Increased Neural Efficiency in the Temporal Association Cortex as the Result of Semantic Task Repetition

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Abstract: We examined the effect of semantic task repetition and of alternating between tasks on cerebral blood flow in three H₂¹⁵O positron emission tomography experiments. We found that repeatedly performing semantic tasks resulted in a reduction in cerebral blood flow to the left temporal association cortex similar to that found in priming experiments even though here there was no repetition of stimuli. Although the same effect was found in two different tasks (word meaning judgments and picture naming), it was only present when the same task was repeated on consecutive scans and not when the subjects alternated from scan to scan between tasks. We propose that there is a neural efficiency which develops in the association cortex of the temporal lobe as a result of repeatedly performing a semantic task. This efficiency is abolished by interruptions such as performing a different task. *Hum Brain Mapp* 29:922–930, 2008. © 2007 Wiley-Liss, Inc.

Key words: priming; middle temporal cortex; association cortex; neural efficiency; task alternation

INTRODUCTION

Neuroimaging studies have looked at several types of changes in brain activity which result from repeating a task or repeatedly being exposed to certain stimuli. Two types of decreases have been noted: a localized decline which results from priming and a nonspecific decline common to many tasks [Paus et al., 1997; Rajah et al., 1998]. In priming experi-

ments, subjects are first engaged in some cognitive task with specific stimuli in a study phase, and then a measure of brain activity is taken while the subjects perform a later task (test phase) with the same stimuli. The analyses carried out compare either brain activity at study and at test with the same stimuli, or activity at test for primed and unprimed stimuli. The results of the priming studies have revealed that the brain areas where decreases occur are dependent on whether or not the stimuli at study and test are in the same format or modality, [Bedgaiyan et al., 2001; Lebreton et al., 2001; Schacter et al., 1999]. When the stimuli at study and at test are in the same modality and the same format, decreases occur primarily in posterior perceptual areas [for overviews, see Gabrieli, 1998; Schacter and Badgaiyan, 2001; Schacter and Buckner, 1998].

Studies which have tried to induce conceptual priming have taken several approaches. One has been to change either the modality or format of the stimuli between study

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and test (e.g., auditory then visual, or pictures then visual words). These findings have shown that priming induces decreases in the lateral and inferior temporal cortex and in the prefrontal cortex [Badgaiyan et al., 2001; Buckner et al., 2000; Lebreton et al., 2001]. Decreases in the left inferior temporal cortex have also been found when subjects were tested on different pictures of the same object at study and test [Simons et al., 2001], when subjects read a word (e.g., peace) then performed a word completion task (e.g., pe___), and when subjects made lexical decisions on semantically primed words [Mummary et al., 1999]. Another approach to exploring conceptual or semantic priming was taken by Demb et al. [1995] who compared priming for repeated items in a semantic task (is the item living or nonliving?) with repeating items in a nonsemantic task (is the word in lower- or upper case?). They found that there was a decrease in activity in the left inferior prefrontal cortex (LIPC) as a result of repeating stimuli in the semantic but not the form-based task. Wagner et al. [1997] probed this finding further and found that both picture repetition and word repetition in a semantic task resulted in reduced activation in the LIPC. It is of note that a common feature of all of these priming experiments has been to show that, in conjunction with the regional decrease in brain activity, subjects also demonstrate greater ease (e.g., decrease in RTs) in processing the primed stimulus than the unprimed.

Studies that have found decreases thought to be nonspecific to the stimuli or task have attributed these decreases to several factors. Paus et al. [1997] found decreases in neocortical areas of the right hemisphere during an auditory signal detection task and suggested they arose from a shift from controlled to automatic attentional processing. Murtha et al. [1996] found activation in the anterior cingulate prior to but not during performance of several simple cognitive tasks. They interpreted these decreases to a change from an anticipatory set to actual performance. Warach et al. [1992] attributed a decrease in cerebral blood flow (CBF) in the frontal and parietal lobes to habituation to the experimental setting. Finally, Rajah et al. [1998] found consistent bilateral CBF decreases over time in the occipital and temporal lobes as the result of the repeated performance of sensori-motor tasks, and ascribed the decrease to habituation in the visual domain.

The finding of decreases across time within the lateral temporal cortex, particularly in the dominant hemisphere when a subject performs a visuomotor task [Rajah et al., 1998] is an important finding with regards to research into the neuroanatomical basis of semantic memory. Semantic memory refers to the capacity to recognize objects, and to understand concepts and their relationship to each other. Lesion studies [Chertkow et al., 1997; Dronkers et al., 2004; Hart and Gordon, 1990; Hillis et al., 2000; McCarthy and Warrington, 1990; Saumier and Chertkow, 2002] provide strong evidence that the left lateral/ventral temporal cortex is the critical area of semantic memory. If this is an area where CBF decreases over scanning time, then its contribution to semantic memory tasks may be systematically underestimated.

In the present study we reexamine this question with a particular interest in the changes in regional CBF (rCBF) due to the repeated performance of a semantic memory task without repetition of stimuli. We ask three questions: (1) what are the changes over time when subjects perform semantic tasks? (2) Are the changes related to an improvement in behavioral performance across blocks as in priming experiments? and (3) Are these changes truly task-independent? To answer these questions we first analyze the data sets of two previously reported PET experiments with respect to the effect of scan order on CBF. In each experiment subjects performed the same semantic task on consecutive scans (Experiment 1, a word meaning task; Experiment 2, a picture naming task) with no repetition of stimuli. The analyses reveal, among other things, a predominantly left lateralized decrease in the middle and inferior temporal cortex. To determine whether this effect is independent of the specific task which is repeated, we then carry out a new experiment in which the subjects alternate from scan to scan between the two semantic tasks (Experiment 3).

MATERIALS AND METHODS

Experiment 1

Consecutive scans of the word meaning (WM) task. This experiment is fully described in Whatmough et al. [2004].

Participants

The participants were 15 healthy elderly individuals [nine women, six men; mean age (s.d.) = 74.3 years (5.6), education = 14.1 years (2.7), mini-mental state examination score (MMSE, maximum = 30, Folstein et al., 1975) = 28.8 (1.0)].

Task and stimuli

During the four task scans subjects viewed on a computer monitor a series of two 2-word pairs such as spade-shovel, spade-carpet, to which they responded by reading aloud the pair of words closest in meaning ("spade-shovel"). Stimuli were presented at a fixed rate of one trial per 3,000 ms with a presentation time of 2,500 ms. The experimenter recorded the responses by pressing on a key at the onset of the second word the participant pronounced (e.g., shovel of the pair spade-shovel). None of the stimuli or trials was repeated. Two factors (semantic class, and level of difficulty) were manipulated in the four-task scans. Two blocks were of concrete concepts (e.g., spade-shovel) and two were of abstract concepts (e.g., oath-vow). One of the blocks of each semantic class was harder than the other so that the four blocks were: easy concrete, hard concrete, easy abstract, and hard abstract. The 15 subjects performed four blocks of trials on four consecutive scans, one block

per scan. The order in which they performed the blocks was counterbalanced across subjects.

Experiment 2

Consecutive scans of the picture naming (PN) task. This experiment is fully described in Whatmough et al. [2002].

Participants

Fourteen healthy elderly individuals participated in this experiment [mean age = 73.1 years (7.2), education = 12.3 years (3.2), MMSE = 28.9 (1.0)].

Task and stimuli

During the four task-scans subjects viewed on a computer monitor a series of pictures which they named aloud. Stimuli were presented at a fixed rate of one per 2,000 ms with a presentation time of 1,000 ms. Experimenter noted all responses for later analysis. None of the stimuli were repeated across blocks. Two factors (semantic class, and level of difficulty) were manipulated in the four-task scans. Two blocks were of animals (e.g., rabbit) and two were of tools (e.g., paint brush). One of the blocks of each semantic class was harder than the other so that the four blocks were: easy animals, hard animals, easy tools, and hard tools. The 14 subjects performed the blocks of trials on four consecutive scans, one block per scan. The order in which they performed the blocks was counterbalanced across subjects.

Experiment 3

WM and PN tasks on alternate scans.

Participants

Nine healthy elderly individuals [six women, three men; mean age = 74.1 years (7.3), education = 15.4 years (3.4), MMSE = 29.3 (.9)] participated in this experiment.

Task and stimuli

There were eight scans in all. The first (pretask) and last (posttask) scans were baseline conditions in which the subjects fixated a black cross on a white background. For the middle six task-scans subjects performed three blocks of WM judgments and three blocks of picture naming (PN), one block per scan. The order of the six task-scans was such that they alternated between the types of task (i.e., WM and PN). The first task scan for five subjects was WM and for four subjects it was PN. The stimuli on the task scans were the same as described in Experiments 1 and 2 above. The blocks, however, were mixed with regard to semantic class (i.e., abstract and concrete for WM, and animals and tools for PN), and level of difficulty was separated into three blocks so that there was an easy, hard,

and harder block of each task. The order of the blocks with regard to level of difficulty was counterbalanced across subjects.

The visual stimuli were presented on a computer monitor positioned above the subjects.

METHODS COMMON TO EXPERIMENTS 1, 2, AND 3

Image Acquisition

Processing of PET and MR scans

PET data were obtained using an ECAT EXACT HR + (CTI/SIEMENS) tomograph at the Montreal Neurological Institute, operating in a three-dimensional acquisition mode. A transmission scan using a Ge-68 rotating rod source was performed at the beginning of each scanning session for the purpose of attenuation correction.

To correct for movement during scanning, all emission scans are aligned with the first emission scan by applying six movement parameters: translational parameters in three dimensions (TransX, TransY, and TransZ) and rotational parameters in three dimensions (RotX, RotY, and RotZ). Poor alignment of the transmission and the emission scans, however, will create inaccuracies in the analysis of PET data [Mesina et al., 2003; Reinders et al., 2002; van den Heuvel et al., 2003]. In this particular study in which we are looking at the change in CBF over consecutive scans the possibility of drawing faulty conclusions from the analyses is particularly strong because it is possible that subjects commonly settle into a particular head position. This would mean that over time there would be an apparent change in CBF over time which would be related to a change in the position of arteries not related to changes in CBF volume. This potential source of error can, however, be addressed given that all in-scanner movement can be accounted for by a combination of the six movement-related parameters. Movement-related error can be minimized by determining the most significant axes of movement and entering these parameters into any subsequent analysis as nuisance variables. To this end for each experiment a principal component analysis was carried out on the six parameters for all scans contributing to the analysis. These analyses identified the movement parameters which explained from 70 to 90% of movement variance in each experiment. These parameters were then entered into the regression analyses as nuisance variables.

The distribution of normalized CBF was measured during each 60 s PET emission scan using the bolus H_2^{15}O methodology [Raichle et al., 1983]. Three-dimensional MR scans (1-mm sagittal slices) from a Philips Gyroscan ACS (1.5T) were also obtained for each participant in a separate session. The CBF images were blurred using a 14-mm Hanning filter and normalized for differences in global blood flow using proportionate normalization, and coregistered with each subject's MRI scan using an automatic

image registration algorithm [Evans et al., 1991; Woods et al., 1992, 1993]. The images were then transformed into the Montreal Neurological Institute standardized proportional stereotaxic space, which is based on the Talairach and Tournoux atlas [1988], using an automatic feature-based algorithm [Collins et al., 1994].

Regression analyses were carried out using an analysis of covariance (ANCOVA), with subjects as the main effect and scan order as the covariate of interest [Paus et al., 1996]. The following model was fitted: $E(y_{ij}) = a_i + b_p s_{ij} + mvt_{ij}$ where y_{ij} is the normalized CBF of subject i on scan j , and s_{ij} is the scan order value given to task scan j . Mvt_{ij} represents movement parameters for subject i on scan j . The subject effect (a_i) and the movement parameters (mvt_{ij}) are removed and the parameter of interest is the slope b_p of the effect of scan order on CBF. The specific movement parameters (any of TransX, -Y, -Z, RotX, -Y, or -Z) that were removed as nuisance variables varied for each experiment. The movement parameters for each experiment and the scan order value for each analysis are provided below.

The t statistic images resulting from the regression analyses were thresholded using the minimum given by a Bonferroni correction and random field theory to account for multiple comparisons [Worsley et al., 1996]. The threshold was calculated based on an estimated gray matter volume over the whole brain of 600 cm³. For a single voxel this yields a threshold of $t > 4.25$ which corresponds to $P < 0.05$ corrected. Significance was also assessed based on the spatial extent of clusters of contiguous voxels, which yields a cluster size $> 1,658$ mm³ for $P < 0.05$ corrected with the method of Friston et al. [1995]. The significance of peaks is reported using the minimum P value of the single peak analysis and cluster analysis. All peaks that reached $P < 0.05$ corrected are reported. Furthermore, for Experiments 2 and 3 predicted peaks that reached $P < 0.001$ uncorrected are also reported which yields a threshold of $t > 3.1$ for a single peak. A region was considered predicted if it reached significance following the regression analyses on the full data set (15 subjects) in Experiment 1.

The following regression analyses searched for areas from the PET data where activation either increased or decreased over time.

Experiment 1. Regression analysis of the four consecutive WM scans [number of scans entered into the regression = subjects (15) $\times$ number of scans (4) = 15 $\times$ 4 = 60]. In this and all other regression analyses the scans were given the regression values of the order in which they were performed (for example, in this case: 1, 2, 3, and 4). A second regression analysis was also carried out on a reduced set of the data from Experiment 1 so that a closer comparison could be made with Experiment 3 in which fewer subjects participated, and in which participants performed only three blocks of each type of task. The reduced data set consisted of the data from task scans 1, 3, and 4 of Experiment 1 for the first four men and first four women who participated (n of scans = 8 $\times$ 4 = 32). The mvt parameters removed were TransX and TransY.

Experiment 2. Regression analysis was carried out on the four consecutive PN scans (n of scans = 14 $\times$ 4 = 56). A second analysis was carried out on the following reduced data set: task scans 1, 3, and 4 and the first four men and first four women who participated (n of scans = 8 $\times$ 4 = 32). The mvt parameters removed were TransX, TransY, TransZ and RotX.

Experiment 3. Four regression analyses were carried out on the following data sets of Experiment 4: (1) on the three interleaved WM scans (n of scans = 9 $\times$ 3 = 27), (2) on the three interleaved PN scans (n of scans = 9 $\times$ 3 = 27), (3) on all six task (WM and PN) scans (n of scans = 9 $\times$ 6 = 54), and (4) on the pretask and posttask fixation scans (n = 9 $\times$ 2 = 18). The mvt parameters removed were TransY, TransZ and RotZ.

RESULTS

Behavioral Results

Word meaning task

One-way repeated measures ANOVA was carried out on both of the WM RT data sets (Experiments 1 and 3) to determine the effect of scan order on RT. They revealed an effect of scan order only in Experiment 1 in which subjects performed the blocks of trials consecutively, $F(3, 42) = 3.3$, $P < 0.05$. Planned comparisons of mean RTs in Experiment 1 revealed that mean RTs were longer on Scan 1 than on Scans 2, 3, and 4, at a significance reaching $P < 0.05$ for all comparisons. The mean difference between Scan 1 and 2 was 134 ms. To better understand this task-learning effect, an additional regression analysis was carried out on the CBF data of WM scan 1 (T1) and WM scan 2 (T2) of the 15 subjects ($n = 15 \times 2 = 30$). There were no other significant differences in RTs among the scans in Experiment 1. There was no effect of scan order in Experiment 3 [$F(2, 16) < 1$]. Mean RTs from Experiments 1 and 3 are plotted in Figure 1a.

Picture naming task

The stimulus presentation rate for this experiment was quite rapid (2,000 ms per trial) and resulted in frequent omissions and some errors. One-way repeated measures ANOVA carried out on the accuracy rate data sets of the PN tasks and revealed scan order had no effect on accuracy rates in Experiment 2 [$F(3, 42) < 1$] or in Experiment 3 [$F(2, 16) < 1$]. Accuracy rates for Experiments 2 and 3 are plotted in Figure 1b.

PET Results

Regression analyses

The regression analyses of Experiments 1 and 2 carried out on both the full (15 subjects) and the reduced data sets (8 subjects) indicated similar results (Tables I and II). The

Figure 1.

Effect of order (a) on RTs in Word meaning task and (b) picture naming under two scan order conditions. Error bars indicate the standard error of the mean.

CBF decreases occurred in two main areas for WM and are illustrated in Figure 2. One area was in the medial frontal cortex, extending from the subcallosal anterior cingulate forward to the medial and superior frontal gyri. CBF modulation in this area has frequently been reported to be related to task difficulty [Paus et al., 1998] and the medial frontal subcallosal region may, among other things, monitor confidence levels [Whatmough et al., 2002].

The second area of decrease in Experiment 1 was in the mid- to posterior portions of the middle and inferior temporal cortex reaching ventrally to the fusiform gyri. This decrease was bilateral but much more extensive in the left hemisphere. Consecutive performance of the PN task (Experiment 2) also induced decreases in the left middle temporal and lateral fusiform gyri. The analysis carried out on the reduced data set of the PN experiment revealed a decrease in the left middle gyrus which was not present in the full data analyses.

Increases across the successive scans of WM task (Experiment 1) occurred in the medial frontal cortex, the supplementary motor cortex, the motor cortex, the frontal eye fields, and in the paracentral lobule. These are areas that would be involved in the physical execution of the task. The increases during consecutive PN scans (Experiment 2) were similar to those during the WM task except that the increase in the motor cortex was left lateralized for PN and right for WM judgments. There was also a substantial increase in the left parahippocampal gyrus over successive performance of the PN task but not during the WM task.

In contrast with Experiments 1 and 2, none of the regression analyses carried out on the data in which subjects alternated between tasks from scan to scan (Experiment 3) revealed any effect of scan order, either positive or negative.

The analysis that investigated looked for changes in CBF from T1 to T2 in Experiment 1 revealed that at this early time frame there was a decrease in CBF principally in the superior frontal cortex and an increase in motor areas (Table III). There was, however, no change in CBF in the middle and inferior temporal cortex. This analysis suggests that the decrease in RTs from T1 to T2 was related to the motor aspects of the task, and that the reduction in RTs reflects a greater ease in responding without necessarily a greater ease in retrieving the semantic representations of the words.

The analysis which compared activation for fixation baseline before and after completing the semantic tasks (Experiment 3, pretask vs. posttask baseline, Fig. 3) revealed a large bilateral decrease in the posterior cingulate cortex. The volume of this cluster was 17.49 cm³. The *t* value and *x*, *y*, *z* coordinates for the cluster peaks were: *t* = -5.8, 4, -31, 26 and *t* = -4.2, 15, -18, 38. The cingulate cortex, in general, is associated with allocation of attention [Mesulam, 2000] and the posterior cingulate in particular with motivated spatial expectancy [Small et al., 2003, 2005]. This is not an area where CBF decreased during the task scans of Experiments 1 and 2.

DISCUSSION

In this study we looked at the changes in performance and rCBF as the result of repeatedly performing two semantic tasks in which there was no repetition of stimuli. The behavioral data underline two differences between the two tasks. First, the mean error rates indicate that the PN task (21%) was more taxing than the WM task (1.5%). Second, the only significant change in performance which resulted from repeatedly performing the tasks was a decrease in response latency after WM T1 when the same task was performed on consecutive scans (Experiment 1).

Despite the lack of improvement in performance as is seen in priming experiments, major changes took place over time in rCBF as the subjects repeatedly performed the

TABLE I. Areas where CBF decreased across successive scans

Region and Brodmann areas	T1, T2, T3, and T4			Reduced data set; T1, T3, and T4 ($n = 8$)		
	t value	Vol. (cm ³)	Coordinates	t value	Vol. (cm ³)	Coordinates
<i>Experiment 1. Word meaning</i>						
L middle and inferior temporal g BA21	-5.7	9.31	-58, -33, -21	-4.4	2.43	-60, -31, -23
R medial and orbital frontal g BA10/11	-4.5	13.85	15, 46, -20	-4.8	9.69	21, 56, -14
R medial front-orbital g BA25/11	-5.2	13.85 ^a	9, 25, -14	-4.5	9.69 ^a	12, 24, -18
L subcallosal ant. cingulate BA25 (including left caudate nucleus)	-4.6 (-3.8)	13.85 ^a 0.85	-9, 17, -11 59, -18, -21	-4.3	1.29	46, -38, -14
R inferior temporal g BA21/20						
<i>Experiment 2. Picture naming</i>						
L middle/inferior temporal g BA20/21	-3.8	0.83	-60, -31, -18	-4.4	1.59	-60, -31, -18
L lateral fusiform g BA37	-4.4	2.06	-42, -52, -15			
L middle frontal g BA10/47				-4.5	1.85	-40, 44, -6

Coordinates refer to the x, y, z coordinates of stereotaxic space of Talairach and Tournoux, [1988]. T -values in parentheses are not significant but are provided for comparison across analyses. Vol = volume, L = left, R = right, g = gyrus, T1 = first scan, T2 second scan etc.

^aThe peak is part of the volume listed above it.

semantic tasks. These changes, however, only occurred when the same task was performed on successive scans. Under conditions of consecutive task performance (Experiments 1 and 2) there was a decline in the left posterior middle/inferior temporal cortex. We suggest that the changes in CBF in the temporal cortex are related to lexico-semantic nature of the tasks. We propose this because the decreases take place in the area that lesion studies indicate are essential for semantic memories: the middle and posterior temporal cortex particularly on the left. The lateralized decline stands in contrast with the Rajah et al. [1998] experiments which found bilateral temporal cortex decreases when subjects performed a sensori-motor task.

We note also that the decline was less pronounced for the more difficult lexical task (i.e., PN). Finally, our results are similar to the lateralized effects of conceptual priming referred to in the Introduction. Here, however, we find the decline in the posterior temporal regions appears over a longer time frame (more than two scans) and that the decline is not associated with superior task performance. It should be noted, however, that in most brain imaging priming experiments, what is being shown is in fact two effects of priming: superior performance plus decreased brain activity. Here we see only decreased brain activity with a maintenance of the same level of performance. We would argue that within this time frame some type of neu-

TABLE II. Areas where CBF increased across successive scans

Region and Brodmann areas	T1, T2, T3, and T4			Reduced data set; T1, T3, and T4 ($n = 8$)		
	t value	Vol (cm ³)	Coordinates	t value	Vol (cm ³)	Coordinates
<i>Experiment 1. Word meaning</i>						
L medial frontal g. BA6	4.5	7.54	-1, 1, 60	4.2	1.96	-3, -1, 54
L superior frontal g. BA6	3.6	7.54 ^a	-15, -17, 63	4.2	1.96 ^a	-3, -2, 62
L paracentral lobule	4.2	7.54 ^a	-11, -35, 53	4.5	2.7	-11, -37, 50
L superior frontal g. BA6	3.7	7.54 ^a	-8, 18, 60	4.5	0.94	-9, 18, 60
R precentral g.	5.9	9.64	38, -26, 62	5.8	2.69	40, -23, 60
	4.2	9.64 ^a	19, -35, 66	5.5	2.69 ^a	42, -23, 57
				5.4	2.69 ^a	38, -25, 60
				5.2	2.69 ^a	43, -26, 60
<i>Experiment 2. Picture naming</i>						
R medial frontal g. BA6	6.5	14.01	1, -18, 60	6.5	13.51	7, -26, 63
Bilateral post-central g. BA5/7	4.6	14.01 ^a	1, -44, 66	5.3	13.51 ^a	-1, -47, 65
R cingulate region	3.6	14.01 ^a	4, -23, 39			
L postcentral g., BA4	4.7	4.31	-35, -26, 54	4.5	3.44	-34, -28, 54
	3.4	4.31 ^a	-25, -21, 39	3.9	3.44 ^a	-25, -16, 62
L precuneus, BA31				4.2	2.54	-8, -57, 30
L cingulate g. BA30				3.9	2.54 ^a	-4, -50, 18
L parahippocampal g. BA30	4.4	1.26	-17, -35, -15	(3.8)	0.29	-16, -31, -6

Notes are provided in Table I.

a. Negative correlations: Areas where CBF decreased over successive scans.

Word meaning task (WM, Expt. 1)

Picture naming task (PN, Expt. 2)

b. Positive correlations: Areas where CBF increased over successive scans.

Word meaning task (WM, Expt. 1)

Picture naming task (PN, Expt. 2)

Figure 2.

Areas where CBF either (a) decreased or (b) increased across successive scans of the Word meaning task (Experiment 1) and the Picture naming task (Experiment 2). The t-value map has been coregistered with the normalized average MR scans of the participants. The Talairach and Tournoux [1988] coordinate of each slice is indicated below each image.

TABLE III. Experiment I: Areas where CBF changed from the first (T1) to the second scan (T2)

Region and Brodmann areas	Vol. (cm ³)	t value	Coordinates
<i>CBF decreases from T1 to T2</i>			
R. sup./medial frontal g. BA9/10	2.80	-4.4	21, 56, 21
R. medial frontal g BA8	2.80 ^a	-8.1	8, 36, 42
R. superior frontal g BA6	0.46	-4.5	19, 18, 63
L. middle frontal g BA6	0.27	-4.4	-34, 12, 44
L. inferior parietal lobule BA40	0.28	-5.0	-47, -47, 54
<i>CBF increases from T1 to T2</i>			
R. cingulus g BA 32	0.49	4.3	1, 13, 39
L. middle frontal g BA8/9	0.29	5.2	-56, 8, 39
R. precentral g BA4	1.50	5.2	35, -19, 66
L. paracentral lobule BA5	0.53	5.6	-4, -31, 51
R. superior temporal g BA22	0.69	4.3	62, -28, 11
L. precuneus BA7	0.93	5.2	-1, -64, 47

Notes are provided in Table I.

ral modification takes place which allows the subject to perform the task more efficiently, that is with less metabolic resources.

To explain the reduction in the association cortex of the temporal lobes, we could perhaps borrow the concept of

Figure 3.

Experiment 3 Regression of Pre- to Post-task baseline conditions: Area where CBF decreased from Pre- to Post.

spreading-activation from cognitive psychology. It was introduced by Collins and Loftus [1975] to account for, among other things, the facilitatory effects of semantic priming. Semantic priming refers to the facilitation which occurs when responding to a word after first seeing a semantically-related word (e.g., nurse after doctor). According to this theory, "activation" of a word spreads to concepts that are semantically related lowering the recognition thresholds of these related concepts, and facilitating the subsequent recognition of related words. The present results may indicate that at the neuronal level, presentation of one word activates and spreads to an array of neurons which are related not only to the word being tested but also to many other associated words. Repeatedly performing a semantic task will lower thresholds enough to reduce the metabolic requirements of the area but not enough to cause faster responding. This would be a characteristic specific to these temporal cortex association areas, for there was no such reduction in the visual cortex (which of necessity would have been involved in the tasks), and there was an increase over time in the sensory-motor cortex which was probably linked to learning the operational aspects of the tasks.

The temporal area in which there was a decline in CBF over time in the consecutive PN task lies within the area where the decrease took place in the consecutive WM task. Despite this, when the tasks were interleaved (Experiment 3) there was no indication that CBF either increased or decreased over time, indicating that the neural set-up which produces the changes when the task is performed consecutively is highly subject to interference or perhaps linked to stimulus format.

The participants in these experiments were elderly and one should ask if these effects generalize to younger populations. This would need to be tested empirically, but we expect that the decreases of consecutive task performance would hold for younger populations given the convergence with priming studies of younger populations. What is less clear is whether the alternating between tasks would have the same effect of interference. Similar experiments with younger subjects need to be carried out in order to evaluate whether they also experience an effect of task interference on rCBF and if so, how great it is. We propose, however, that, in an elderly population there is evidence of short-term (within an hour) neural efficiency within the association cortex of the temporal lobes. This capacity of the cortex to adapt is highly subject to the effects of interference by the performance of another task. In this population both increases and decreases in CBF over time were dependent on task order in that they were not observed when the subjects alternated between tasks.

From a methodological point of view, these experiments bring to light aspects to consider with regards to protocol and analyses of semantic tasks and brain imaging. One is that "semantic areas" can become more efficient with task repetition in that subjects can maintain the same level of performance and yet require less and less CBF. This may

explain why some studies fail to find semantic specific activation in temporal areas despite adequate testing [Roskies et al., 2001]. One solution to this problem might be to compare the first task scan rather than an average of all task scans with baseline when carrying out subtractions. A second aspect to consider is that in PET experiments in which there are 10-min pause between task scans, experimenters should consider that events such as lively conversations occurring during the interscan pauses have the potential of altering the pattern of rCBF during subsequent scans.

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