

Covert Auditory Attention Generates Activation in the Rostral/Dorsal Anterior Cingulate Cortex

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Abstract

■ The anterior cingulate cortex (ACC) is believed to mediate conscious information processing or high-capacity attention. However, previous functional imaging studies have largely relied on tasks that involve motor function as well as attention. The work from our group utilizing an auditory continuous performance task demonstrated increased activity in a caudal division of the ACC that borders the supplementary motor area (SMA). Activity in this region was attributed to motor responding as well as attention. In the present study, we used ^{15}O H_2O positron emission tomography (PET) to map brain activation during nonmotor, covert auditory attention. Our hypothesis was that a different region within the ACC, anterior to the SMA, would be active during covert attention (CA). Six men and six women were asked to monitor aurally presented syllables presented at a 1-sec

interstimulus interval. During the CA condition, subjects were asked to continuously discriminate target (.19 probability) from nontarget stimuli. Simultaneous recording of event-related potentials (ERPs) confirmed the discrimination of target and nontarget stimuli and the allocation of attention capacity. Comparison of the monitored versus nonmonitored presentation of stimuli demonstrated significant activity in a rostral/dorsal division of the right ACC, anterior to SMA. Other regions of activation included the lateral prefrontal cortex and posterior superior temporal gyrus in the left hemisphere, consistent with neurocognitive models of language and vigilance. We conclude that a rostral/dorsal subdivision of the right ACC is specific for conscious attention during auditory processing, in contrast to premotor response formation. ■

INTRODUCTION

The role of the anterior cingulate cortex (ACC) in attention and motor control has been a topic of intense interest in recent years. While the ACC is a primary substrate for conscious information processing and response formation (Posner, 1994; Posner & Rothbart, 1991), it is also widely recognized as an integral region for premotor function (Picard & Strick, 1996; Devinsky, Morrell, & Vogt, 1995; Vogt, Nimchinsky, Vogt, & Hof, 1995; Paus, Petrides, Evans, & Meyer, 1993). The ACC includes Brodmann's areas (BA) 24, 25, and 32 on its rostral border and more caudal areas BA 24' and 32' (Vogt et al., 1995). Research indicates that these broad rostral and caudal divisions subservise different processes: The rostral division is critical for processing affective stimuli, while caudal areas subservise cognitive and motor performance (Devinsky et al., 1995). Cytoarchitectural data from monkey and human demonstrate that BA 24' and 32', which border the supplementary motor area (SMA), possess layer V pyramidal cells that are directly involved in the motor system (Vogt et al., 1995). In addition,

electrical stimulation of caudal ACC gives rise to tonic posturing of the contralateral forearm and wrist (Diehl et al., 2000). It is likely that these caudal subdivisions of the ACC are modality specific (e.g., oral vs. manual response) with respect to premotor control (Picard & Strick, 1996; Paus et al., 1993). Indeed, data from one case study (Turken & Swick, 1999) suggest that performance accuracy on attention tests is highly dependent upon whether an oral or manual response is required.

Heretofore, the behavioral tasks employed in neuroimaging research have failed to differentiate the contribution of neural networks underlying attention versus other functions. Most attentional studies have employed tasks that involve a range of other cognitive operations such as finger tapping, word generation, Stroop conflict, semantic processing, and working memory, among others (Paus et al., 1993). Furthermore, most neuroimaging studies of attention have been conducted in the visual modality, and several auditory studies requiring only attention or easy target/nontarget discriminations have failed to demonstrate reliable ACC activity (Grady et al., 1997; O'Leary et al., 1996; Reinsel et al., 1995; Cohen et al., 1988). Benedict et al. (1998), however, found right ACC activity during execution of a more difficult auditory

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task, the continuous performance test, an established clinical procedure designed to quantify attention deficits in patients with neurologic and psychiatric disorders (Benedict et al., 1994; Parasuraman & Haxby, 1993; Cornblatt, Lenzenweger, & Erlenmeyer-Kimling, 1989; Nuechterlein, Parasuraman, & Jiang, 1983). The procedure requires a button-press response following target presentations without requiring the manipulation of information in working memory. Targets are embedded within a stream of nontarget stimuli, usually at a probability of .15–.25. The task is made difficult by degrading stimulus quality, thereby lowering the signal-to-noise ratio. This auditory task was associated with activation in right caudal ACC (BA 24c'), in comparison to a passive listen control condition (Benedict et al., 1998). However, the activation task in this study, like most other positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) studies (Paus, Koski, Caramanos, & Westbury, 1998), involved motoric responding in order to measure performance.

Overt responses are necessary when investigators seek to measure or confirm that tasks are performed correctly and that attention is allocated to the primary task under investigation. Yet such measurement presents an interesting conundrum: While it is important to measure or confirm conscious processing, neural activity associated with these behavioral (manual, oral) responses confounds the interpretation of activity on PET or fMRI imaging. A few studies have employed covert responding tasks such as counting targets (Grady et al., 1997; Reinsel et al., 1995), but such procedures confound neural networks that underlie processes such as calculation and working memory with those mediating only conscious attention. The conundrum extends to psychological theory as well. According to Posner (1994) and Posner and Rothbart (1991), the so-called bottleneck of attention that gives rise to consciousness occurs when individuals prepare for a behavioral (or motor) response. Thus, the precise distinction among attention, response preparation, and motor function is unclear.

In the present study, we endeavored to study conscious attention covertly, by asking participants to mentally note targets without responding orally or manually. To ascertain the extent to which attentional capacity was allocated to the task, we measured event-related potentials (ERPs) during the covert attention (CA) condition. We predicted that contrasts designed to map attentional networks would give rise to increased rCBF in a dorsal division of the ACC distinguishable from the traditional cognitive/motor caudal zone.

RESULTS

Behavioral Results

Six male and six female volunteers were presented with human voiced syllables during PET. There were no

gender effects with respect to age, education, or any neuropsychological test score.

During the motor attention (MA) condition, subjects pressed response buttons after detecting a target syllable. The control for this task was a motor-only (MO) condition that required self-paced, random button presses without target/nontarget discrimination. During the CA condition, subjects attended to stimuli in order to mentally recognize targets. The control task was a listen-only (LO) condition requiring that subjects merely listen to stimuli. Each condition was repeated across two blocks, separated by a rest condition. The order of task presentation was counterbalanced to control for alertness/arousal effects.

On the MA task, mean true-positive rate was 0.83 ($SD = 0.09$) and false-positive rate was 0.02 ($SD = 0.01$). Overall performance as measured by Pr (Snodgrass & Corwin, 1988), which accounts for true-positive and false-positive rates, did not differ significantly between the first and second administrations of the MA task.

Total responses (i.e., number of button presses, including false positives) during MA and MO were highly correlated (Pearson $r = .81$, $p < .001$). There was a statistical trend ($p = .07$) toward more responses during the MA (55.1, $SD = 9.5$) than MO (48.8, $SD = 16.4$) condition and the number of MO responses ranged widely from 21 to 75. Total responses during MO were also reliably correlated with target/nontarget discrimination accuracy (Pr) during MA ($r = .74$, $p < .001$). These behavioral data suggest that subjects employed a variety of cognitive strategies during the MO task and that these strategies involved attention to some extent. There were no behavioral data for analysis obtained from the non-motor tasks.

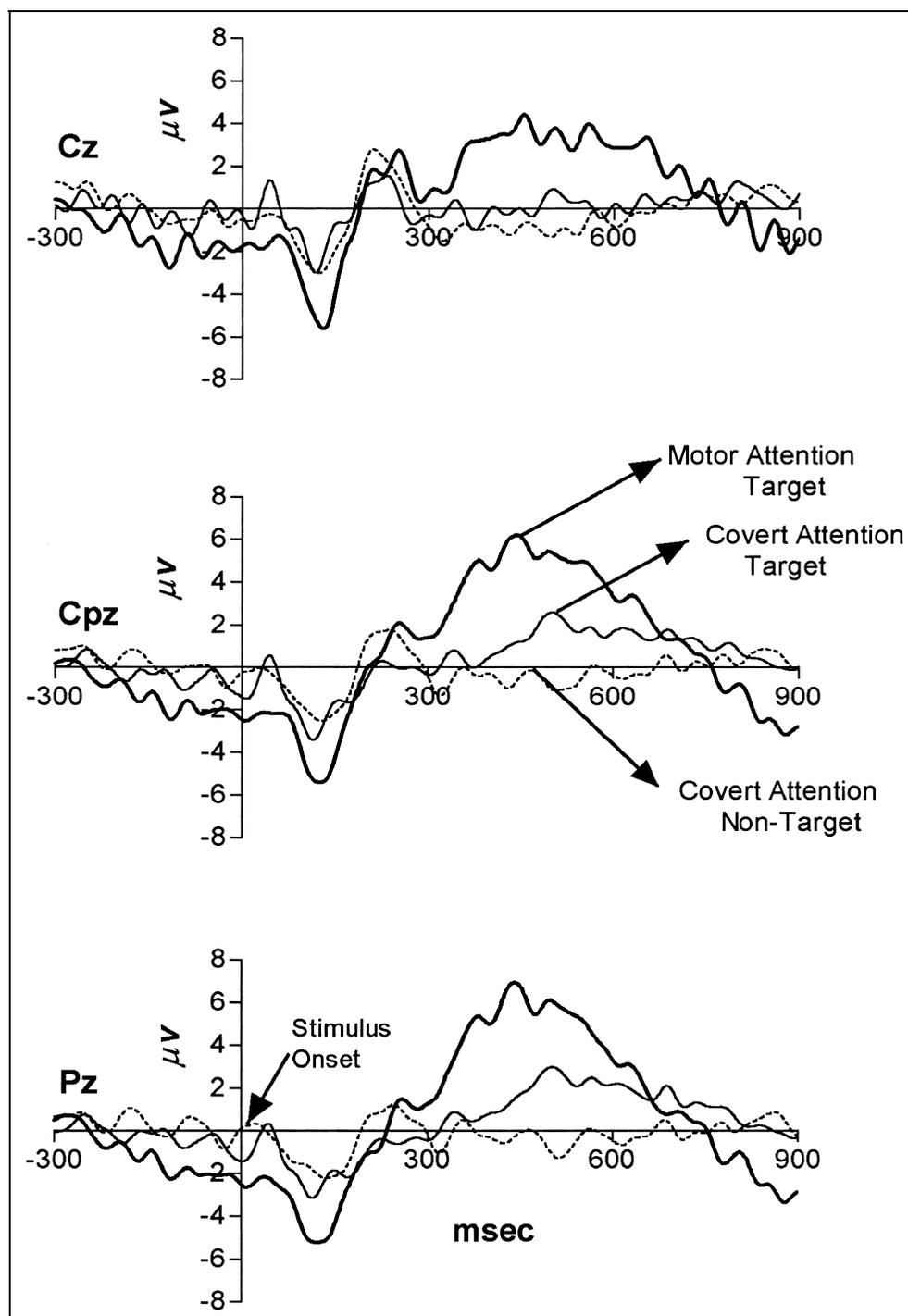
Electrophysiology

A 4 (MA target, CA target, MA nontarget, CA nontarget) \times 3 (Cz, Cpz, Pz) ANOVA for amplitude effects yielded a significant interaction ($p < .01$, Figure 1). The target P3 amplitude for MA was significantly higher ($p < .01$) than the target P3 amplitude for CA at all midline scalp sites, but best seen at Cpz. The targets in both tasks elicited higher P3 amplitude than their respective nontargets (MA, $p < .05$; CA, $p < .05$). No amplitude differences were seen in the P3 window between MA nontargets and CA nontargets. Analysis of latency effects revealed that P3 latency was longer for CA than MA, irrespective of lead ($p < .05$).

Imaging

The PET data were used to generate areas of increased rCBF in statistical parametric mapping (SPM) $\{Z\}$ images (Figure 2) and statistics pertaining to the each significant region (Table 1). The SPM contrast comparing MA and MO yielded one small reliable region of elevated rCBF

Figure 1. Central–parietal waveforms for MA and CA conditions. Testing of univariate effects revealed that MA target P3 amplitude was significantly higher ($p < .01$) than CA target amplitude at all midline scalp sites, although most clearly evident at Cz. The CA target P3 amplitude was significantly higher than P3 amplitude for nontargets ($p < .05$). Analysis of latency effects revealed that P3 latency was longer for CA than MA, irrespective of lead ($p < .05$).

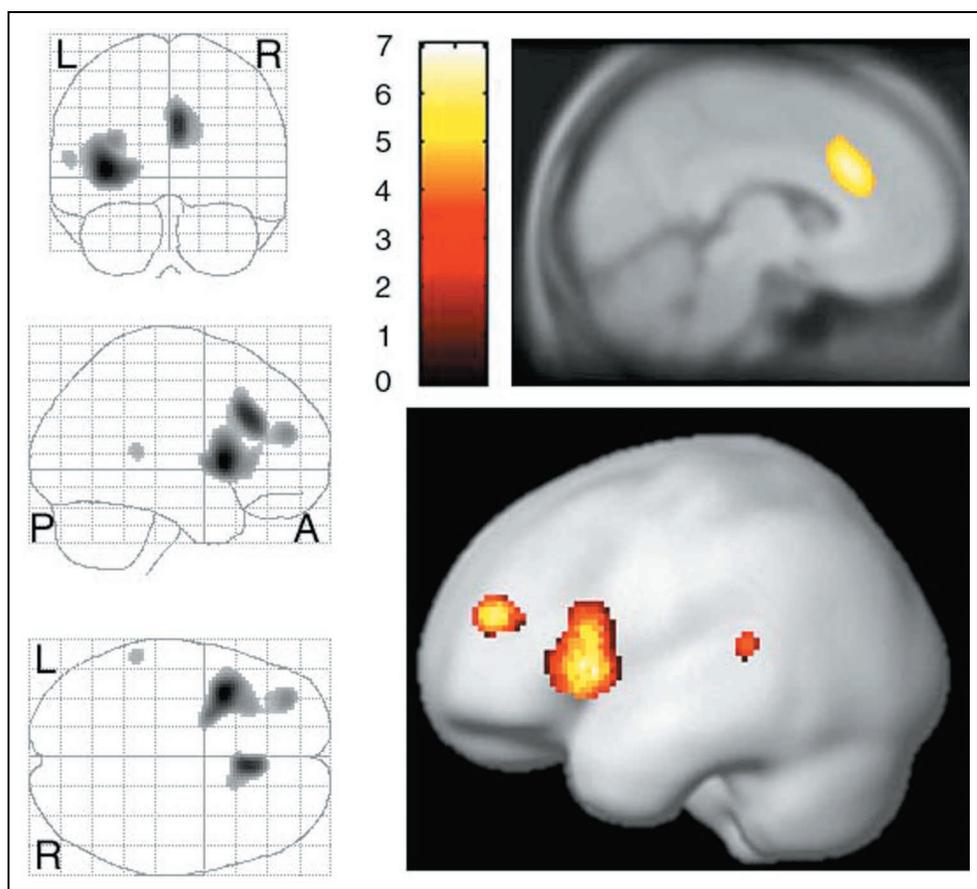


(corrected $p = .04$), focused in the left primary sensory/motor cortex. This contrast also revealed a weakly activated site in the caudal ACC ($x = -4$, $y = 0$, $z = 50$, uncorrected $p < .001$) proximal to SMA.

The CA – LO contrast is shown in Figure 2 at the conservative threshold of $p = .00001$, corrected for multiple comparisons, to separate more clearly the various maxima. Statistical details are presented in Table 1. The contrast revealed a reliable region of activation

within the right ACC. The activity is clearly localized in BA 32', in the dorsal aspect of the cingulate gyrus. This contrast revealed three other regions of activity. First, there was a large area of increased rCBF in the left hemisphere extending posteriorly from lateral prefrontal cortex encompassing the operculum, insular cortex, and areas of premotor cortex. Imaging this region using the more stringent criteria (Figure 2) revealed two distinct subregions: The first located on the lateral aspect of the

Figure 2. Three orthogonal SPM $\{Z\}$ projections are shown on the left at an uncorrected threshold of $p = .00001$. Image orientation: A = anterior; P = posterior; R = right; L = left. CA is contrasted against passive listening (LO) to identical stimuli (CA – LO) where CA requires discrimination of targets from nontargets. The top right image is through a parasagittal plane that passes through the site of maximal activation in the right ACC. The bottom right panel shows SPM $\{Z\}$ values rendered on to the lateral surface of the left hemisphere and demonstrates activation in the premotor cortex, the lateral frontal cortex, and the posterior portion of the superior temporal gyrus.



left frontal cortex, encompassing BA 46 and 10; and the second located in premotor cortex, BA 6 and 44. Finally, another significant area of activation was focused in the posterior temporal cortex, posterior to A1.

Since the CA and LO tasks were each presented in separate blocks, we sought to determine whether this block design affected the results of our analysis. Specifically, did the fact that subjects had performed the MA task affect subsequent performance of subsequent CA tasks? Two approaches were used. In the first, we performed a cognitive conjunction analysis in which we

identified common activations in the CA – LO contrast in each of the two blocks. As expected, this analysis yielded results that were virtually identical to those shown in Figure 2. In the second approach, we looked for differences between blocks using two contrasts: block1 (CA – LO) – block2 (CA – LO) and block2 (CA – LO) – block1 (CA – LO). Neither of these tests for interactions yielded significant results at the voxel level.

Comparisons of men and women (voxel by voxel t tests, corrected) in all contrasts revealed no significant sex differences with regard to brain activation.

Table 1. Data Derived From SPM Analysis, CA – LO Contrast

Region	Cluster Size Corrected p	Voxel Threshold Corrected p	x	y	z	Localization
Left premotor	.000	.000	–36	12	4	BA 44, 45
Left lateral frontal cortex		.005	–32	48	20	middle frontal gyrus, BA 46/10
Right ACC	.000	.000	6	26	30	cingulate gyrus, BA 32
Left temporal lobe	.002	.026	–58	–38	12	posterior superior temporal gyrus, BA 22

DISCUSSION

We employed a version of the CPT that required only auditory processing and target identification. By subtracting a passive listening from an active attentional state, we isolated areas of the brain that are active during motor-free or covert auditory attention. PET imaging revealed activity in the right ACC, as well as in regions of the left hemisphere that correspond with language function. These data support the hypothesis that the right ACC is part of an anterior attentional network that is not motor-dependent.

ACC and Attention

One model of the ACC's role in attention poses that the lateral prefrontal cortex sends signals to the ACC where the execution of adaptive responses is initiated (Posner, 1994; Posner & Peterson, 1990). This view of the ACC is probably too general. Devinsky et al. (1995) proposed that two cognitive subdivisions of the ACC can be distinguished: a mid or rostral/dorsal division (BA 32'), where cognitive or conscious processing begins, and a caudal area (BA 24c') that mediates initiation of a modality-specific motor response. Our results, which demonstrate activity only in the rostral/dorsal division, support this conceptualization. The lateral prefrontal cortex may interact with this "pure cognitive" division, which has reciprocal connections with the premotor caudal zone for motor preparation. Because no motor response was required in our study, only the more rostral area was activated. We previously found that attention to syllables with motor responding produced activity in the caudal aspect of ACC (BA 24c', $x = 0$, $y = -10$, $z = 44$) proximal to the SMA (Benedict et al., 1998). The locus of activation reported in the present study ($x = 6$, $y = 26$, $z = 30$) is clearly anterior to this previously described region.

Another interpretation of our finding is that increased activity in this rostral/dorsal subregion of the ACC is related to input from primary or secondary auditory cortex. Koski and Paus (2000) and Paus (2000) have pointed out that there are modality specific differences in activity within the frontal cortex during attention. For example, many visual attention studies have demonstrated activity in the frontal eye fields whereas the ventrolateral frontal cortex has been commonly observed during auditory attention (Paus, 2000). Certain regions of the ACC may also be positioned to receive input from specific sensory regions, either directly, or via other regions within the prefrontal cortex. Arguing against this interpretation of rostral/dorsal activity is our prior observation of a peak within the caudal ACC during auditory attention with motor responding (Benedict et al., 1998). Nevertheless, replication of the current finding using activation tasks in the visual modality or a direct comparison of auditory and visual CA PET activity would be of interest in future research.

Our subjects were instructed to monitor auditory stimuli but not respond either orally or manually. As such, our findings are not compatible with a response preparation model of the ACC-mediated attention (Posner & Dehaene, 1994; Posner & Peterson, 1990). Rather, the data would seem to support more recent theories that conceptualize the role of the ACC as one of processing conflicts during response competition (Carter et al., 2000; Carter, Botvinick, & Cohen, 1999). In our study, subjects were asked to evaluate each stimulus, analyze its quality, and determine whether it was a target or nontarget. The covert response of denoting the target was contingent upon such stimulus evaluation. Such effortful discrimination presumably requires increasing levels of processing capacity, and gives rise to consciousness. Response preparation also requires attentional capacity, but this function appears to be mediated by a more posterior division of the ACC.

Methodological Considerations

ACC activity during conscious processing or attention has been observed in multiple behavioral tasks. Unfortunately, it is difficult to isolate the effects of attention from other cognitive operations. The paradigmatic Stroop procedure, for example, involves visual processing, reading, color naming, and impulse control, as well as attention. Thus, it is not surprising that a recent Stroop-based fMRI study identified activation in 31 regions of interest (Peterson et al., 1999). While an interregional correlation analysis suggested coupling of the ACC with many of these regions, the complexity of the task makes it difficult to identify the specific attentional elements in this neurocognitive network. The advantage of the continuous performance task employed here is that ancillary cognitive operations were substantially reduced and the demand for attention capacity was high. Indeed, the only nonattention operation required in our study involved the perception of very basic or simple auditory stimuli. Changes in rCBF have been studied before with the standard CPT paradigm (Benedict et al., 1998; Cohen et al., 1988), but these studies included motoric responding. In this study, we circumvented this problem by monitoring a late component ERP that demonstrated greater attention allocation for target as opposed to nontarget stimuli during CA. Monitoring of covert processing during PET was attempted previously (Tzourio et al., 1997). However, the activation task required easy discriminations of low- (750 Hz) and high- (1790 Hz) pitched tones rather than degraded stimuli, only early ERPs were studied, and the ACC activity was of marginal significance ($p = .07$).

The MO/MA contrast was also intended to localize cerebral activity associated with auditory attention while controlling for the influence motor output. This experimental manipulation was not successful despite pilot work using the same protocol wherein the MO and MA

conditions generated nearly identical numbers of total responses. Unfortunately, in the present study, there was a modest difference in response rate between these conditions. Moreover, target discrimination accuracy during MA was correlated with total number of responses during MO, suggesting that the latter condition also involved attention. We also found that the frequency of responding during MO was highly variable, suggesting that multiple cognitive strategies were employed across subjects. Altogether, there is evidence that the control task was not sufficiently automated. In retrospect, we believe that subjects should have been given more practice with the MO task prior to imaging.

The CA/LO contrast was more successful in that motor function was controlled directly by asking subjects not to respond orally or manually. Covert tasks pose the problem of verifying mental activity during imaging. We addressed this problem by comparing late component ERPs that followed target and nontarget stimuli. The P3 amplitude difference between target and nontarget stimuli for both MA and CA tasks suggests that an attention network was activated despite the absence of a motor response. However, we note that P3 latency was longer for LA than MA, suggesting that subjects took longer to process the targets when no motor response was required.

Language-Related Activation

Three left hemisphere regions—lateral prefrontal cortex, premotor cortex, and posterior temporal cortex—were significantly more active when target/nontarget discriminations were compared to a passive listening state. Such a finding was expected because more elaborate auditory/language processing was required during CA. Monitoring the sequential presentation of phonemes is similarly associated with activity in the left posterior/superior temporal gyrus, as well as in the Broca's area (Demonet et al., 1992). Other findings suggest that the observed activity in the Broca's area may also be explained by subvocalization of the articulatory loop component of working memory (Demonet, Price, Wise, & Frackowiak, 1994a, 1994b). Activity in the lateral prefrontal cortex has been reported in studies requiring verbal working memory (Braver et al., 1997; D'Esposito et al., 1995; Jonides et al., 1993; Petrides, Alivisatos, Meyer, & Evans, 1993), particularly when the central executive component is strongly emphasized (Cohen et al., 1997). However, our activation task did not require manipulation of information in working memory. Moreover, we did not find activity in the left parietal cortex (BA 39 and 40), another region associated with verbal working memory (Barch et al., 1997). The lateral prefrontal activity observed in this study may represent further cognitive activity related to evaluating syllables in this unusual cognitive task (i.e., being told to mentally note but not respond to targets) or some

aspect of problem solving other than the manipulation of information on line.

METHODS

Subjects

Twelve right-handed healthy volunteers (six men, six women) participated in the study after providing written informed consent in accordance with guidelines approved by a university institutional review board. Mean age for the sample was 25.1 ($SD = 5.9$) years.

The subjects were screened with audiometric (250–8000 Hz of 20-dB hearing level) and neuropsychological (1.5 SD of normal) procedures, as well as MRI.

Activation Tasks

A NeuroScan computer network system (NeuroScan, Herndon, VA) was used to present human-voiced English syllables ending with /a/ and beginning with either a stop or nasal consonant. Eight speakers (four men, four women) were employed to generate the stimuli, which were then degraded and edited to 200 msec in length. The stimuli were digitized at a rate of 41000 Hz for a duration of 200 msec. The end points were smoothed utilizing a Hanning Window with a 5-msec rise/fall time. Left and right channels were limited to a sound pressure level of 80 dB. The degraded stimuli were created by passing the original stimuli through a low-pass filter with a break frequency of 1150 Hz and a slope rate of 24 dB/octave. The final pool of 128 stimuli was employed for each behavioral task, thereby limiting repetition, and in turn, participant learning of specific stimulus–response pairings. These stimuli were found to be matched in difficulty in a pilot study employing 15 student volunteers. The syllables were presented via foam cushion insert earphones. The peak sound pressure level approximated 90 dB. The interstimulus interval was 1 sec and the target probability rate was .19. Each sequence lasted approximately 5 min and included 333 stimuli.

There were four activation tasks: MA, MO, CA, and LO. During MA, subjects discriminated among the stimuli in order to identify targets with a rapid, bilateral thumb-press response. During MO, subjects performed a well-practiced, bilateral thumb-press task while listening to syllables. There was no specified target syllable and button presses were self-paced. Subjects were trained to respond at a frequency approximating the rate of target syllable presentations during MA. The task was practiced for 15–30 min at the end of the neuropsychological assessment and again immediately prior to scanning. Practice was intended to automate the task such that no or little attention would be required. During CA, subjects discriminated the stimuli so that a designated target could be recognized or identified. No motor response was required. Subjects were told to mentally note or recognize when a target syllable was presented,

and to avoid covert speech and all motoric responding (manual or vocal). During LO, subjects were instructed to merely listen to the auditory stimuli.

All subjects underwent two sets of trials, separated by a resting scan (nine scans total). Tasks were presented in counterbalanced order with the stipulation that within each modality control conditions (LO, MO) preceded active attention states (CA, MA). Target syllables included: /ba/, /da/, /pa/, and /ma/.

Electrophysiological Recording

Electrophysiological (EEG) data were collected from nine subjects. One subject's responses were lost to technical error. The first two subjects in the series were not collected due to changes in the EEG acquisition protocol. A 32-lead electrode cap (Quick-Cap, NeuroScan, Sterling, VA) was used, in accordance with the 10–20 system. The scalp electrodes were referenced to left and right mastoids. Eye movements were recorded with vertical electrooculogram (VEOG) and horizontal electrooculogram (HEOG) electrodes. Continuous EEG was collected with NeuroScan amplifiers. A low-frequency filter at 0.1 Hz and a high-frequency filter at 100 Hz were used. A 60-Hz filter was also employed. The sampling rate was at 500 Hz (2 msec). Continuous EEG was divided into 1700-msec epochs. The epoch window was set between 300 msec prestimulus and 1400 msec poststimulus onset. Prior to averaging, the data were filtered offline (25 Hz low pass, 0.3 Hz high pass). The 300-msec prestimulus waveform was used for baseline correction. Artifact rejections were set at $\pm 200 \mu\text{V}$ for scalp electrodes and $\pm 100 \mu\text{V}$ for HEOG. The VEOG correction was performed using the method of Semlitsch, Anderer, Schuster, and Presslich (1986). Separate averages were created for the target and nontarget stimuli of the MA and CA tasks. Averages for each subject were created to yield a grand average for both target and nontarget stimuli within each task. The grand averages were used to derive a template for P3 identification. The P3 response was identified as the maximum positive deflection (baseline to peak) occurring between 300 and 700 msec poststimulus. The peaks corresponding to P3 at Cz, Cpz, and Pz for targets and nontargets during MA and CA tasks were subjected to a repeated measures ANOVA. Data for three subjects were not included in the analyses due to technical problems. In addition, data for one subject were not obtained for the MA condition.

PET

Subjects underwent ^{15}O H₂O PET and ERP recording simultaneously, in a single session, during which they performed the auditory tasks described above. Earphones were inserted into the subject's ears and the subject was positioned in the PET scanner. Examples of each single auditory stimulus were presented to insure

accurate comprehension of target and nontarget stimuli during the transmission scan.

Subjects were positioned in a Siemens ECAT 951/31R tomograph, modified for 3-D data collection, so that the inferior image plane coincided with the canthomeatal line. Etymotic ER3A insert earphones were placed in the external auditory meatus of both ears. To reduce ambient noise even further, Cabot Safety Model 3000 earmuffs or Bose Active Noise Suppression headset were placed over both ears. Head position was maintained by means of an individually fitted thermo-plastic mask. After a 20-min transmission scan, nine emission scans were obtained. Each scan began with the slow intravenous injection of a bolus (15-sec injection followed by a 15-sec flush) of 7 mCi or less of ^{15}O H₂O as a tracer of CBF. Activation procedures began 20 sec prior beginning the injection and continued throughout the scan. The initial 60 sec of emission data, timed from the arrival of the ^{15}O H₂O in the brain, were used for image reconstruction (random coincidence correction, measured attenuation, Hann filter, cutoff frequency 0.4 cycles per pixel) and analysis.

Images were converted to the Analyze format and analyzed by SPM (Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997). Images were corrected for between-scan movement, normalized into standard space, and normalized to a common mean CBF value by an analysis of covariance. A 15-mm Gaussian smoothing filter was employed to increase the signal-to-noise ratio, condition the data to conform with the requirements of Gaussian field theory, and to minimize confounding of results due to individual anatomical differences. PET images were mapped onto a common stereotaxic framework based on the atlas of Talairach and Tournoux (1988) using stereotaxic normalization (Friston et al., 1995). A 15-mm Gaussian filter was employed to reduce spatial uncertainty. Unless otherwise specified, all analyses were performed using a Z threshold of 3.09 corresponding to $p = .001$ (corrected for multiple comparisons). The contrasts were designed to isolate attention while controlling for motor activity. MA was contrasted against MO, and CA was contrasted against LO. ERPs following target and nontarget stimuli were collected to confirm that the MA and CA states were associated with allocation of attention. The MO and MA conditions were compared for total number of responses to insure balance of motor activity across condition.

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REFERENCES

- Barch, D. M., Braver, T. S., Nystrom, L. E., Forman, S. D., Noll, D. C., & Cohen, J. D. (1997). Dissociating working memory from task difficulty in human prefrontal cortex. *Neuropsychologia*, *35*, 1373–1380.
- Benedict, R. H. B., Harris, A. E., Markow, T., McCormick, J., Nuechterlein, K., & Asarnow, R. (1994). The effects of attention training on information processing in schizophrenia. *Schizophrenia Bulletin*, *20*, 537–545.
- Benedict, R. H. B., Lockwood, A. H., Shucard, D. W., Shucard, J. L., Wack, D., & Murphy, B. (1998). Functional neuroimaging of sustained and selective attention in the auditory modality. *NeuroReport*, *9*, 121–126.
- Braver, T. S., Cohen, J. D., Nystrom, L. E., Jonides, J., Smith, E. E., & Noll, D. C. (1997). A parametric study of prefrontal cortex involvement in human working memory. *Neuroimage*, *5*, 49–62.
- Carter, C. S., Botvinick, M. M., & Cohen, J. D. (1999). The contribution of the anterior cingulate cortex to executive processes in cognition [Review, 62 refs]. *Reviews in the Neurosciences*, *10*, 49–57.
- Carter, C. S., Macdonald, A. M., Botvinick, M., Ross, L. L., Stenger, V. A., Noll, D., & Cohen, J. D. (2000). Parsing executive processes: Strategic vs. evaluative functions of the anterior cingulate cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *97*, 1944–1948.
- Cohen, J. D., Perlstein, W. M., Braver, T. S., Nystrom, L. E., Noll, D. C., Jonides, J., & Smith, E. E. (1997). Temporal dynamics of brain activation during a working memory task [see comments]. *Nature*, *386*, 604–608.
- Cohen, R. M., Semple, W. E., Gross, M., Holcomb, H. H., Dowling, M. S., & Nordahl, T. F. (1988). Functional localization of sustained attention: Comparison to sensory stimulation in the absence of instruction. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology*, *1*, 3–20.
- Cornblatt, B. A., Lenzenweger, M. F., & Erlenmeyer-Kimling, L. (1989). The continuous performance test, identical pairs version: II. Contrasting attentional profiles in schizophrenic and depressed patients. *Psychiatry Research*, *29*, 65–85.
- Demonet, J., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J. L., Wise, R., Rascol, A., & Frackowiak, R. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain*, *115*, 313–317.
- Demonet, J., Price, C., Wise, R., & Frackowiak, R. S. J. (1994a). A PET study of cognitive strategies in normal subjects during language tasks: Influence of phonetic ambiguity and sequence processing on phoneme monitoring. *Brain*, *117*, 671–682.
- Demonet, J., Price, C., Wise, R., & Frackowiak, R. S. J. (1994b). Differential activation of right and left posterior Sylvian regions by semantic and phonological tasks: A positron-emission tomography study in normal subjects. *Neuroscience Letters*, *182*, 25–28.
- D'Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., & Grossman, M. (1995). The neural basis of the central executive system of working memory. *Nature*, *378*, 279–281.
- Devinsky, O., Morrell, M. J., & Vogt, B. A. (1995). Contributions of the anterior cingulate cortex to behaviour. *Brain*, *118*, 279–306.
- Diehl, B., Dinner, D. S., Mohamed, A., Najm, I., Klem, G., LaPresto, E., Bingaman, W., & Luders, H. O. (2000). Evidence of cingulate motor representation in humans. *Neurology*, *55*, 725–728.
- Frackowiak, R. S. J., Friston, K. J., Frith, C. D., Dolan, R. J., & Mazziotta, J. C. (1997). *Human brain function*. New York: Academic Press.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. P., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, *2*, 189–210.
- Grady, C. L., Van Meter, J. W., Maisog, J. M., Pietrini, P., Krasuski, J., & Rauschecker, J. P. (1997). Attention-related modulation of activity in primary and secondary auditory cortex. *NeuroReport*, *8*, 2511–2516.
- Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S., & Mintun, M. A. (1993). Spatial working memory in humans as revealed by PET [see comments]. *Nature*, *363*, 623–625.
- Koski, L., & Paus, T. (2000). Functional connectivity of the anterior cingulate cortex within the human frontal lobe: A brain-mapping meta-analysis. *Experimental Brain Research*, *133*, 55–65.
- Nuechterlein, K. H., Parasuraman, R., & Jiang, Q. (1983). Visual sustained attention: Image degradation produces rapid sensitivity decrement over time. *Science*, *220*, 327–329.
- O'Leary, D. S., Andreason, N. C., Hurtig, R. R., Hichwa, R. D., Watkins, G. L., Ponto, L. L., Rogers, M., & Kirchner, P. T. (1996). A positron emission tomography study of binaurally and dichotically presented stimuli: Effects of level of language and directed attention. *Brain and Language*, *53*, 20–39.
- Parasuraman, R., & Haxby, J. V. (1993). Attention and brain function in Alzheimer's disease: A review. *Neuropsychology*, *7*, 242–272.
- Paus, T. (2000). Functional anatomy of arousal and attention systems in the human brain. *Progress in Brain Research*, *126*, 65–77.
- Paus, T., Koski, L., Caramanos, Z., & Westbury, C. (1998). Regional differences in the effects of task difficulty and motor output on blood flow response in the human anterior cingulate cortex: A review of 107 PET activation studies [Review, 94 refs]. *NeuroReport*, *9*, R37–R47.
- Paus, T., Petrides, M., Evans, A. C., & Meyer, E. (1993). Role of the human anterior cingulate cortex in the control of oculomotor, manual, and speech responses: A positron emission tomography study. *Journal of Neurophysiology*, *70*, 453–469.
- Peterson, B. S., Skudlarski, P., Gatenby, J. C., Zhang, H., Anderson, A. W., & Gore, J. C. (1999). An fMRI study of Stroop word-color interference: Evidence for cingulate subregions subserving multiple distributed attentional systems [Review, 100 refs]. *Biological Psychiatry*, *45*, 1237–1258.
- Petrides, M., Alivisatos, B., Meyer, E., & Evans, A. C. (1993). Functional activation of the human frontal cortex during the performance of verbal working memory tasks. *Proceedings of the National Academy of Sciences, U.S.A.*, *90*, 878–882.
- Picard, N., & Strick, P. L. (1996). Motor areas of the medial wall: A review of their location and functional activation. *Cerebral Cortex*, *6*, 342–353.
- Posner, M. I. (1994). Attention: The mechanisms of consciousness [Review, 37 refs]. *Proceedings of the National Academy of Sciences, U.S.A.*, *91*, 7398–7403.
- Posner, M. I., & Dehaene, S. (1994). Attentional networks. *Trends in Neurosciences*, *17*, 75–79.
- Posner, M. I., & Peterson, S. E. (1990). The attentional system of the human brain. *Annual Review of Neuroscience*, *25*–42.
- Posner, M. I., & Rothbart, M. K. (1991). Attentional mechanisms and conscious experience. In A. D. Milner & M. D. Rugg (Eds.), *Neuropsychology of consciousness*. New York: Academic Press.

- Reinsel, R. A., Veselis, R. A., Feshchenko, V. A., Diresta, G. R., Mawlawi, O., Beattie, B., Silbersweig, D., Stern, E., Blasberg, R., Macapinlac, H., Finn, R., Goldsmith, S., & Larson, S. (1995). Target detection and the prefrontal cortex. *Annals of the New York Academy of Sciences*, 769, 393–397.
- Semlitsch, H. V., Anderer, P., Schuster, P., & Presslich, O. (1986). A solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. *Psychophysiology*, 23, 695–703.
- Snodgrass, J. C., & Corwin, J. (1988). Pragmatics of measuring recognition memory: Applications to dementia and amnesia. *Journal of Experimental Psychology, General*, 117, 34–50.
- Talairach, J., & Tournoux, P. (1988). *A coplanar stereotaxic atlas of the human brain*. Stuttgart: Thieme.
- Turken, A. U., & Swick, D. (1999). Response selection in the human anterior cingulate cortex. *Nature Neuroscience*, 2, 920–924.
- Tzourio, N., Massiou, F. E., Crivello, F., Joliot, M., Renault, B., & Mazoyer, B. (1997). Functional anatomy of human auditory attention studied with PET. *Neuroimage*, 5, 63–77.
- Vogt, B. A., Nimchinsky, E. A., Vogt, L. J., & Hof, P. R. (1995). Human cingulate cortex: Surface features, flat maps, and cytoarchitecture. *Journal of Comparative Neurology*, 359, 490–506.