
Brain Activations Associated with Shifts in Response Criterion on a Recognition Test

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Abstract Sensitivity and bias can be manipulated independently on a recognition test. The goal of this fMRI study was to determine whether neural activations associated with manipulations of a decision criterion would be anatomically distinct from neural activations associated with manipulations of memory strength and episodic retrieval. The results indicated that activations associated with shifting criteria (a manipulation of bias) were located in bilateral regions of the lateral cerebellum, lateral parietal lobe, and the dorsolateral prefrontal cortex extending from the supplementary motor area. These regions were anatomically distinct from activations in the prefrontal cortex produced during memory-based retrieval processes (manipulations of sensitivity), which tended to be more medial and anterior. These later activations are consistent with previous studies of episodic retrieval. Determining patterns of neural activations associated with decision-making processes relative to memory processes has important implications for Cognitive Neuroscience, including the use of these patterns to compare memory models in different paradigms.

Résumé La sensibilité et le biais peuvent être manipulés de façon indépendante lors d'une épreuve de reconnaissance. L'objectif de cette étude par IRMF consistait à déterminer si les activations des neurones afférentes aux manipulations du critère de décision différent, du point de vue anatomique, de celles qui sont afférentes aux manipulations de la force de la mémoire et du recouvrement épisodique. Les résultats ont démontré que les activations associées au déplacement du critère (manipulation du biais) se situaient dans les parties bilatérales du cervelet latéral, le lobe pariétal latéral et le cortex préfrontal dorsolatérale, s'étendant à partir de l'aire motrice supplémentaire. Ces zones différaient du point de vue anatomique de celles activées dans le cortex préfrontal lors d'opérations de recouvrement basé sur la mémoire (manipulation de la sensibilité), qui elles, avaient tendance à être davantage médianes et antérieures. Ces activations plus tardives correspondent aux résultats d'études antérieures sur le

recouvrement épisodique. L'établissement des patrons d'activation des neurones associée aux opérations de prise de décision relatives aux processus mnémoniques comporte d'importantes implications pour la neuro-science cognitive, y compris le recours à ces patrons pour comparer les modèles de la mémoire selon différents paradigmes.

There are both single and dual process models of recognition memory. Donaldson (1996) and Hirshman and Henzler (1998) argued that most recognition phenomena could be explained by a unidimensional continuum of strength or familiarity with different decision rules for different recognition tasks. Others have proposed dual process models consisting of conscious recollection and familiarity (Mandler, 1980; Yonelinas, 1997). In both types of models, the participants have to arrive at a decision as to whether or not a particular item has been presented. Signal detection theory has often been used to describe the decision process (Green & Swets, 1966/1974; Murdock, 1974). Signal detection theory consists of two parts: separate distributions of old and new items along a strength of evidence continuum, and a decision criterion along that continuum for judging whether an item is old or new. Two parameters are used to characterize signal detection: d' , which represents the separation of the old and new distributions on the strength of evidence continuum, and beta, which reflects the placement of the decision criterion on that same continuum. Several manipulations have been developed for varying the two parameters independently of one another. For instance, d' can be manipulated by varying the number of presentations of individual items or their a priori strength without affecting beta. Beta can be manipulated through instructions, payoffs, and the respective percentages of old and new items. Our primary goal in this research is to see if we can identify the neural structures that are active during manipulations of d' and during manipulations of beta. Since the two para-

meters can be manipulated independently of one another, we expected to find differences in the patterns of neural activations.

Neuroimaging has been used in a wide variety of memory studies pertinent to the ones we report. Many studies that require episodic retrieval have produced activations primarily in the prefrontal cortex (Buckner, 2000; Cabeza & Nyberg, 2000), although other brain regions have also been associated with episodic memory, including the medial temporal lobe, the parietal lobe, the cerebellum, the thalamus, and the retrosplenium (Milner, Squire, & Kandel, 1998; Schacter & Wagner, 1999; Ungerleider, 1995). Different aspects of episodic retrieval have been measured: 1) global retrieval (comparing a retrieval task with a rest), 2) retrieval success (comparing successful retrieval with unsuccessful retrieval), and 3) retrieval effort (comparing difficult retrieval with less difficult retrieval). Each of these manipulations produces differential activations of the prefrontal cortex (Buckner et al., 1998a, b; Cabeza & Nyberg, 2000; Henson et al., 2000; Wagner, Desmond, Glover, & Gabrielli, 1998), more often in the right hemisphere than the left (Nyberg, Cabeza, & Tulving, 1996; Nyberg et al., 2000; Tulving et al., 1994). Examining the neural activations associated with manipulations of the signal detection parameters against these more traditional comparisons may help to clarify the neural processes involved in memory.

Many neuroimaging studies have looked at activations in the brain associated with decision-making (Bechara et al., 1998; Dove et al., 2000; Elliott, Rees, & Dolan, 1999; MacDonald, 2000; O'Doherty et al., 2001), but no neuroimaging study has directly investigated orthogonal manipulations of sensitivity and criterion as defined in signal detection theory. If criterion effects are an important part of the memory process, we should see distinct patterns of activation for manipulations of criteria that are anatomically separate from activations associated with the memory-based manipulations of episodic retrieval. In this study, conditions in which participants' criteria were manipulated on a trial-by-trial basis (shifting criteria) were compared to conditions in which participants' criteria remained stable.

We used a within-participants design. Participants were scanned during a recognition test of previously studied words. Criterion, or beta, was manipulated during the recognition test by presenting words in one of two colours. Participants were instructed to respond liberally to words in one colour, and conservatively to words in another colour. Therefore, in randomly alternating blocks of trials, some blocks consisted of an exclusively liberal criterion, some blocks consisted of an exclusively conservative criterion, and some blocks consisted of liberal and conservative criteria randomly

mixed. This design allowed for a specific contrast between mixed criterion and stable criterion (criterion shifts). Furthermore, crossed with manipulations of criteria were manipulations to d' . Some blocks contained words that were presented three times during the study session (representing high d' blocks) and other blocks contained words presented only once (representing low d' blocks). In addition, blocks of a rest condition were interspersed. This further allowed for specific contrasts between recognition and rest (global retrieval), high d' and low d' (retrieval success), and low d' and high d' (retrieval effort).

Method

PARTICIPANTS

Nine participants (2 males) took part in exchange for course credit in an Introductory Psychology class or for \$20. The ages ranged from 18 to 25 years old. All functional magnetic resonance imaging was conducted at the Dartmouth Brain Imaging Center. The use of human participants and fMRI procedures followed a protocol approved by The Committee for the Protection of Human Participants at Dartmouth College.

BEHAVIOURAL PARADIGM

All words used for both study and test procedures were chosen from the Toronto Word Pool (Friendly, Franklin, Hoffman, & Rubin, 1982) with the constraint that there were no obvious groups of highly related words. Prior to scanning, participants studied 168 words. The words were presented at the centre of a computer monitor for 500 msec each. The rate of presentation was one word every second. Fifty-six of the 168 words were presented three times during the study session, nonconsecutively and in random order. The thrice-repeated words were used during the high d' blocks, while the words presented once were used during the low d' blocks.

Test words were presented during scanning using a back-projection system. Participants took part in two functional runs consisting of a series of recognition test blocks and rest blocks. One hundred and twelve "old" words and 80 "new" words were presented during the tests. Participants had a button box in each hand for responding. The right button corresponded to "old," meaning they remembered seeing the word during the study session, and the left button corresponded to "new," meaning they did not remember seeing the word. The words for the recognition test were presented either in green or in red. Participants were instructed to adjust their criteria for judging whether a word was "old" or "new" depending on the colour of the word. For example, if the word was green then the participant was to be very liberal in responding "old." If the word was red then the participant was to be very

TABLE 1
Conditions During Functional Imaging Other Than Rest

	Criterion		
	Mixed	Conservative	Liberal
High d'	MH	CH	LH
Low d'	ML	CL	LL

conservative in responding “old.” Detailed instructions were provided to elucidate the meanings of conservative and liberal.

The paradigm for the recognition test was designed using alternating blocks of trials (see Table 1 for the conditions represented in each block). Each block consisted of six trials. Half the blocks consisted of three “old” words and three “new” words, while the other half consisted of four “old” words and two “new” words. The words within a block were randomly ordered. A trial began with a word (either in green or in red) presented for 1 second, followed by 3 seconds of a blank screen during which the participant was instructed to respond. Each functional run consisted of 20 blocks, with the blocks within each functional run being randomly ordered. Four of the blocks represented a mixed criteria – high d' (MH) condition. Three words were in green and three words were in red, randomly intermixed. The “old” words for those blocks had been presented three times during the study session. Two blocks represented a liberal criterion (high d' (LH) condition. The only difference from the MH condition was that all the words were in green. Two blocks represented a conservative criterion – high d' (CH) condition, with all the words in red. Four blocks represented a mixed criteria – low d' (ML) condition, two blocks represented a liberal criterion – low d' (LL) condition, and two blocks represented a conservative criterion – low d' (CL) condition. These low d' blocks were identical to the previous high d' blocks except that the “old” words had been presented only once during the study session. There were four rest blocks. Instead of words, a row of “Xs” was presented with the same timing parameters as in the recognition blocks. The participants were instructed to respond to each new row of Xs by alternately pressing the left and right buttons.

FMRI IMAGING PARAMETERS

A single fMRI session consisting of two functional runs (244 scans each) was obtained for each participant. Functional images were acquired with gradient-recalled echoplanar imaging (TR = 2,000 ms, TE = 35 ms, RF flip angle = 90°, gradient-echo pulse sequence, 27 contiguous axial slices at 5 mm thick, and an in-plane resolution of 64 x 64 pixels in a FOV of 24 cm, producing

TABLE 2
Contrasts Made During Analysis

Shifting Criteria	(MH+ML)-(LH+CH+LL+CL)
Global Retrieval	(MH+LH+CH+ML+LL+CL)-(REST)
Retrieval Success	(MH+LH+CH)-(ML+LL+CL)
Retrieval Effort	(ML+LL+CL)-(MH+LH+CH)

voxels of 3.75 mm x 3.75 mm x 5 mm) (Kwong et al., 1992; Ogawa et al., 1992) on a 1.5T GE SIGNA Echospeed MRI scanner (General Electric, Milwaukee, WI) equipped with high-performance gradients (revision LX 8.3; maximum amplitude 4.0mT/m; slew rate 150 mT/m/s). Twenty 7-slice, T1-weighted structural images were also obtained for each participant in the same slice prescription as the functional scans (TR = 650 msec, TE = 6.6 ms, fast spin-echo pulse sequence, with an in-plane resolution of 192 x 192 pixels in a FOV of 24 cm, producing voxels of 1.25 mm x 1.25 mm x 5 mm). High resolution, T1-weighted structural images were acquired as well using a 3-D SPGR pulse sequence (TR = 25 ms, TE = 6 ms, RF flip angle = 25°, bandwidth = 15.6 kHz, voxel size = .9375 mm x 1.25 mm x 1.2 mm). Foam padding was used for head stabilization.

FMRI ANALYSIS

Data were analyzed using Statistical Parametric Mapping (SPM99b; Wellcome Department of Cognitive Neurology, London, UK) (Friston et al., 1995). Motion correction to the first functional scan was performed within each participant using a six-parameter rigid-body transformation. The 27-slice structural image was then co-registered to the high-resolution structural image, and the resulting transformation parameters were applied to the mean of the motion-corrected images and all motion-corrected functional images. Using mutual information co-registration, the functional images were then directly co-registered to the high-resolution structural image. Spatial normalization to the Montreal Neurological Institute template (Talairach & Tournoux, 1988) was performed by applying a 12-parameter affine transformation followed by a nonlinear warping using basis functions (Ashburner & Friston, 1999). All transformations were computed sequentially with one reslice operation at the end, and the functional images were written with 3 mm x 3 mm x 3 mm voxels. The spatially normalized scans were smoothed with an 8-mm isotropic Gaussian kernel to accommodate anatomical differences across participants. These smoothed and normalized images were then used for statistical analysis.

A random-effects model was used to make statistical inferences (Friston et al., 1999). Each time series was

TABLE 3
Behavioural Measures of Sensitivity and Bias as a Function of Condition

	Fixed Blocks				Mixed Blocks			
	CH	CL	LH	LL	MH(c)	ML(c)	MH(l)	ML(l)
hits	57%	39%	81%	72%	64%	41%	73%	63%
false alarms	19%	7%	45%	39%	8%	10%	42%	46%
bias	1.59	2.87	0.78	1.05	2.63	3.05	0.89	1.00
d'	1.14	1.20	1.11	1.02	1.88	1.19	1.03	0.54
con. B / lib. B	2.23		0.92		2.84		0.95	
high d' / low d'	1.13	1.11			1.46	0.87		

high-pass filtered (cutoff = 240 s), and any global signal intensity differences were removed. For each participant, and for each voxel, simple t contrasts were based on a general linear model that included covariates for each of the seven conditions within each functional run. The group analyses reported in Figures 1 and 2, and in Table 4, were then based on one-sample t -tests that, for each contrast, included the voxel-wise parameter estimates from each participant with a threshold for significance of $p < .01$ (uncorrected for multiple comparisons) and a minimum voxel extent of 10. This relatively liberal threshold was used because random-effects analyses are very conservative already.

Results

BEHAVIOURAL RESULTS

As in previous studies, participants were able to shift their criteria on a trial by trial basis (Wolford & Miller, submitted). Beta (β) or bias is the height of the “old” distribution at the criterion value divided by the height of the “new” distribution at the same value. A β value less than 1 indicates a liberal response bias, while a β value greater than 1 indicates a conservative response bias. As shown in Table 3, participants followed instructions. Overall, bias was significantly higher in the conservative conditions (2.54) than in the liberal conditions (0.94) (repeated measures ANOVA, $F(1,8) = 30.42$, $p = .001$). Participants were also slightly more conservative in the low d' conditions, $F(1,8) = 7.71$, $p = .024$. However, there was no interaction between criteria conditions and d' conditions. Interestingly, there was a significant interaction between criteria conditions and fixedness conditions. Both conservative and liberal biases became more conservative during the mixed criteria blocks than during the fixed criterion blocks, but the conservative bias (2.23 to 2.84) was affected more than the liberal bias (0.92 to 0.95). Clearly, participants were able to shift their criterion between conservative and liberal judgments during the mixed blocks.

The number of presentations influenced d' as expected. In blocks in which the studied words were shown three times (high d' conditions), d' averaged

1.30. In blocks in which the studied words were only shown once (low d' condition), d' averaged 0.99. Though the number of presentations had the desired effect, it was not significant and not as large as in previous work (see Wolford & Miller, submitted). However, there was a significant interaction between d' conditions and fixedness conditions, $F(1,8) = 17.38$, $p = .003$. As shown in Table 3, the d' manipulation seemed to be more effective in the mixed criteria blocks than in the fixed criterion blocks.

fMRI RESULTS

The main focus of this study was to investigate patterns of activation associated with shifting decision criteria, and to determine whether those patterns are distinct from patterns of activation associated with memory-based retrieval processes. As discussed earlier, episodic memory retrieval can be manipulated in a variety of ways. In order to ensure that shifting criteria is distinct from other retrieval processes, the study was designed to allow for different contrasts to be made (see Table 2). Regions associated with shifting criteria were assessed by contrasting blocks in which participants shifted their criteria at least twice, with blocks in which participants maintained a particular criterion (either liberal or conservative). This contrast collapsed across the two d' conditions. The three memory-based retrieval processes investigated in this study were global retrieval, retrieval success, and retrieval effort. To examine global retrieval, regions that are associated with the act of retrieving a past event, rest conditions were subtracted from all conditions involving recognition (a combination of mixed and stable criteria blocks). Retrieval success, regions that are associated with successful retrieval versus less successful retrieval, included all high d' conditions minus all low d' conditions. Retrieval effort, regions that are associated with more effortful retrieval versus less effortful retrieval (essentially the inverse of the previous contrast), included all low d' conditions minus all high d' conditions. Table 3 shows the significant clusters of activation above threshold at the group level for each of the

TABLE 4
Group-level Activations

Contrast	Region	BA	Talairach			Size	
			x	y	z	voxels	t
Shifting Criterion mixed criteria "minus" stable criterion	(L MFG)	(6/8/9)	-33	6	42	350	6.04
	(L SFG)	(8)	-9	39	51	26	6.01
	(L AC)	(32)	-12	21	30	130	5.53
	(R MFG)	(6/8/9)	42	3	39	112	5.45
	L IPL	(40)	-45	-48	45	122	4.83
	R Cb		33	-66	-30	2504	9.32
	R IPL	(40)	45	-45	30	"	5.32
	L Cb		-33	-63	-39	"	8.70
Global Retrieval recognition "minus" rest	(L IFG)	(47)	-39	27	0	1167	15.11
	(R IFG)	(47)	36	21	-9	675	12.38
	(L AC)	(32)	-9	24	42	916	9.69
	(R AC)	(32)	3	24	42	"	9.30
	L PAG	(39)	-30	-60	36	192	8.91
	R Pc	(19)	39	-66	39	174	7.14
	R Cb		3	-54	-36	266	7.40
	L Cb		-6	-33	-27	"	4.44
Retrieval Success high <i>d'</i> "minus" low <i>d'</i>	(R MeFG)	(6)	0	39	33	64	4.87
	R Thal		15	-33	18	114	12.16
	L Caud		-12	6	15	195	8.38
	L MTL		-36	-3	-15	59	6.69
	L Cb		-3	-45	-24	183	8.29
	R Cb		3	-72	-21	"	5.88

BA = Brodmann's area, MFG=middle frontal gyrus, SFG=superior frontal gyrus, AC=anterior cingulate, IPL=inferior parietal lobule, Cb=cerebellum, IFG=inferior frontal gyrus, PAG=parietal angular gyrus, Pc=precuneus, MeFG=medial frontal gyrus, Thal=thalamus, Caud=caudate, MTL=medial temporal lobe.

Note: Clusters of activation above threshold ($p < .01$; minimum voxel extent: 10) are reported as a function of contrast. The stereotaxic coordinates and corresponding *t* values are for the voxel with the statistical maxima within each cluster.

first three contrasts. Table 4 shows the significant clusters of activation at the individual level for retrieval effort.

As shown in the glass brain in Figure 1 (see page 173), a general pattern of activation emerges for shifting criteria. The most significant areas of activation include large regions of the lateral right and left cerebellum that roughly extend into the right and left parietal lobe. Within the frontal lobes, significant clusters of activation appear in the superior and lateral regions of the prefrontal cortex from the supplementary motor area (SMA) of BA 8 to more anterior regions of the left middle frontal gyrus (BA 9). This pattern of activation was quite distinct from global retrieval or retrieval success. The strongest activations for global retrieval occurred in the inferior and lateral regions of the prefrontal cortex, and in the anterior cingulate. The only region associated with global retrieval that overlapped regions associated with shifting criteria was the anterior cingulate. Retrieval success produced a significant cluster of activation in the prefrontal cortex, the medial frontal gyrus (BA 6), and several clusters in subcortical regions, most notably in the left medial temporal lobe.

Again, none of the regions associated with retrieval success overlapped with regions associated with shifting criteria.

As for the retrieval effort contrast, individual analysis revealed significant focal clusters of activation in the anterior regions of the prefrontal cortex (see Figure 2 on page 175 and Table 5). A group level analysis, however, revealed no significant clusters of activation within the frontal lobes above the threshold of $p < .01$ and a voxel extent greater than 10. The lack of significant clusters of activation at the group level may be due to the relatively small behavioural difference in *d'*. The variability across participants of the location of activation within the anterior prefrontal cortex may also be contributing to the lack of significance at the group level. Nevertheless, at the individual level the activations are consistent with previous studies on episodic retrieval effort (Andreasen et al., 1995; Rugg et al., 1998; Schacter et al., 1996). Furthermore, in none of the nine participants did activations associated with retrieval effort overlap with activations associated with criterion shift.

TABLE 5
Frontal Lobe Activations for Individual Participants During Retrieval Effort

Contrast	Sbj	Region	BA	Talairach			Size	
				x	y	z	voxels	t
Retrieval Effort	CC	R MFG	(10)	39	60	3	61	5.21
	BB	R IFG	(47)	18	15	-15	30	4.08
	KB	R MFG	(10)	30	51	-9	56	6.32
	JL	R IFG	(47)	9	33	-18	190	7.09
low d' "minus" high d'	EE	R SFG	(11)	18	51	-18	78	5.80
	SC	L MeFG	(11)	-9	51	-15	34	4.86
	" "	R SFG	(11)	21	54	-18	24	3.82
	HG	L SFG	(9)	-15	60	33	110	6.22
	NL	R MFG	(47)	45	45	-9	19	3.45
	BK	R SFG	(11)	36	54	-15	5	2.95

Note: Clusters of activation in the frontal lobes above threshold ($p < .001$; minimum voxel extent: 10) are reported for each participant. The stereotaxic coordinates and corresponding t values are for the voxel with the statistical maxima within each cluster. Below the dotted line are activations in two participants at a lower threshold ($p < .01$; no minimum voxel extent).

Discussion

The results from this study confirmed our hypothesis that neural activations associated with manipulations of a decision criterion would be anatomically distinct from neural activations associated with manipulations of memory strength and episodic retrieval, based on cognitive models that state that these two processes are functionally independent. The following discussion makes three points. 1) Activations associated with shifting criteria are consistent with related studies on decision-making. 2) Activations associated with manipulations of episodic retrieval have replicated previous neuroimaging studies. 3) Establishing a pattern of brain activity associated with shifting criteria distinct from storage-based aspects of episodic retrieval has important implications in memory research.

REGIONS ASSOCIATED WITH SHIFTING CRITERIA

As the results indicate (see the glass brains in Figure 1), there is a clear difference between the general pattern of activation associated with shifting criteria and the general patterns of activation associated with global retrieval, retrieval success, and retrieval effort. More significant activations took place in the posterior regions of the brain than the frontal regions during shifting criteria, while more significant activations take place in the frontal regions than posterior regions during global retrieval. Regions of activation for shifting criteria include the lateral cerebellum, lateral parietal lobe, anterior cingulate, and the supplementary motor area and adjoining areas of the dorsolateral prefrontal cortex.

The strongest activations associated with shifting criterion occur in the lateral regions of the right and left

cerebellum. This is consistent with studies that show that patients with cerebellar damage are impaired on tasks that require coordination of rapid shifts in attention between stimulus-response alternations (Courchesne et al., 1994), though subsequent neuroimaging studies indicate that this regional activation may be limited to a remapping of the motor responses and does not necessarily involve attentional shifts (Bischoff-Grethe, Ivry, & Grafton, 2001). There is some activation of the cerebellum associated with the other retrieval tasks as well, though these activations are much more medial and much smaller in extent. Lateral parietal regions, more so than the cerebellum, are strongly associated with shifts in spatial orientation and attention (Corbetta, 1998; Corbetta et al., 2000; Hopf & Mangun, 2000; Hopfinger, Buonocore, & Mangun, 2000; Platt & Glimcher, 1999). In this study, the lateral parietal regions of the right and left inferior parietal lobule were more active during shifting criteria than during stable criteria, and these regions did not overlap with parietal regions active during the other retrieval tasks.

Two frontal lobe regions produced significant clusters of activation during criterion shifts. One of the regions was in the dorsolateral prefrontal cortex with statistical maxima in the left and right supplementary motor area (BA 6). In the left prefrontal cortex particularly, this activation extends anterior and inferior along the middle frontal gyrus to BA 9. Activity in the supplementary motor area is consistent with several neuroimaging studies on task-switching (Dove et al., 2000) and shifts in attention (Bischoff-Grethe et al., 2001; Corbetta, 1998; Corbetta et al., 2000; Hopfinger et al., 2000). These areas of activation in the dorsolateral pre-

frontal cortex did not overlap with any of the clusters of activation observed during global retrieval, retrieval effort, or retrieval success. One area of overlap we did observe in the frontal lobes was the anterior cingulate. This region is thought to underlie response selection and initiation of action (Cabeza et al., 1997; Shallice et al., 1994) and performance monitoring (MacDonald et al., 2000). Performance monitoring and response selection could be important components in criterion shifts as well as other retrieval tasks.

REGIONS ASSOCIATED WITH EPISODIC RETRIEVAL

The specific episodic retrieval processes investigated in this study include global retrieval, retrieval success, and retrieval effort. These retrieval processes are known to produce differential activation in the prefrontal cortex (Cabeza & Nyberg, 2000). In this study, global retrieval, defined as maintaining attention on a retrieval task, primarily produced clusters of significant activation in the inferior frontal gyrus bilaterally (BA 47) and in the anterior cingulate bilaterally (BA 32), consistent with previous neuroimaging studies (Cabeza et al., 1997; Wagner et al., 1998b). Retrieval success, defined as monitoring the product of retrieval, produced clusters of significant activation primarily in subcortical regions (including the right thalamus, left caudate, and left medial temporal lobe) and in the right medial frontal gyrus (BA 6), also consistent with previous studies (Andreasen et al., 1995; Tulving et al., 1994b, 1996). Retrieval effort, defined as performing a demanding retrieval search, did not produce significant clusters of activation at the group level. But an analysis of individual participants did indicate consistent clusters of activation in the anterior prefrontal cortex, more right than left hemisphere (BA 10, 11, and 47), also consistent with previous studies on retrieval effort (Andreasen et al., 1995; Rugg et al., 1998; Schacter et al., 1996a).

IMPLICATIONS FOR MEMORY RESEARCH

An important goal of cognitive neuroscience is to establish how selected regions of the brain are involved in particular cognitive processes. This study investigated the question of how the brain is differentially involved in decision-making processes relative to memory processes. One important implication of establishing a pattern of activation associated with shifting criteria dissociated from retrieval-based analyses is that those patterns of activations can be used to compare memory models in different paradigms.

Recently, many investigators have attempted to distinguish brain activity underlying false memories from true memories (see Schacter, Norman, & Koutstaal, 1998, for review) with little success other than some activity in the primary sensory cortex during the

retrieval of true memories (Fabiana, Stadler, & Wessels, 2000; Schacter et al., 1996b). Most of these studies have utilized a word association paradigm that produces "false memories" by creating a high percentage of false alarms (Roediger & McDermott, 1995). False alarms on a recognition test can arise for a variety of reasons. The phenomenon may be explained as "remembering" something that did not occur (Roediger & McDermott, 1995; see Roediger 1996 for review), or it may be explained as a series of criterion shifts sensitive to meta-memory variables (Miller & Wolford, 1999). Often, a false alarm is behaviourally indistinguishable as to whether it occurred due to some storage-based process or due to a criterion shift (Miller & Wolford, 1999; Wickens & Hirschman, 2000; Wixted & Stretch, 2000). However, the neural activations underlying a shift in criteria may be quite different from the neural activations underlying the retrieval of a stored event, allowing us to distinguish between criterion and storage explanations of false memories.

Further studies will need to be conducted to fully determine brain regions underlying shifts in criteria. Furthermore, this study raises several important questions: 1) Do uninstructed shifts in criterion produce similar activations as instructed shifts, 2) Are the neural structures underlying criterion shifts on a recognition test similar to neural structures underlying criterion shifts on other types of tasks, and 3) How do shifts in criteria differ, in terms of anatomical structures, from other shifts in attention? As a first step, we have shown that decision processes involved in recognition memory can be distinguished at the neural level from storage-based retrieval processes.

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References

- Andreasen, N. C., O'Leary, D. S., Cizadlo, T., Arndt, S., Rezai, K., Watkins, G. L., Ponto, L. L., & Hichwa, R. D. (1995). II. PET studies of memory: Novel versus practiced free recall of word lists. *Neuroimage*, 2, 296-305.
- Ashburner, J., & Friston, K. J. (1999). Nonlinear spatial normalization using basis functions. *Human Brain Mapping*, 7, 254-266.
- Bechara, A., Damasio, H., Tranel, D., & Anderson, S. W. (1998). Dissociation of working memory from decision making within the human prefrontal cortex. *Journal of Neuroscience*, 18, 428-437.

- Bischoff-Grethe, A., Ivry, R. B., & Grafton, S. T. (2001). *Cerebellar involvement in motor remapping rather than attention*. Seventh Annual Meeting of the Organization for Human Brain Mapping, Brighton, England.
- Buckner, R. (2000). Neuroimaging of memory. In M.S. Gazzaniga (Ed.), *The cognitive neurosciences*. (pp. 817-828). Cambridge, MA: MIT Press.
- Buckner, R. L., Koustaal, W., Schacter, D. L., Dale, A. M., Rotte, M., & Rosen, B. R. (1998a). Functional-anatomic study of episodic retrieval using fMRI: II. Selective averaging of event-related fMRI trials to test the retrieval-success hypothesis. *Neuroimage*, 7, 163-175.
- Buckner, R. L., Koustaal, W., Schacter, D. L., Wagner, A. D., & Rosen, B. R. (1998b). Functional-anatomic study of episodic retrieval using fMRI: I. Retrieval effort vs. retrieval success. *Neuroimage*, 7, 151-162.
- Cabeza, R., Kapur, S., Craik, F. I. M., McIntosh, A. R., Houle S., & Tulving, E. (1997). Functional neuroanatomy of recall and recognition: A PET study of episodic memory. *Journal of Cognitive Neuroscience*, 9, 254-265.
- Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, 12(1), 1-47.
- Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Science*, 95, 831-838.
- Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience*, 3, 292-297.
- Courchesne, E., Townsend, J., Akshoomoff, N. A., Saitoh, O., Yeung-Courchesne, R., Lincoln, A. J., James, H. E., Haas, R. H., Schreibman, L., & Lau, L. (1994). Impairment in shifting attention in autistic and cerebellar patients. *Behavioral Neuroscience*, 108, 848-865.
- Donaldson, W. (1996). The role of decision processes in remembering and knowing. *Memory & Cognition*, 24, 523-533.
- Dove, A., Pollman, S., Schubert, T., Wiggins, C. von-Cramon, D. Y. (2000). Prefrontal cortex activation in task switching: An event-related fMRI study. *Cognitive Brain Research*, 9, 103-109.
- Elliott, R., Rees, G., & Dolan, R. J. (1999). Ventromedial prefrontal cortex mediates guessing. *Neuropsychologia*, 37, 403-411.
- Fabiani, M., Stadler, M. A., & Wessels, P. M. (2000). True but not false memories produce a sensory signature in human lateralized brain potentials. *Journal of Cognitive Neuroscience*, 12, 941-949.
- Friendly, M., Franklin, P. E., Hoffman, D., & Rubin, D. C. (1982). The Toronto Word Pool: Norms for imagery, concreteness, orthographic variables, and grammatical usage for 1,080 words. *Behavior Research Methods & Instrumentation*, 14, 375-399.
- Friston, K. J., Holmes, A. P., & Worsley, K. J. (1999). How many participants constitute a study? *Neuroimage*, 10, 1-5.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. B., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 2, 189-210.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley. Reprinted 1974 by Krieger, Huntington, NY.
- Henson, R. N. A., Rugg, M. D., Shallice, T., & Dolan, R. J. (2000). Confidence in recognition memory for words: Dissociating right prefrontal roles in episodic retrieval. *Journal of Cognitive Neuroscience*, 12, 913-923.
- Hirshman, E., & Henzler, A. (1998). The role of decision processes in conscious recollection. *Psychological Science*, 9, 61-65.
- Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: An electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, 111, 1241-1257.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, 3, 284-291.
- Kwong, K. K., Belliveau, J. W., Chesler, D. A., Goldberg, I. E., Weiskoff, R. M., Poncelet, B. P., Kennedy, D. N., Hoppel, B. E., Cohen, M. S., Turner, R., Cheng, H. M., Brady, T. J., & Rosen, B. R. (1992). Dynamic magnetic resonance imaging of human brain activity during primary sensory stimulation. *Proceedings of the National Academy of Science*, 89, 5675-5679.
- MacDonald, A. W. III., Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science*, 288, 1835-1838.
- Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review*, 87, 252-271.
- Miller, M. B., & Wolford, G. L. (1999). Theoretical commentary: The role of criterion shift in false memory. *Psychological Review*, 106, 398-405.
- Milner B., Squire L. R., Kandel E. R. (1998). Cognitive neuroscience and the study of memory. *Neuron*, 20, 445-468.
- Murdoch, B. B. (1974). *Human memory: Theory and data*. Potomac, Maryland: Erlbaum.
- Nyberg, L., Cabeza, R., & Tulving, E. (1996). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin & Review*, 3, 135-148.
- Nyberg, L., Habib, R., Tulving, E., Cabeza, R., Houle, S., Persson, J., & McIntosh, A. R. (2000). Large scale neurocognitive networks underlying episodic memory. *Journal of Cognitive Neuroscience*, 12, 163-173.
- O'Doherty, J., Kringelbach, M. L., Rolls, E. T., Hornak, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature*

- Neuroscience*, 4, 95-102.
- Ogawa, S., Tank, D. W., Menon, R., Ellermann, J. M., Kim, S. G., Merkle, H., & Ugurbil, K. (1992). Intrinsic signal changes accompanying sensory stimulation: Functional brain mapping with magnetic resonance imaging. *Proceedings of the National Academy of Science*, 89, 5951-5955.
- Platt, M. L., & Glimcher, P. W. (1999). Neural correlates of decision variables in parietal cortex. *Nature*, 400, 233-238.
- Roediger, H. L. III. (1996). Memory illusions. *Journal of Memory and Language*, 35, 76-100.
- Roediger, H. L. III, & McDermott, K. B. (1995). Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 21, 803-814.
- Rugg, M. D., Fletcher, P. C., Allan, K., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1998). Neural correlates of memory retrieval during recognition memory and cued recall. *Neuroreport*, 8, 262-273.
- Schacter, D. L., Alpert, N. M., Savage, C. R., Rauch, S. L., & Albert, M. S. (1996a). Conscious recollection and the human hippocampal formation: Evidence from positron emission tomography. *Proceedings of the National Academy of Science*, 93, 321-325.
- Schacter, D. L., Norman, K. A., & Koutstaal, W. (1998). The cognitive neuroscience of constructive memory. *Annual Review of Psychology*, 49, 289-318.
- Schacter, D. L., Reiman, E., Curran, T., Yun, L. S., Bandy, D., McDermott, K. B., and Roediger, H. L. III. (1996b). Neuroanatomical correlates of veridical and illusory recognition memory: Evidence from positron emission tomography. *Neuron*, 17, 267-274.
- Schacter, D. L., & Wagner, A. D. (1999). Medial temporal-lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus*, 9, 7-24.
- Shallice, T., Fletcher, P., Frith, C. D., Grasby, P., Frackowiak, R. S. J., & Dolan, R. J. (1994). Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature*, 368, 633-635.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the brain*. New York: Thieme.
- Tulving, E., Kapur, S., Craik, F. I. M., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Science*, 91, 2016-2020.
- Tulving, E., Markowitsch, H. J., Craik, F. I. M., Habib, R., & Houle, S. (1996). Novelty and familiarity activations in PET studies of memory encoding and retrieval. *Cerebral Cortex*, 6, 71-79.
- Ungerleider, L. G. (1995). Functional brain imaging studies of cortical mechanisms for memory. *Science*, 270, 760-775.
- Wagner, A. D., Desmond, J. E., Glover, G., & Gabrieli, J. D. E. (1998a). Prefrontal cortex and recognition memory: fMRI evidence for context-dependent retrieval processes. *Brain*, 121, 1985-2002.
- Wagner, A. D., Poldrack, R. A., Eldridge, L. L., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1998b). Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. *Neuroreport*, 9, pp. 3711-3717.
- Wolford, G. L., & Miller, M. B. Support for a criterion-shift explanation of false memories. Manuscript submitted for publication.
- Yonelinas, A. P. (1997). Recognition memory ROCs for item and associative information: The contribution of recollection and familiarity. *Memory & Cognition*, 25, 747-763.

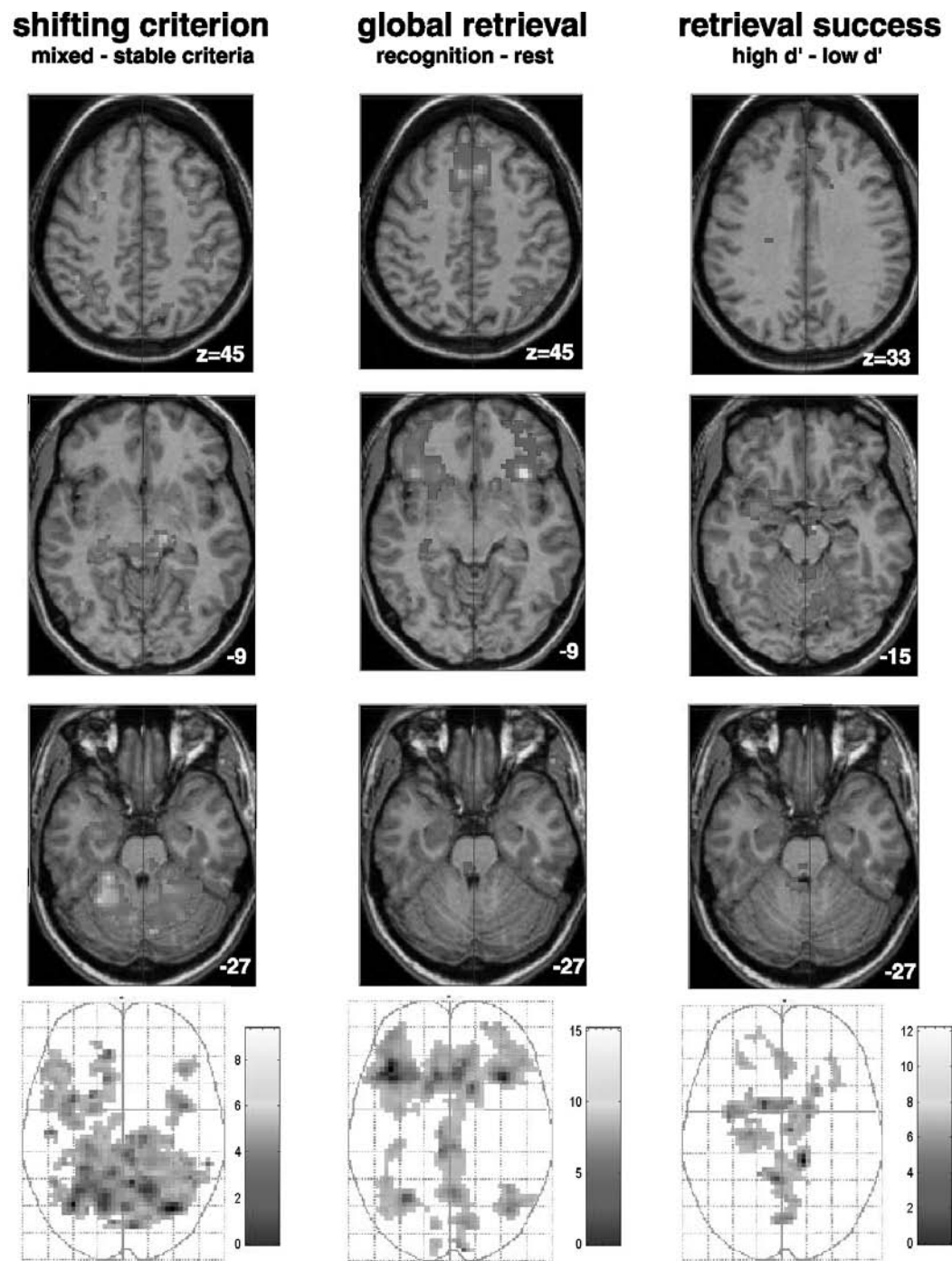


Figure 1. Group-level activations for shifting criterion, global retrieval, and retrieval success. Three axial slices are shown below each contrast with the z coordinates in Talairach space reported in the lower right corner of each image. The functional data are superimposed over a spatially normalized high-resolution anatomical image. Below these three images are glass brain representations revealing all clusters of activations above threshold ($p < .01$; minimum voxel extent: 10) throughout the whole brain for each contrast. Next to the glass brain representations are the scales for that particular contrast given in t values, with significant activations reported for any voxel having a t value greater than or equal to 2.90 (based on the threshold mentioned above). As the images indicate, activations during shifting criterion were much more extensive in the posterior regions of the brain, including lateral regions of the cerebellum and parietal lobe, with some activations in the dorsolateral regions of the prefrontal cortex including the supplementary motor area. While activations during global retrieval were much more extensive in the prefrontal cortex, primarily in the inferior frontal gyrus and the anterior cingulate. Activations during retrieval success were more extensive in medial regions of the brain, including the medial frontal gyrus and the medial temporal lobe.

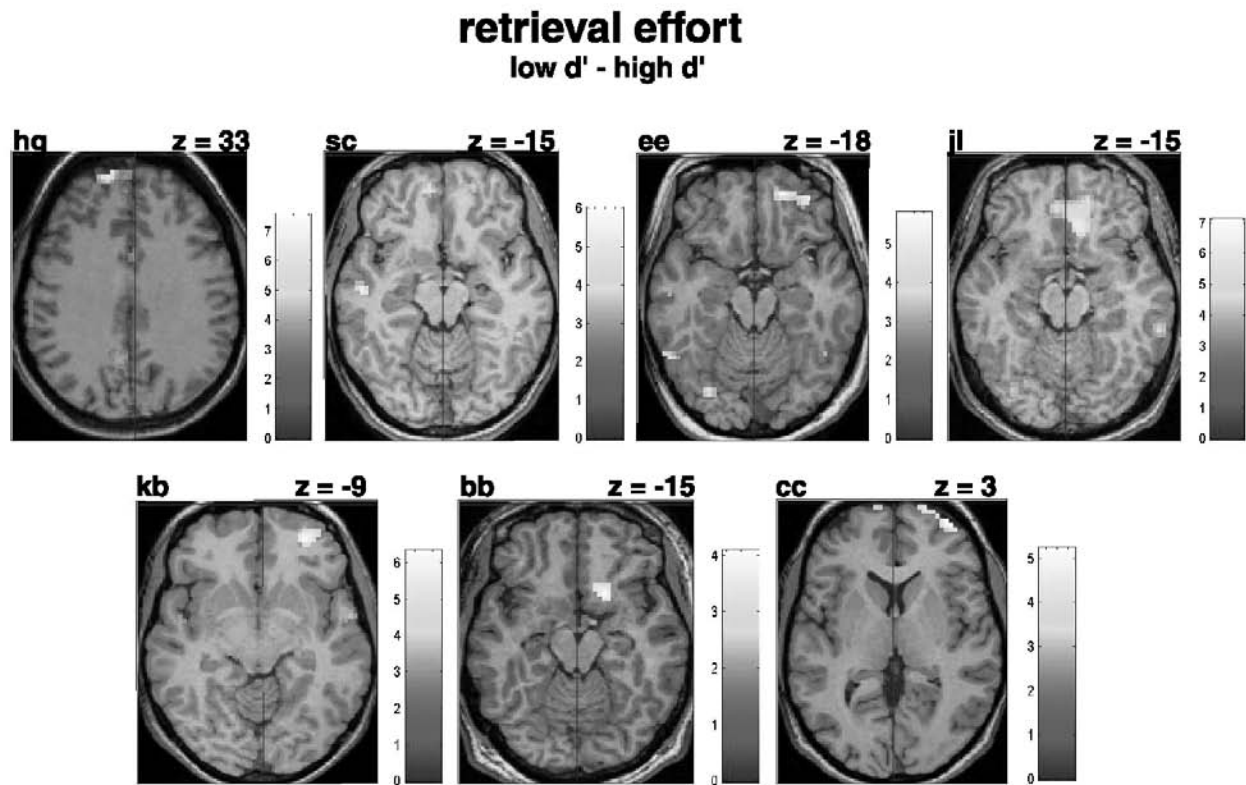


Figure 2. Clusters of significant activations for individual participants during retrieval effort. Axial slices are shown for seven of the nine participants that produced clusters of frontal lobe activations above a significant threshold ($p < .001$; minimum voxel extent: 10). The z coordinates of each axial slice are reported in Talairach space. The functional data are superimposed over corresponding spatially normalized high-resolution anatomical images of each participant. Next to each image are the scales for that particular participant given in t values, with significant activations reported for any voxel having a t value greater than or equal to 3.10 (based on the threshold mentioned above). The locations of these clusters of activations are primarily in the anterior and inferior regions of the prefrontal cortex, including Brodmann areas 9, 10, 11, and 47.