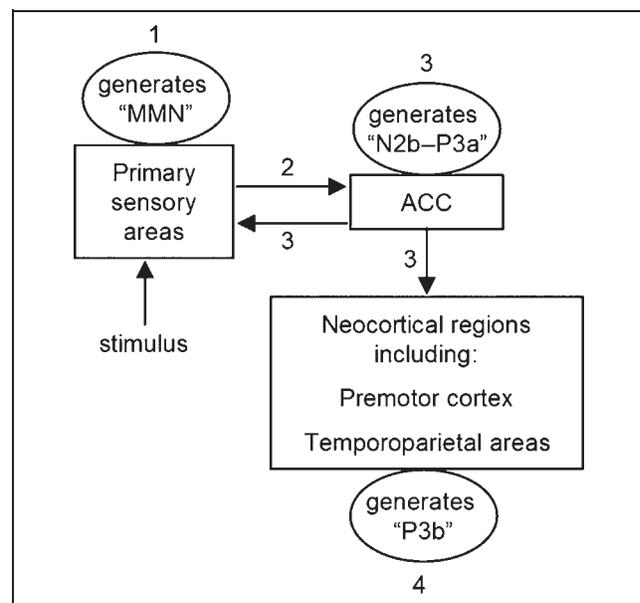
### Temporal Dynamics of ACC and Primary Sensory Cortex Responses

Converging evidence from ERPs provides further insight into the temporal dynamics underlying the modulatory effects of the ACC. Detection of infrequent stimuli evoked large N2b and P3 components in ERPs for both modalities. Dipole modeling, based on fMRI activations, showed large N2b response in the ACC at about 200 msec. Large P3 responses at about 310 msec in the auditory modality and at 370 msec poststimulus in the visual modality were also observed in the ACC. At these latencies, amplitudes in the ACC were more than twice as large as the amplitudes in other activated regions, including early sensory areas. For both tasks, ERP topography at the latency of the P3 response in the ACC showed a peak located over frontal and central electrodes, suggesting that this response in the ACC indexes the P3a component. Our data also suggest

that slow-wave responses (after 350 msec poststimulus) observed for all dipoles, except the dipole in the ACC, are related to the P3b component. Corresponding ERP scalp topography showed a centroparietal distribution that is typically observed for the P3b component (for a review, see Näätänen, 1992). These results extend prior ERP findings, which have suggested frontocentral source for the P3a and centroparietal source for P3b (Elting, van Weerden, van der Naalt, De Keyser, & Maurits, 2003).

Our dipole analysis also showed that, in each modality, primary sensory regions (Heschl gyrus and striate cortex) generate detectable signals about 50 msec prior to N2b response in the ACC. The ERP scalp topography corresponding to these deflections showed a negative peak over central electrodes at 159 msec poststimulus for the auditory oddball task, and over centro-occipital electrodes at 208 msec poststimulus for the visual oddball task. The latency and topography of these responses suggest an early sensory detection of a difference between infrequent and frequent stimuli, analogous to a mismatch negativity component (Tales, Newton, Troscianko, & Butler, 1999; Näätänen, 1992).

We visualize these changes in terms of a dynamic reentrant interaction between the primary sensory areas



**Figure 6.** Schematic model of bottom-up and top-down interactions underlying attentional control. Stage 1: About 150 msec poststimulus, primary sensory areas detect an infrequent stimulus as indexed by the MMN component of the ERP. Stage 2: This bottom-up MMN signal is transmitted to other brain regions, notably the ACC. Stage 3: About 200–300 msec poststimulus, the ACC generates a top-down control signal, as indexed by N2b–P3a ERP components. This signal is simultaneously transmitted to primary sensory areas and other neocortical regions. Stage 4: About 300–400 msec poststimulus, neocortical regions, notably the premotor cortex and temporoparietal areas, respond to attentional shift with a signal that is indexed by the P3b ERP component.

and the ACC (Figure 6). Initially, primary sensory areas detect a deviant stimulus; information about a deviant stimulus is conveyed to multiple cortical regions, including the ACC. During the interval corresponding to the N2b–P3a complex, the ACC then sends a modulatory signal back to sensory areas and other cortical regions, including the IPC, as shown by fMRI activations. P3b activity reflects the resultant response in multiple cortical regions, as shown in our dipole model. Consistent with this view, the N2b component (Näätänen & Picton, 1986; Näätänen et al., 1982; Renault & Lesevre, 1979) has been thought to index a controlled or conscious orientation to deviant and novel environmental stimuli (Renault, Ragot, Lesevre, & Remond, 1982; Ritter, Simson, Vaughan, & Friedman, 1979), and the P3a has been associated with attentional reorientation and reallocation of attention to relevant stimuli (e.g., Barcelo, Perianez, & Knight, 2002; Escera, Alho, Schroger, & Winkler, 2000; Courchesne, Hillyard, & Galambos, 1975; Squires, Squires, & Hillyard, 1975). Intracranial recordings using visual and auditory oddball tasks (Baudena, Halgren, Heit, & Clarke, 1995) have also suggested the existence of N2b generators in the ACC and more widespread P3b generators in the ventrolateral prefrontal cortex, hippocampus, superior temporal gyrus, intraparietal sulcus, and rhinal cortex (for a review, see Halgren, Marinkovic, & Chauvel, 1998). Scalp EEG recordings of patients with brain lesions have shown that lesions in the temporoparietal junction severely reduce the amplitude of the P3b component, but not the N2b (for a review, see Soltani & Knight, 2000). These findings indicate that the ACC is the major generator of brain responses that, around 200 msec poststimulus, engender attentional shift whose effects are manifest over widely distributed cortical regions, including the primary sensory cortex. Taken together, our combined fMRI and ERP findings provide new evidence for a dynamic process that involves both bottom–up and top–down interactions underlying attentional control. Such interactions provide a distributed brain mechanism by which neural activity is amplified to favor the selection, maintenance, and manipulation of task-relevant information while diminishing neural activity in regions handling task-irrelevant information (Milham, Erickson, et al., 2002).

### Acknowledgments

It is a pleasure to thank two anonymous reviewers for their comments and suggestions. This research was supported by grants from the Norris Foundation, the Swiss National Science Foundation, and the National Institutes of Health (grants HD40761 and HD47520 to V. M.).

Reprint requests should be sent to S. Crottaz-Herbette, PhD, or V. Menon, PhD, Department of Psychiatry and Behavioral Sciences, Stanford University School of Medicine, 401 Quarry Road, Stanford, CA 94305, or via e-mail: herbette@stanford.edu or menon@stanford.edu.

The data reported in this experiment have been deposited with the fMRI Data Center (www.fmridc.org). The accession number is 2-2005-120HQ.

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