

Priming within and across Modalities: Exploring the Nature of rCBF Increases and Decreases

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Neuroimaging studies suggest that within-modality priming is associated with reduced regional cerebral blood flow (rCBF) in the extrastriate area, whereas cross-modality priming is associated with increased rCBF in prefrontal cortex. To characterize the nature of rCBF changes in within- and cross-modality priming, we conducted two neuroimaging experiments using positron emission tomography (PET). In experiment 1, rCBF changes in within-modality auditory priming on a word stem completion task were observed under same- and different-voice conditions. Both conditions were associated with decreased rCBF in extrastriate cortex. In the different-voice condition there were additional rCBF changes in the middle temporal gyrus and prefrontal cortex. Results suggest that the extrastriate involvement in within-modality priming is sensitive to a change in sensory modality of target stimuli between study and test, but not to a change in the feature of a stimulus within the same modality. In experiment 2, we studied cross-modality priming on a visual stem completion test after encoding under full- and divided-attention conditions. Increased rCBF in the anterior prefrontal cortex was observed in the full- but not in the divided-attention condition. Because explicit retrieval is compromised after encoding under the divided-attention condition, prefrontal involvement in cross-modality priming indicates recruitment of an aspect of explicit retrieval mechanism. The aspect of explicit retrieval that is most likely to be involved in cross-modality priming is the familiarity effect. © 2001 Academic Press

Priming refers to a change in the ability to identify or produce an item as a consequence of a specific prior encounter with it (Tulving and Schacter, 1990) and is considered a type of implicit or nondeclarative memory (e.g., Graf and Schacter, 1985; Schacter *et al.*, 1993;

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Squire, 1994). Priming effects have been demonstrated when targets are studied and tested either in the same sensory modality (within-modality priming) or in different sensory modalities (cross-modality priming; e.g., Bassili *et al.*, 1989; McClelland and Pring, 1991; Schacter and Graf, 1989).

Neuroimaging studies have consistently reported that within-modality priming is associated with reduced activity in regions of extrastriate cortex when study and test items were presented visually (priming related increases in activity have been reported under certain task conditions, cf, Henson, Shallice and Dolan, 2000; Schacter *et al.*, 1995; for review see, Schacter and Buckner, 1998; Wiggs and Martin, 1998). Surprisingly, we observed the same pattern (reduced extrastriate activation) when study and test items were presented aurally (Badgaiyan *et al.*, 1999; see also, Buckner *et al.*, 2000). In contrast, neuroimaging studies of cross-modality priming have not revealed changes in extrastriate cortex. Instead, cross-modality priming is associated with increased regional cerebral blood flow (rCBF) in the prefrontal cortex and decreased rCBF in regions of superior temporal cortex (Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999).

The rCBF decrease in extrastriate cortex during within- but not cross-modality priming suggests that the decrease is related to modality-specific perceptual processes. However, it is unclear what aspects of perceptual processing are related to extrastriate decreases during within-modality priming. This question is especially salient in relation to auditory priming, because extrastriate cortex has not been previously linked with auditory processing (for discussion, see Badgaiyan *et al.*, 1999).

Behavioral studies have shown that within-modality auditory priming includes two components. One component reflects memory for specific features of a stimulus (e.g., speaker's voice), and a second component involves an abstract phonological or lexical representation of the stimulus that is unaffected by the change in acoustic features (Church and Schacter, 1994; Goldinger, 1996; Jackson and Morton, 1984; Schacter and

Church, 1992; Sheffert, 1998). It is unknown whether decreases in extrastriate cortex during within-modality auditory priming reflect memory for feature-specific information and therefore occur only when target items share the same features at study and test. Alternatively, such decreases may reflect memory for abstract lexical information, and therefore occur even when presented items have different features at study and test.

Similarly, it is not clear which features of cross-modality priming are responsible for increased rCBF in prefrontal cortex. Based on the findings of previous neuroimaging (Schacter *et al.*, 1997) and neuropsychological (Curran *et al.*, 1999; Jacoby *et al.*, 1993) studies, we have suggested that increased prefrontal rCBF during cross-modality priming could reflect some aspect of explicit retrieval (cf. Badgaiyan *et al.*, 1999; Schacter and Badgaiyan, 2001). To test this idea, we examined cross-modality priming following encoding under full- and divided-attention conditions. Behavioral experiments have indicated that dividing attention at encoding significantly reduces explicit retrieval but has no effect on priming in a word stem completion task (Debner and Jacoby, 1994; Jennings and Jacoby, 1993). These findings have clear implications for cross-modality priming: if attention is divided at encoding, it should reduce or abolish the contribution of explicit retrieval to the priming effect. If, therefore, prefrontal activation during cross-modality priming is associated with explicit retrieval, dividing attention at encoding should reduce or eliminate this activation.

The two experiments reported here used positron emission tomography (PET) to characterize the nature of rCBF changes during within-modality and cross-modality auditory priming. In experiment 1, rCBF changes in within-modality auditory priming on a word stem completion task were studied under same- and different-voice conditions. The goal of the experiment was to determine whether changes in extrastriate cortex are observed during within-modality priming only when the study and test items have similar perceptual features or whether such changes occur even when perceptual features differ between study and test items. In experiment 2, we studied cross-modality priming after encoding was carried out under full- or divided-attention conditions to determine whether the prefrontal activations observed during cross-modality priming are associated with explicit retrieval.

MATERIALS AND METHODS

The experimental protocols were approved by the institutional review board and informed consent was obtained from all volunteers. The volunteers were native English speaking college students and had normal or corrected to normal vision and hearing. They were right handed as assessed by the modified Edinburgh handedness inventory (Raczkowski *et al.*, 1974). The

exclusion criteria included a history of prolonged use of a prescription or recreational drug, a neurological or psychiatric condition, claustrophobia, and significant prior radiation exposure. Subjects were advised not to use alcohol within 24 h and tobacco within 3 h of the scheduled scan time.

Experiment 1. Volunteers ($n = 8$) were selected to roughly match the age and gender ratio (range, 18–27 years, mean = 20 years, three females, five males) of the participants of our earlier priming experiments (Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999).

The experiment was conducted using an auditory word stem completion task. During the study task, subjects heard a list of 60 words (30 target and 30 filler words in random order) presented over headphones (2 s/word). The study task required subjects to rate the pleasantness of each word on a 1–3 scale using a numeric keypad and responding with the right hand. The words were recorded in two different voices—one male and one female. An equal number of target and filler words were assigned to each voice. Approximately three minutes after the study task, auditory word stems (first syllables) were presented, either in the voice in which subjects had studied target words (same-voice condition) or in a different voice (different-voice condition). Each block was composed of a different set of words and stems, and subjects were scanned while they provided completions to auditory word stems that could be completed with previously studied words (priming scan) or could not be completed with previously studied words (baseline scan). There were separate blocks for priming and baseline word stems.

In each word stem completion block, 30 auditory word stems were presented (3 s/stem), the first 10 during the prescan window and the final 20 during the actual scan. Subjects were asked to speak aloud the first word that came to mind beginning with each stem. They were told to avoid proper nouns and were assured that there were no right or wrong answers. The first ten stems in each block were derived from both studied and nonstudied words; half were presented in a male voice and the other half in a female voice. In the priming scans, the final 20 stems came from the studied list. In the same-voice condition, the final 20 stems were recorded in the same voice in which target words had been studied, whereas in the different-voice condition the final 20 stems were presented in a voice that was different from the one used at study. Thus, in each block, half of the stems were presented in a male voice and the other half in a female voice. In the baseline blocks, none of the final 20 stems could be completed with a studied word. An equal number of stems were presented in a male and female voice and PET scans were obtained during completion of the final 20 stems.

The study-test blocks were repeated to obtain two priming and two baseline blocks for each of the two

conditions—same-voice and different-voice. Thus, each subject was scanned eight times during the experiment. During the word stem completion task, responses were recorded on a tape recorder, and response latencies were recorded with a microphone connected to a PsyScope button box (Macwhinney *et al.*, 1997).

Target materials consisted of a list of common English words, each having a unique first syllable. The criteria used for the selection of words were described earlier (Badgaiyan *et al.*, 1999). Selected words were divided into two lists (A and B) which were balanced according to word frequency (Kucera and Francis, 1967), number of syllables and number of possible completions. Each word was recorded in both a male and a female voice on a computer using SoundEdit. The first syllable of each word was used as an auditory word stem, and each stem had at least six possible completions. The stems were prepared by editing words to retain only the first syllable. For half of the subjects, list A was used as the study list and list B as the baseline list; for the other half the assignment of lists to conditions was reversed. All words and stems were recorded in both male and female voice for counterbalancing. The words were counterbalanced across subjects to ensure that each word occurred equally often in the same-voice and different-voice conditions, in the priming and the baseline scans, and at different scan sequences. During the stem completion, subjects were asked to focus on a cross hair that was always displayed at the center of a computer monitor.

Experiment 2. Volunteers ($n = 8$) were selected to roughly match the age and gender ratio (range 18–22 years, mean = 20 years; four females, four males) of the participants of experiment 1.

The experiment was conducted using a visual cross-modality priming task following encoding under full- or divided-attention conditions. In the full attention condition, subjects studied a list of 60 (30 target and 30 filler) words presented aurally over a headphone (3 s/word). They were asked to rate the pleasantness of each word on a 1–3 scale using a numeric keypad and responding with the right hand. Later, visual word stems were presented (3 s/stem; upper case; news gothic; 24 point; bold) on the center of a monitor. The stems consisted of the first three letters of either studied (priming scans) or nonstudied (baseline scans) words and each stem had at least six possible completions. Subjects were asked to speak aloud the first word that came to mind beginning with a stem. They were told to avoid proper nouns and were assured that there were no right or wrong answers. In each study block, subjects studied 60 (30 target and 30 filler) words. Study blocks were followed by a priming block or by a baseline stem completion block (30 stems/block). The first 10 stems in each block, presented during the prescan window, came from both studied and nonstudied

words. All of the final 20 stems presented during actual scanning were derived either from studied (priming) or nonstudied (baseline) words.

In the divided-attention condition, stem completion blocks were similar to that in the full-attention condition. During the study phase, however, in addition to making a pleasantness judgement on aurally presented words, subjects were instructed to track the numbers appearing on the monitor (a number every 3 s), and to press a key when a number repeats. An initial pilot study suggested that the full-attention condition elicited greater priming than did the divided-attention condition. We therefore reduced the number of study words in the divided-attention condition to 45 (30 target and 15 filler) words per block, to achieve similar priming effects in the two conditions (see Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999). The study-test blocks were repeated to obtain two priming and two baseline blocks for each of the two conditions—full-attention and divided-attention, each subject was therefore, scanned eight times. During the stem completion task, responses were recorded on a tape recorder, and response latencies were recorded with a microphone connected to a PsyScope button box (Macwhinney *et al.*, 1997). Subjects were scanned during completion of the final 20 stems.

Target materials consisted of a list of common English words, each having a unique word stem. The criteria used for the selection of words were same as described in experiment 1. Words were recorded in a female voice on a computer using SoundEdit, and were counterbalanced across subjects to ensure that each word occurred equally often in the full- and divided-attention conditions, in the priming and the baseline blocks and at different scan sequences.

PET data acquisition and analysis. Procedures used for data acquisition and treatment were similar to those used in the earlier experiments (Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999). Scans were obtained during the word stem completion task using a GE Scanditronix (Uppsala) model PC4096 (15-slice) whole body tomograph. An individually molded plastic facemask was used to minimize head motion during the experiment. At time zero, the stem completion task was started along with the PET camera and continued for 90 s. At 30 s radioactive tracer inhalation (^{15}O labeled carbon dioxide) and emission data acquisition began. Tracer inhalation and data acquisition lasted for 60 s. The camera recorded data in five second epochs for a total of 90 s. The data before radioactivity is started are used, to correct for background activity from prior scans. Only the data between 30–90 s were used to form the images used in the analysis. A washout period of approximately 10 min was allowed between successive scans. To allow adequate tracer inhalation, subjects were instructed to take a deep breath after saying

each word. Since they had to say a word every 3 s, they were practiced to synchronize breathing to exhale while making a voice response and inhale in the intervening period.

After image reconstruction, PET data from each subject were treated as follows: a correction was computed to account for head movement (rigid body translation and rotation) using a least squares fitting technique (Alpert *et al.*, 1996). The mean across all conditions was formed and used as input to determine the transformation to the standard coordinate system of Talairach and Tournoux (1988). This transformation was computed by deforming the 10 mm parasagittal brain-surface contour to match the contour of a reference brain (Alpert *et al.*, 1993). Following spatial normalization, scans were filtered with a two-dimensional Gaussian filter, full width at half maximum set to 20 mm. Statistical analysis followed the theory of statistical parametric mapping (Friston *et al.*, 1991; Friston *et al.*, 1995; Worsley *et al.*, 1992). Data were analyzed with SPM95 (from the Wellcome Dept. of Cognitive Neurology, London, UK). The PET data at each voxel, normalized by the global mean, were considered to be the independent variable and analyzed with a univariate linear statistical model. The statistical model considered subjects (eight) as block effects and scan conditions (four) as the main effects (residual $df = 53$), explicitly accounting for replicate measurements in a fashion equivalent to repeated measures ANOVA. It was assumed that there was no interaction between subjects (i.e., block effect) and scan conditions. Hypothesis testing was performed using the method of planned contrasts at each voxel.

We set thresholds for significance according to the theory of Gaussian fields (Friston *et al.*, 1991; Friston *et al.*, 1995; Worsley *et al.*, 1992). When no localizing hypothesis or prior experimental data were available, a threshold of $z = 4.2$ was considered significant. We settled for this value because a threshold of 4.2 is considered significant for unplanned comparisons according to the theory of Gaussian fields when the search volume is whole brain (for calculation and discussion see Friston *et al.*, 1991; Worsley *et al.*, 1996). When we had a priori hypotheses that localized the putative activation to a specific anatomic region, we considered a threshold of $z = 3.09$ to be significant. This threshold ($z = 3.09$) constitutes a compromise between a low threshold uncorrected for multiple comparisons ($z = 1.96$) and a higher threshold ($z = 4.2$) suggested for unplanned comparisons (see Worsley *et al.*, 1996).

RESULTS

Experiment 1

Behavioral data. Significantly more target words were produced during priming scans (where word

TABLE 1
Behavioral Responses in the Same-Voice and Different-Voice Conditions

	Block 1	Block 2	Mean
Same-voice			
Target completion (percentage of target words used)			
Studied words	38.1	40.6	39.4
Baseline words	13.8	16.9	15.3
Studied-baseline	24.4	23.7	24.1
Response latency (ms)			
Studied words	1711	2000	1855
Baseline words	2034	1954	1994
Baseline-studied	323	46	139
Different-voice			
Target completion (percentage of target words used)			
Studied words	39.4	34.3	36.9
Baseline words	16.2	15.0	15.6
Studied-baseline	23.2	19.3	21.3
Response latency (ms)			
Studied words	1957	1930	1944
Baseline words	2028	1993	2010
Baseline-studied	71	63	66

stems could be completed with studied items) than during the baseline scans (where stems could not be completed with studied words) both in the same-voice ($t_{15} = 7.67$; $P < 0.0001$) and different-voice ($t_{15} = 13.73$; $P < 0.0001$) conditions (Table 1). Although there was a slightly higher level of priming in the same-voice (39.4%) than in the different-voice condition (36.9%), the difference did not approach statistical significance ($t_{15} = 0.91$; $P > 0.37$). The percentage of target words generated during the first and the second priming blocks also did not differ significantly in either condition, suggesting that the subjects did not use intentional retrieval strategies. Such strategies would have inflated target completion rates in the second block (see Badgaiyan *et al.*, 1999). Analysis of variance showed no effect of either block sequence ($F_{1,14} = 0.85$; $P > 0.80$) or voice condition ($F_{1,14} = 0.89$; $P > 0.36$). The block sequence \times voice condition interaction was also not statistically significant ($F_{1,14} = 2.00$; $P > 0.17$).

Mean response times in the same-voice (1855 ms) and different-voice (1944 ms) priming conditions were less than those observed in the baseline conditions (1994 and 2010 ms). Collapsed across the same-voice and different-voice conditions, response times were significantly shorter for the primed conditions compared to the baseline ($t_{31} = 2.75$; $P < 0.01$). The difference, however, was only marginally significant in the same-voice ($t_{15} = 2.04$; $P = 0.059$) and different-voice ($t_{15} = 2.10$; $P = 0.053$) conditions when considered separately. There was no significant effect of either block sequence ($F_{1,14} = 3.04$; $P > 0.1$) or voice condition ($F_{1,14} = 2.31$; $P > 0.15$). The block sequence \times voice

Priming < Baseline

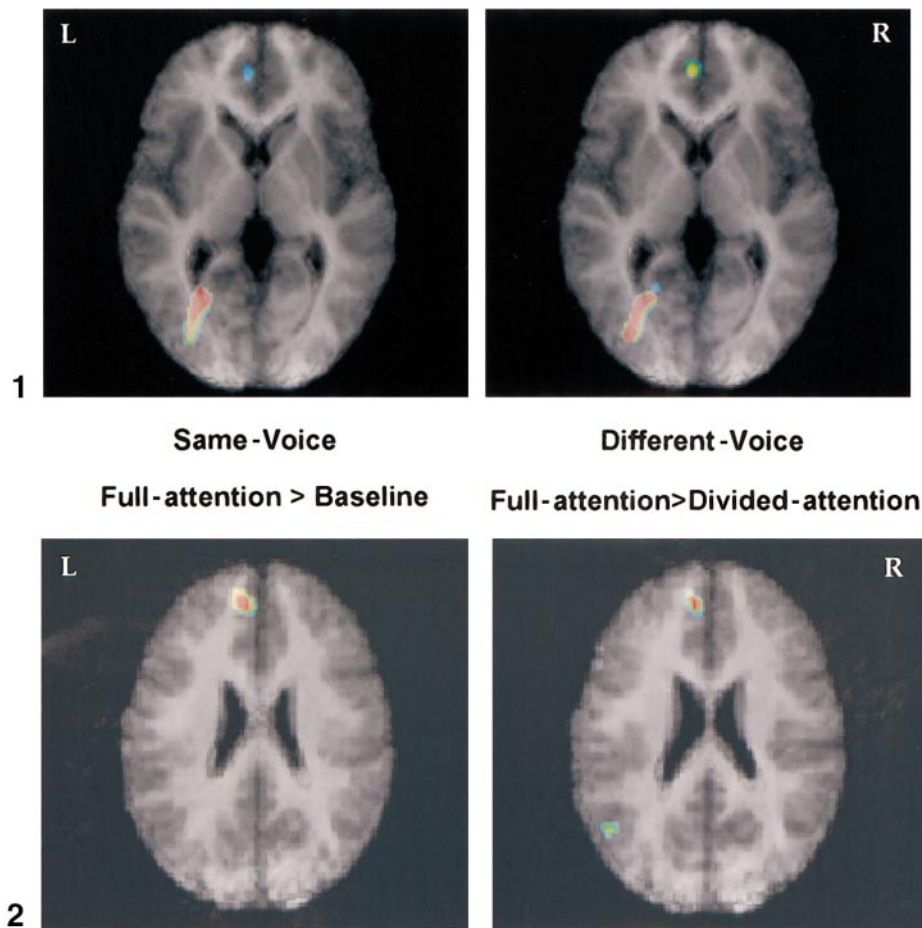


FIG. 1. Statistical parametric maps (SPM) showing significant rCBF changes in the extrastriate cortex in within-modality auditory priming under the same-voice and different-voice conditions, as compared to the stem completion baseline. Reduced rCBF was observed in both same- and different-voice conditions. The maps are superimposed over averaged structural SPGR/MRI images that were transformed to Talairach space. Atlas coordinates are provided in Table 2.

FIG. 2. Statistical parametric maps (SPM) showing significant rCBF changes in the medial prefrontal cortex in cross-modality visual priming following encoding under full- and divided-attention conditions. Increased rCBF was observed in full-attention condition, both in comparison with the divided-attention and the baseline condition. In divided-attention condition, there was no rCBF increase in the prefrontal cortex. A second activation seen in the left superior temporal gyrus in the full-attention vs divided-attention contrast was not significant statistically. The maps are superimposed over averaged structural SPGR/MRI images that were transformed to Talairach space. Atlas coordinates are provided in Table 4.

condition interaction was also not significant ($F_{1,14} = 7.44$; $P > 0.16$).

rCBF data. As compared to the baseline, reduced rCBF was observed at four cortical locations in the same-voice condition (Fig. 1; Table 2): extrastriate cortex (including BA 19), medial prefrontal cortex (BA 9/10), precuneus (BA 7), and angular gyrus (BA 39/40). There was also a trend suggesting decreased rCBF in dorsal prefrontal cortex (BA 9/10). These reductions are generally in the same areas where we previously reported reduced rCBF during within-modality auditory priming (Badgaiyan *et al.*, 1999). In the present experiment, however, we observed decreased rCBF

only in the left extrastriate cortex, whereas the reduction was bilateral in the earlier experiment.

In the different-voice condition, we observed reduced rCBF in each of the four areas where reductions were observed in same-voice condition (Fig. 1; Table 2). There were additional reductions, at or near threshold for significance, in the right middle temporal gyrus (BA 37) and dorsolateral prefrontal cortex (BA 9). We also observed evidence of increased rCBF in the left middle temporal gyrus (BA 38/21) in the different-voice condition. However, the direct comparison between PET images of the same-voice and different-voice conditions did not reveal any significant rCBF changes. No re-

TABLE 2

Regions Showing Significant rCBF Changes in the Same- and Different-Voice Conditions Compared to the Baseline Condition

Condition and cortical area		Talairach coordinates (x, y, z)	Z score
Same-voice			
rCBF decreases	1. Medial prefrontal (BA 10)	-8, +50, +0	6.62
	2. Extrastriate cortex (BA 19)	-20, -58, +4	5.88
	3. Precuneus (BA 7)	+0, -46, +44	5.81
	4. Angular gyrus (BA 39/40)	+42, -46, +24	5.23
	5. Dorsal prefrontal (BA 9/10)	-4, +56, +28	3.44
Different-voice			
rCBF decreases	1. Medial prefrontal (BA 10)	-6, +48, +0	6.56
	2. Angular gyrus (BA 39/40)	+42, -46, +24	5.75
	3. Extrastriate cortex (BA 19)	-20, -56, +4	5.37
	4. Precuneus (BA 7)	+0, -46, +44	4.50
	5. Dorsal prefrontal (BA 10)	-6, +58, +28	4.25
	6. Dorsolat. prefrontal (BA 9)	+36, +42, +36	4.19
	7. Dorsolat. prefrontal (BA 9)	-36, +30, +36	3.94
	8. Middle temporal gyrus (BA 37)	+42, -58, +8	3.13
rCBF increase	1. Middle temporal gyrus (BA 38/21)	-26, +6, -28	4.56

gions showing significant rCBF increases were found in either the same-voice priming condition of the present experiment, or in the within-modality priming condition of previous experiments (Badgaiyan *et al.*, 1999).

Experiment 2

Behavioral data. To confirm that the divided-attention encoding condition reduces explicit retrieval in a cross-modality protocol, we conducted a pilot study in which eight volunteers were given a visual word stem completion task that was similar to the one used in this experiment. The pilot task, however, differed from the task given to the subjects that were scanned (described under Materials and Methods) in two ways: the study list length (60 words) was the same in the full- and divided-attention conditions, and subjects were asked to complete word stems using a studied word. There was significantly greater recall ($t_{31} = 4.00$; $P < 0.001$) in the full-attention (52.9%) than in the divided-attention condition (32.7%), indicating that division of attention during encoding significantly reduces explicit retrieval in the cross-modality condition.

Analysis of behavioral data obtained during the scan (using the cross-modality priming protocol described under Materials and Methods) revealed similar degrees of priming in the full- (39.1%) and divided- (38.1%) attention conditions (Table 3). Significantly more target words were produced during priming than in the baseline condition following encoding under full-attention ($t_{15} = 11.46$; $P < 0.001$) and divided-attention ($t_{15} = 10.28$; $P < 0.001$). The percentage of target words generated during the first and the second priming blocks did not differ significantly in either condition. Analysis of variance showed no effect of either block

sequence ($F_{1,14} = 0.02$; $P > 0.88$) or attention condition ($F_{1,14} = 0.36$; $P > 0.56$). The block sequence \times attention condition interaction was also not statistically significant.

Mean response times in the full- (1172 ms) and divided-attention (1213 ms) priming conditions were less than those observed in the baseline condition (1318 and 1368 ms). Collapsed across full- and divided-attention conditions, response times were significantly shorter ($t_{31} = 4.00$; $P < 0.001$) in the priming blocks as compared to those in the baseline blocks. There was no

TABLE 3

Behavioral Responses under Full- and Divided-Attention Conditions			
	Block 1	Block 2	Mean
Full-attention			
Target completion (percentage of target words used)			
Studied words	39.4	38.8	39.1
Baseline words	17.5	18.1	17.8
Studied-baseline	21.9	20.7	21.3
Response latency (ms)			
Studied words	1211	1216	1213
Baseline words	1338	1398	1368
Baseline-studied	127	182	155
Divided-attention			
Target completion (percentage of target words used)			
Studied words	37.5	38.7	38.1
Baseline words	17.5	16.3	16.9
Studied-baseline	20.0	22.4	21.2
Response latency (ms)			
Studied words	1210	1134	1172
Baseline words	1301	1334	1318
Baseline-studied	91	200	146

TABLE 4

Regions Showing Significant rCBF Changes in the Full- and Divided-Attention Conditions

Condition and cortical area	Talairach coordinates (x, y, z)	Z score
Full-attention (compared to baseline)		
rCBF increase Medial prefrontal (BA 9)	-6, 46, 24	3.75
rCBF decrease Sup. temporal gyrus (BA 22)	-62, -36, 4	2.69
Divided-attention (compared to baseline)		
rCBF decrease Sup. temporal gyrus (BA 22)	-60, -36, 4	2.88
Full-attention minus divided-attention		
rCBF increase Medial prefrontal (BA 9)	-14, 52, 28	3.12

significant effect of either block sequence ($F_{1,14} = 0.87$; $P > 0.77$), or attention condition ($F_{1,14} = 0.73$; $P > 0.41$). The block sequence \times attention condition interaction was also not significant.

rCBF data. As compared to the baseline, in the full-attention priming condition rCBF increased in medial prefrontal cortex (BA 9; Fig. 2) and decreased in superior temporal gyrus (BA 22). These rCBF changes were generally in the same areas where we observed similar changes in earlier cross-modality priming experiments with both auditory (Badgaiyan *et al.*, 1999) and visual (Schacter *et al.*, 1999) stem completion tasks. Even though the peak of the most significant prefrontal activation in this experiment was located slightly to the left of the midline, the activation was localized mainly in the anterior right hemisphere, as observed in the previous cross-modality priming experiments. In the divided-attention condition, a trend for reduced rCBF was observed in superior temporal gyrus (BA 22). This reduction was in the same area where reduced rCBF was observed in the full-attention condition of this experiment, and the visual cross-modality priming condition of the earlier experiment (Schacter *et al.*, 1999). There were no significant rCBF changes in any other cortical areas (Table 4). Direct comparison of the PET images observed under full- and divided-attention conditions revealed a significant rCBF increase in the medial prefrontal cortex (BA 9) in the full-attention condition ((Fig. 2; Table 4).

DISCUSSION

Decreased Extrastriate rCBF in Within-Modality Priming

In previous experiments we found priming-related rCBF reductions in extrastriate cortex (BA 19) during within-modality, but not during cross-modality, auditory and visual priming (Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999). By demonstrating that reduced

rCBF in extrastriate cortex is associated with priming in the same-voice condition, the present data confirm our earlier observations. In addition, we found similar priming-related rCBF reductions in extrastriate cortex in the different-voice condition, thus providing further evidence that reduced rCBF in the extrastriate area is observed when the sensory modality of stimulus presentation is held constant between study and test (Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999). Taken together, the results suggest that the priming-related rCBF reduction in the extrastriate area is sensitive to a study-to-test change of sensory modality, but not to changes in stimulus features within the same modality. This observation appears to hold for both auditory and visual priming. In within-modality visual priming experiments, reduced activity in the extrastriate area has previously been reported when the letter case of target words (upper or lower) was changed between study and test (Badgaiyan and Posner, 1996, 1997; Buckner *et al.*, 1995).

More generally, patterns of rCBF changes were quite similar in the same-voice and different-voice conditions: the regions that showed priming-related rCBF reductions in the same-voice condition (left extrastriate, medial prefrontal, precuneus, and right angular gyrus) also showed significant reductions in the different-voice condition. This similarity between the same- and different-voice conditions contrasts markedly with our earlier experiments, which revealed no overlap between areas showing priming-related decreases during within-modality priming and those showing decreases (or increases) during cross-modality priming (Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999).

In the different-voice condition however, priming-related changes (at or near the threshold for significance) were observed in two additional regions that were not observed in the same-voice condition: decreases in dorsolateral prefrontal cortex bilaterally, and an increase in the middle temporal gyrus. We must be cautious about interpreting these changes because the direct comparison between the same- and different-voice conditions failed to produce any significant effects. However, it may be worth noting that the regions exhibiting priming-related changes in the different-voice condition have been implicated in functions associated with speech discrimination, such as speech monitoring (McGuire *et al.*, 1996), word comprehension (Binder *et al.*, 1996), and pitch discrimination (Zatorre *et al.*, 1994). It is possible that these changes indicate the recruitment of auditory discrimination processes during different-voice priming that are not recruited during same-voice priming. Perhaps when the priming task requires identification of a target that had been studied previously in a different voice, additional cortical processing is required to "normalize" (cf., McClelland and Elman, 1986; Green *et al.*, 1991) the stimulus so that the normalized test stimuli can be matched

with the studied items. These additional areas may be involved in the processing of auditory information required to achieve such normalization—a “second cycle” of search that is activated when a mismatch is indicated between the acoustic properties of a test cue and those of a previously studied item (Badgaiyan, 2000; Schacter and Badgaiyan, 2001).

The foregoing suggestions still leave open the question of what role extrastriate cortex plays in auditory priming. We have previously discussed in detail possible mechanisms that may account for the involvement of extrastriate cortex in auditory priming (Badgaiyan *et al.*, 1999). One of the possible accounts that we discussed involves the use of visual imagery. Perhaps subjects created visual images of auditorily presented words during the study task and retrieved those images during primed auditory stem completion performance. However, by this account we should have observed increased rCBF—not decreased rCBF—in extrastriate cortex during auditory priming because visual imagery is associated with increased activation in the extrastriate area (Cohen *et al.*, 1996; D’Esposito *et al.*, 1997; Cabeza *et al.*, 1997). Thus, use of visual imagery during the study task and priming test does not offer a plausible account of our results. A related idea is that auditory processing may have activated orthographic features of target items during baseline stem completion performance (e.g., Tanenhaus *et al.*, 1980). If extrastriate cortex is involved with orthographic processing and representation (e.g., Petersen *et al.*, 1990), then the observed rCBF decreases may reflect corresponding decreases in orthographic processing after auditory priming. This notion, however, would lead us to expect increased extrastriate activation in the baseline stem completion task relative to fixation. However, no such increases were observed in our earlier experiment (Badgaiyan *et al.*, 1999).

Another possible explanation of extrastriate decreases may be suppression of visual processing during auditory task performance, similar to the cross-modal suppression effect in auditory cortex observed during visual attention (Haxby *et al.*, 1994). However, it seems an unlikely explanation because we did not observe significant extrastriate rCBF decreases in the baseline auditory stem completion condition compared to fixation in the auditory priming experiment (Badgaiyan *et al.*, 1999). If the observed decrease resulted from suppression of visual regions as a consequence of attention to auditory stimuli, the effect should have been observed in the baseline condition as well as in the priming condition.

An additional possible mechanism that we discussed earlier (Badgaiyan *et al.*, 1999) is based on the hypothesis that a part of the extrastriate cortex has a non-visual function that supports within-modality priming both in the visual and auditory domain. The part of the extrastriate cortex that is most likely to support such a

function is the area V3A, located within BA 19. This area has a distinct neuroanatomical and neurochemical profile and it receives input both from the visual and non-visual cortical areas (cf, Zilles and Clarke, 1997; Tootell *et al.*, 1997). This region is extensively connected to the subcortical and cortical areas outside occipital visual cortex, and is not dependent on input from primary visual cortex for activation (Girard *et al.*, 1991). Even though this area is classically associated with visual motion detection (Galletti *et al.*, 1990), recent studies suggest that V3A mediates multimodal and possibly cognitive functions. Neuroimaging experiments have shown activation in this area in response to auditory stimuli (Bookheimer *et al.*, 1998) and recent animal experiments indicate that the activity in the neurons of area V3A is modulated by a variety of nonretinal functions that include attention, anticipation, and memory (Nakamura and Colby, 2000). It, however, remains to be determined how the activities in V3A area are associated with priming-related rCBF reductions, but the possible link seems worth considering and exploring.

Further, because the extrastriate cortex is involved in priming under both same- and different-voice conditions, it appears that the extrastriate mechanism is capable of ignoring or “removing” surface features of stimuli to allow identification of a within-modality stimulus with a different surface feature (i.e., voice) than a previously studied item (for discussion see Badgaiyan, 2000). Whatever the exact nature of the contributions made by this area to auditory priming, the present results can help to guide the search for an answer by showing that the relevant processes in the extrastriate cortex operate at a sufficiently abstract level to survive study-to-test changes between the voices of different speakers. However, our previous results (Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999) suggest that such processes are not so abstract that they operate across sensory modalities.

Our findings converge nicely with those of Buckner *et al.* (2000), who used functional magnetic resonance imaging (fMRI) technique to examine priming on repeated visual and auditory stem completion tasks. They found that both visual and auditory priming was accompanied by reduced activity in a region of inferior temporal cortex, anterior and lateral to the extrastriate region observed in the present study, that is not normally associated with auditory processing. Buckner *et al.* suggested that the priming-related reduction in inferior temporal cortex is associated with the operation of amodal lexical processes. Because they examined only within-modality (visual and auditory) priming, it is not known whether similar reductions would be observed across modalities, in contrast to the effects we have observed. Studies that examine the issue would help to determine whether the effects observed

by Buckner *et al.* operate at a similar level of abstraction to those documented in our experiments.

Increased Prefrontal rCBF in Cross-Modality Priming

In earlier experiments on cross-modality priming, we had observed increased rCBF in the prefrontal cortex (Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999). Because prefrontal activation is generally associated with conscious recollection (for a recent review see Rugg and Wilding, 2000), we studied cross-modality priming under full- and divided-attention conditions to evaluate the possible association between prefrontal activation and explicit retrieval. Experiments that have used visual stimuli at both study and test have observed that dividing attention during encoding significantly reduces conscious recollection while preserving the priming effect (Debner and Jacoby, 1994; Jennings and Jacoby, 1993). We found similar reductions of explicit retrieval in the cross-modality condition (see Results). If, therefore, the prefrontal activation is associated with the recruitment of an aspect of explicit retrieval mechanism, dividing attention at study should abolish this activation. Consistent with this prediction, we observed increased rCBF in prefrontal cortex in the full- but not in divided-attention condition (Table 4). This observation is in agreement with the cognitive studies that have shown that some aspect of explicit retrieval mechanism is associated with cross-modality priming (Jacoby *et al.*, 1993).

Prefrontal activations have been implicated in a number of different aspects of explicit retrieval (for a recent review see Rugg and Wilding, 2000). The anterior prefrontal cortex (the activation observed in the present experiment), however, has most frequently been associated with the retrieval of recently studied items (Buckner *et al.*, 1995; Rugg *et al.*, 1998; Tulving *et al.*, 1994; cf., Badgaiyan and Posner, 1997). Activation in an area close to the one observed in this experiment ($x, y, z = -9, 42, 24$) has recently been reported in an experiment concerning explicit retrieval when subjects expressed a feeling of familiarity that they had studied a particular item, but had no specific recollection of it (Henson *et al.*, 1999). Cross-modality priming might involve similar processes. After completing a stem using the first word that came to mind, subjects may experience a feeling of familiarity with a previously studied word. This interpretation is supported by a cognitive study reported by Richardson-Klavehn and Gardiner (1996). They have shown that cross-modality priming on the stem completion test is associated with some form of conscious awareness that completed words appeared earlier in the target list, but does not involve intentional or voluntary retrieval of studied items. Understanding why such "involuntary explicit memory" or feelings of familiarity occur for cross-modality priming, but not for within-modality

priming, is an important question for future neuroimaging and cognitive investigations.

In addition to the prefrontal activation, we also observed decreased rCBF in superior temporal gyrus (BA 39/40) in earlier cross-modality priming experiments (Badgaiyan *et al.*, 1999; Schacter *et al.*, 1999). In the present experiment, the decrease (or a trend) was observed under both full- and divided-attention conditions. This observation supports our earlier hypothesis that the decrease is associated with some aspect of phonological or lexical processing, which should occur under both full- and divided-attention conditions (Badgaiyan *et al.*, 1999). This hypothesis is based on the findings of a number of cognitive studies that have suggested that cross-modality priming is mediated by some form of abstract lexical representation involved in phonological input or output processing (e.g., Curran *et al.*, 1999; Kirsner *et al.*, 1989; Weldon, 1991). It is interesting to note that recent neuroimaging studies have obtained evidence of polysensory representation in the left superior temporal gyrus. Since a congruent cross-modal (visual-auditory) stimulus elicits greater activation as compared to an incongruent stimulus, it has been suggested that the left superior temporal cortex is involved in cross-modal binding (Calvert *et al.*, 2000). Attenuated activity obtained in cross-modality priming condition could therefore suggest a reduction in demand for cross-modal binding for the primed items, as compared to nonprimed baseline items. In light of these convergent findings, the next step for neuroimaging studies is to specify the exact nature of the contributions made by the left superior temporal region to cross-modality priming effects.

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