

When less means more: deactivations during encoding that predict subsequent memory

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In event-related functional MRI (fMRI) studies, greater activity for items that are subsequently remembered (R-items) than for items that are subsequently forgotten (F-items), or Dm effect (Difference in memory), has been attributed to successful encoding operations. In contrast, regions showing a reverse DM effect (revDM = F-items > R-items) have been linked to detrimental processes leading to forgetting. Yet, revDMs may reflect not only activations for F-items (aFs) but also deactivations for R-items (dRs), and the latter alternative is more likely to reflect beneficial rather than detrimental encoding processes. To investigate this issue, we used a paradigm that included a fixation baseline and could distinguish between the two types of revDMs (aF vs. dR). Participants were scanned while encoding semantic associations between words or perceptual associations between words and fonts, and their memory was measured with associative recognition tests. For both semantic and perceptual encoding, dR effects were found in dorsolateral prefrontal, temporoparietal, and posterior midline regions. In contrast with a prior study that attributed revDMs in these regions to detrimental processes, the present results suggest that these effects reflect beneficial processes, that is, the efficient reallocation of neurocognitive resources. At the same time, aF effects were found in other regions, such as the insula, and these are more consistent with an interpretation in terms of detrimental processes. Whereas most fMRI studies of encoding have focused on activation increases, the present study indicates that activation decreases are also critical for successful learning of new information.

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Introduction

With the advent of event-related functional MRI (fMRI), it has now become possible to investigate the neural correlates of

episodic memory encoding on a trial-by-trial basis and with high spatial resolution. The most powerful method available to investigate episodic encoding with fMRI is the subsequent memory paradigm. This method was originally developed for the analysis of event-related brain potentials (Paller et al., 1987) and later applied to fMRI (Brewer et al., 1998; Wagner et al., 1998). In this paradigm, subjects are scanned while encoding a list of items, and the results of a subsequent memory test are used to classify encoded items as either “remembered” (R) or “forgotten” (F). Greater activity for R-items than for F-items is known as the DM (difference in memory), and it is assumed to reflect successful encoding operations (Brewer et al., 1998; Davachi and Wagner, 2002; Fletcher et al., 2003; Kirchoff et al., 2000; Morcom et al., 2003; Otten et al., 2001; Rypma and D’Esposito, 2003; Wagner et al., 1998). Conversely, greater activity for F-items than for R-items, or reverse DM (revDM), has been attributed to detrimental processes during encoding that lead to subsequent forgetting (Otten and Rugg, 2001). In the present study, we provide evidence that revDMs are not necessarily detrimental and may instead reflect successful reallocation of processing resources.

Although occasionally reported in subsequent memory studies, few fMRI studies have focused on negative correlates of remembering (Otten and Rugg, 2001; Reynolds et al., 2004; Wagner and Davachi, 2001). Otten and Rugg (2001) were the first to emphasize regions showing greater activity for F-items than for R-items. They scanned participants during incidental encoding of single words (living–nonliving task), and then measured their memory using a recognition test. In two experiments with a similar paradigm, they found revDMs in dorsolateral prefrontal cortex (PFC), posterior midline (posterior cingulate, medial parietal), and inferior parietal regions. According to Otten and Rugg, these findings “clearly demonstrate the existence of cortical regions where enhanced activity during word processing is associated with less-effective encoding of the words into memory” (p. 1529). They suggested that secondary processes drained processing resources available for successful encoding of the items (see also Reynolds et al., 2004). One possibility is that these secondary processes involved the selection of information relevant to the living–

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nonliving distinction from working memory. Another possibility is that these secondary processes involved task-switching operations, which were required because living–nonliving trials were randomly interleaved with other kinds of trials. In sum, Otten and Rugg interpreted revDMs as reflecting processes detrimental to encoding.

Inherent to this interpretation is the assumption that revDMs are driven by processes associated with F-items rather than by processes associated with R-items. Yet, given that cognitive processes can lead to both activations and deactivations with respect to a resting baseline, there are at least two different kinds of revDMs. As illustrated in Fig. 1, a revDM (F-item > R-item) may occur not only when F-items elicit a greater activation than R-items (*aF-revDM*, or simply *aF*) but also when R-items elicit a greater deactivation than F-items (*dR-revDM*, or simply *dR*). This distinction is important because it leads to different interpretations of revDMs.

Several functional neuroimaging studies (Binder et al., 1999; Mazoyer et al., 2001; McKiernan et al., 2003; Raichle et al., 2001; Shulman et al., 1997) have associated cognitive performance not only with activations, but also with selective deactivations in a small set of brain areas including the posterior midline and temporoparietal areas identified by Otten and Rugg (2001). It has been proposed that these regions form a default network involved in specific cognitive processes, which are thought to take place during conscious rest, and that these processes are suspended when a demanding cognitive task is being performed leading to deactivations in these areas (Greicius et al., 2003; Raichle et al., 2001). Support for a default network composed of regions that are tonically active comes from metabolic findings showing that during passive rest an equilibrium exists in the brain between local oxygen supply and oxygen consumption, which allows for a long-term continuing level of neural activity (Raichle et al., 2001). Interestingly, the magnitude of such task-induced deactivations (TIDs, McKiernan et al., 2003) tends to increase with task demands. This indicates that TIDs play a role in successful task performance reflecting efficient reallocation of processing resources from “default” to task-relevant processes (McKiernan et al., 2003; Raichle et al., 2001). Hence, in view of these findings, it is possible that revDMs do not reflect processes detrimental for encoding occurring during F-items (aF), but rather processes

beneficial for encoding (efficient allocation of resources) occurring during R-items (dR).

To distinguish between aF and dR, it is necessary to compare R-items and F-items not only to each other but also to a resting baseline. Such a comparison was not reported by Otten and Rugg (2001) (see however, Reynolds et al., 2004; Wagner and Davachi, 2001), and hence, this study could not distinguish between the two patterns depicted in Fig. 1. To address this issue, we conducted an fMRI study including a fixation baseline. Additionally, we investigated revDMs for two different kinds of information. Participants were scanned while encoding semantic associations between words (semantic condition) or perceptual associations between words and the fonts in which they were written (perceptual condition), and their memory was measured with associative recognition tests. revDMs were separately measured for the semantic condition and the perceptual condition, and the overlap between the two conditions was isolated using a conjunction analysis. Verifying that revDMs can be replicated across different encoding conditions is critical to make sure that deactivations during R-items are reliable and that activations during F-items are not due to noise. Additionally, it provides information about whether these effects are related to particularities of the tasks employed.

In sum, to clarify the meaning of revDMs, we identified reliable revDMs across two different encoding conditions, semantic and perceptual, and classified them as either dR or aF. We defined dRs as revDMs in which R-items showed a significant deactivation from the baseline, and we defined aFs as revDMs in which F-items showed a reliable activation from the baseline. We assumed that dRs reflect processes beneficial for encoding, whereas aFs reflect processes detrimental for encoding. On the basis of Otten and Rugg's (2001) results, we predicted revDMs in dorsolateral PFC, posterior midline, and inferior parietal regions (see also Wagner and Davachi, 2001). On the basis of studies showing deactivations in posterior midline and inferior parietal regions during demanding cognitive tasks (Binder et al., 1999; Mazoyer et al., 2001; McKiernan et al., 2003; Raichle et al., 2001; Shulman et al., 1997), we expected that these regions would show dRs rather than aFs.

Methods

Subjects

The subjects were 14 healthy volunteers (4 females) with an average age of 19.8 (SD = 1.7) years. They were all students at Duke University who were paid for their participation. The subjects' written informed consent was obtained according to the Declaration of Helsinki and the study was approved by the Duke University Institutional Review Board.

Materials

The critical materials were abstract nouns selected from the MRC Psycholinguistic database (<http://www.psy.uwa.edu.au/MRCDataBase/mrc2.html>). The words were 4–11 letters in length and of moderate frequency.

Memory task

The memory task included two encoding conditions, semantic and perceptual, which were alternated across eight experimental

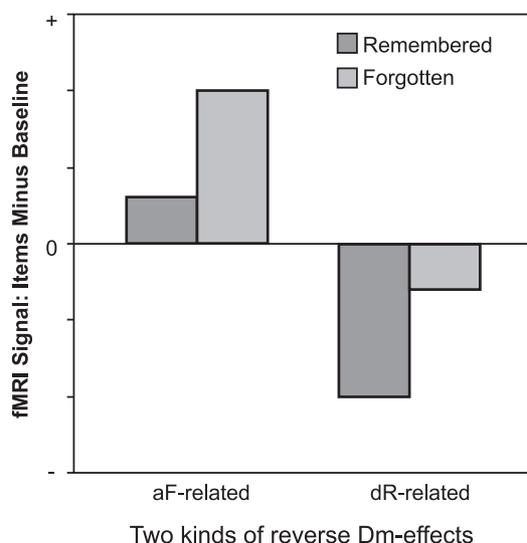


Fig. 1. Simulated data illustrating two kinds of reverse Dm (revDM) effects.

runs. The order of the conditions was counterbalanced across subjects. Each experimental run consisted of an encoding block and a retrieval block separated by a 30-s delay. During semantic encoding blocks, two words in plain font were displayed next to each other in the center of the screen. Subjects were instructed to rate the semantic relatedness of the words on a 4-point scale (1 = low; 4 = high) and, at the same time, to try to memorize the word pair (intentional encoding). Retrieval was tested by presenting pairs identical to the ones studied and pairs made by recombining words from different studied pairs. Participants indicated whether each pair was identical or recombined and their level of confidence (1 = definitely identical, 2 = probably identical, 3 = probably recombined, 4 = definitely recombined). During perceptual encoding blocks, the font in which the two words were presented varied across trials. Subjects were instructed to memorize the font with the word pair, while rating the aesthetic quality of the font together with the particular words that made up the pair (1 = low; 4 = high). Retrieval was tested in a similar manner except that recombined pairs consisted of studied pairs presented in the font of a different studied pair. The trials were presented for 3.4 s and followed by an interval ranging between 0 and 5.4 s. This interval was defined as baseline in the fMRI analysis (see below). Participants were encouraged to respond within the time that the word pair was displayed on the screen. Responses were not included in the analyses when the response time exceeded this period. The number of study trials per block was 29, yielding a total of 116 encoding trials per condition.

fMRI scanning

Images were collected using a 4-T GE scanner. Scanner noise was reduced with ear plugs and head motion, with foam pads and tape. Stimuli were presented with LCD goggles (Resonance Technology, Inc.), and behavioral responses were recorded with a four-key fiber optic response box (Resonance Technology, Inc.). Anatomical scanning started with a T1-weighted sagittal localizer series. The anterior (AC) and posterior commissures (PC) were identified in the mid-sagittal slice, and 34 contiguous oblique slices were prescribed parallel to the AC–PC plane. High-resolution T1-weighted structural images were acquired with a 450-ms repetition time (TR), a 9-ms echo time (TE), a 24-cm field of view (FOV), a 256² matrix, and a slice thickness of 1.9-mm. Functional scanning employed an inverse spiral sequence with a 1700-ms TR, a 6-ms TE, a 24-cm FOV, a 64² image matrix, and a 60° flip angle. Thirty-four contiguous slices were acquired with the same slice prescription as anatomical images. Slice thickness was 3.75-mm, resulting in cubic 3.75-mm³ isotropic voxels.

fMRI analyses

Data were analyzed using SPM99 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, <http://www.fil.ion.ucl.ac.uk/spm>). After discarding the first four volumes, time series were corrected for differences in slice acquisition times and realigned. Anatomical images were coregistered with the functional images. Next, both anatomical and functional images were spatially normalized to a standard stereotaxic space using the Montreal Neurological Institute (MNI) templates implemented in SPM99 and resliced to a resolution of 3 × 3 × 3 mm. The coordinates were later converted to Talairach and Tournoux's space (Talairach and Tournoux, 1988) using software available online

(http://www.mrc_cbu.cam.ac.uk/Imaging/mnispace/html). Finally, the volumes were spatially smoothed using an 8-mm isotropic Gaussian kernel.

For each subject, trial-related activity was assessed by a convolving vector of the onset times of the stimuli with a synthetic hemodynamic response function. The general linear model, as implemented in SPM99, was used to model the effects of interest and other confounding effects (e.g., head movement and magnetic field drift). Statistical Parametric Maps were identified for each participant by applying linear contrasts to the parameter estimates for the events of interest, resulting in a *t* statistic for every voxel. In both semantic and perceptual conditions, we coded three trial types: fixation baseline, R-items, and F-items. R-items included only those with high-confidence responses, because we were interested in recollection rather than familiarity or guessing. In this paper, we report only revDM findings. DM findings and retrieval results will be reported in a separate publication.

For both R- and F-items, activity increases and decreases relative to the fixation baseline were assessed using an uncorrected threshold of $P = 0.001$ with an extent threshold of five contiguous voxels. We chose a fixation baseline in view of previous reports that specifically related default network activity to passive rest (e.g., Raichle et al., 2001), although we recognize that identification of activations and deactivations is partly dependent on the particular baseline that is used (e.g., Stark and Squire, 2001). Next, we identified regions showing greater activity for F- than for R-items (i.e., semantic revDM and perceptual revDM). Because our analyses were mainly hypothesis driven focusing on regions reported in the study by Otten and Rugg, and because we restricted our search volume by using an inclusive masking procedure, we applied a slightly lower threshold ($P = 0.05$, uncorrected, cluster size > 5) for these comparisons. The resulting T maps were masked (inclusively, $P = 0.001$, uncorrected) either with the contrast F-item > fixation or the contrast fixation > R-item to distinguish between aFs and dRs, respectively. Finally, we assessed commonalities across tasks by inclusively masking the T maps corresponding to semantic and perceptual revDMs.

Results

Behavioral results

The proportion of correctly recognized identical pairs (hits) was 0.67 (SD = 0.05) in the semantic condition and 0.63 (SD = 0.05) in the perceptual condition. High-confidence hits (R-items in fMRI analyses) were 71% of total hits in the semantic condition and 51% of total hits in the perceptual condition. This difference was significant ($P < 0.001$). The false alarm rates to recombined trials were 0.27 (SD = 0.12) for the semantic condition and 0.38 (SD = 0.17) for the perceptual condition. This difference was also significant ($P = 0.006$).

During semantic encoding, reaction times (RTs) were 2099 ms (SD = 264 ms) for R-items and 2152 ms (SD = 378 ms) for F-items. During perceptual encoding, RTs were 1861 ms (SD = 386 ms) for R-items and 1919 ms (SD = 407 ms) for F-items. A 2 (condition: semantic vs. perceptual) × 2 (item type: R vs. F) ANOVA on RT data yielded a significant effect of condition (semantic > perceptual, $P < 0.001$) but no significant effect of item type ($P > 0.25$) or condition × item type interaction ($P > 0.96$). This suggests that potential differences in encoding activity

Table 1
Brain regions showing dR- and aF-related revDMs

Region	Side	A	Perceptual			<i>t</i> values			Semantic			<i>t</i> values		
			<i>x</i>	<i>y</i>	<i>z</i>	R-items	F-items	revDM	<i>x</i>	<i>y</i>	<i>z</i>	R-items	F-items	revDM
<i>dRs</i>														
Dorsolateral PFC	Right	9	23	31	41	-4.43	-2.30	2.44	27	42	26	-3.71	-0.19	5.11
Temporoparietal cortex	Right	39/40	60	-43	30	-6.99	-6.57	3.80	49	-49	48	-4.17	-0.07	4.34
	Left	39/40	-52	-59	10	-4.10	-1.15	2.26	-	-	-	-	-	-
Posterior midline regions	-	7/23	-11	-46	34	-8.49	-2.95	3.36	8	-46	24	-5.03	-2.77	5.91
		31	-4	-13	39	-3.42	-2.77	2.03	4	-20	40	-6.7	-3.14	9.5
Somatosensory cortex	Right	3	60	-13	22	-4.14	-0.41	4.07	-	-	-	-	-	-
	Right	3	27	-30	58	-5.17	-2.44	3.91	-	-	-	-	-	-
<i>aFs</i>														
Insular cortex	Left	-	-42	8	7	-0.18	2.80	4.13	-	-	-	-	-	-
Somatosensory cortex	Left	4	-34	-24	54	1.65	4.59	3.57	-	-	-	-	-	-
Thalamus	Right	-	8	-4	-7	0.66	6.08	2.97	-	-	-	-	-	-

between R- and F-items cannot be accounted for by the amount of time spent on processing each item.

fMRI results

The top part of Table 1 lists regions showing dRs. In the semantic condition, these effects were found in right dorsolateral PFC, right temporoparietal cortex, and the posterior midline cortex. All these regions showed deactivations that were more pronounced for R-items than for F-items, not reaching significance for the latter in right dorsolateral PFC and right temporoparietal regions. In the perceptual condition, dRs were found in the same regions, and additionally, in left temporoparietal and right somatosensory areas. Finally, a conjunction analysis was used to identify dR effects common to both semantic and perceptual conditions. As illustrated

in Fig. 2, these shared dRs were found in right dorsolateral PFC (Fig. 2a), posterior midline regions, including posterior cingulate and precuneus (Fig. 2b), and right temporoparietal cortex (Fig. 2c).

The bottom part of Table 1 lists regions showing aFs. In the semantic condition, there were no aFs, but in the perceptual condition, several regions showed greater activity for F-items than for R-items. These regions included the left insular cortex, left motor–somatosensory cortex, and the right thalamus. The aF in the left insula is shown in Fig. 3.

Discussion

The goal of the present study was to investigate the meaning of revDMs, that is, greater activity for subsequently forgotten items

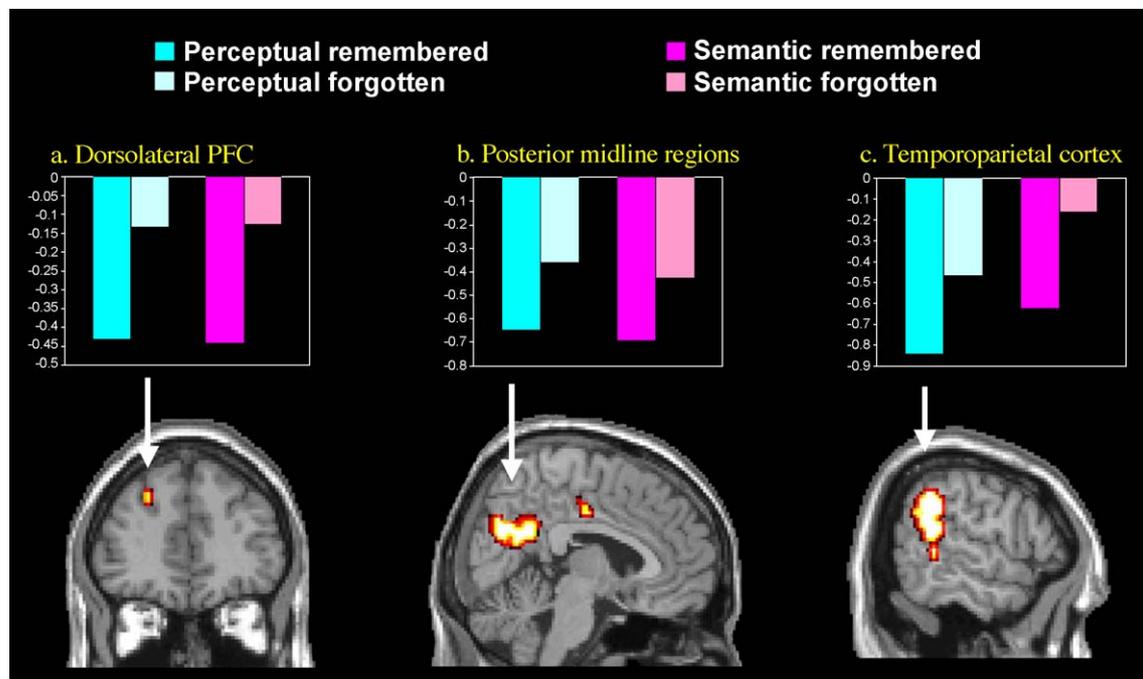


Fig. 2. (a–c) Brain regions showing greater deactivations for R- than for F-items (dRs) during both perceptual and semantic encoding (conjunction analysis). The bar graphs indicate effect sizes for R- and F-items relative to the fixation baseline.

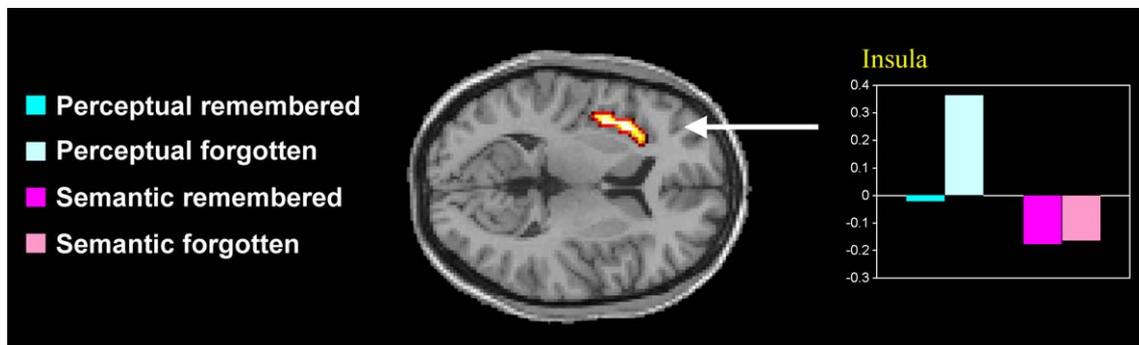


Fig. 3. The left insula showed greater activation for F- than for R-items (aF) during perceptual encoding. The bar graphs indicate effect sizes for R- and F-items relative to the fixation baseline.

(F-items) than for subsequently remembered items (R-items). revDMs may be due to greater deactivations for R-items (dRs) or to greater activations for F-items (aFs). The present study results yielded two main findings. First, right dorsolateral PFC, right temporoparietal, and posterior midline regions showed dRs, which are likely to reflect processes beneficial for encoding. Second, in the perceptual condition, a few regions including the insula showed aFs, which are likely to reflect processes detrimental for encoding. Below, we discuss these two findings.

revDMs due to deactivations for R-items (dRs)

A conjunction analysis revealed a set of regions that showed revDMs during both semantic and perceptual encoding conditions. These regions included right dorsolateral PFC, right temporoparietal, and posterior midline (posterior cingulate and precuneus) regions. Although the locations of the revDMs were entirely right-sided in our study, these are essentially the same regions that showed revDMs in the study by Otten and Rugg (2001). That study also employed a conjunction analysis to identify revDMs common to two conditions, which in their study was the same living–nonliving task in two different experiments (i.e., different groups of participants). Thus, taking together their study and ours, revDMs in the same set of regions were found in three different conditions and three different groups of participants. Thus, revDMs in right dorsolateral PFC, right temporoparietal cortex, and posterior midline regions seem to be robust and generalizable. Although it is worth noting that in another study (Wagner and Davachi, 2001) the right dorsolateral PFC did not show a revDM for reasons that are still unclear.

However, the interpretations of the revDM network in Otten and Rugg's and in our study are quite different. Otten and Rugg attributed their revDMs to secondary processes (e.g., selection from working memory, task switching) that drained resources available for successful encoding operations. This interpretation intrinsically assumes that the revDMs reflected processes associated with F-items, which led to greater activity for F- than for R-items. However, given that a comparison with a low-level baseline was not reported, it is unknown if the revDMs reflected activations for F-items (aFs) or deactivations for R-items (dRs). In the present study, we reported such a comparison and found that revDMs in right dorsolateral PFC, right temporoparietal cortex, and posterior midline regions overlapping with the ones identified by Otten and Rugg were dRs rather than aFs (see also Wagner and Davachi, 2001). Thus, our study suggests that these regions are associated with processes associated with R-items, and hence, likely to be

beneficial rather than detrimental for encoding. This alternative interpretation rests on the assumption that processes beneficial for cognitive processing may lead to deactivations.

As mentioned, this assumption is consistent with evidence that a small set of brain regions, including temporoparietal and posterior midline areas, consistently shows deactivations relative to resting baselines when demanding cognitive tasks are being performed (Binder et al., 1999; Mazoyer et al., 2001; McKiernan et al., 2003; Raichle et al., 2001; Shulman et al., 1997). One explanation of these task-induced deactivations (TIDs, McKiernan et al., 2003) is that they reflect the reallocation of neuro-cognitive resources to the task at hand. This hypothesis predicts that, as task demands increase, deactivations should become more pronounced. This prediction was confirmed by a recent fMRI study. In this study (McKiernan et al., 2003), participants discriminated between a target and other speech-like sounds, and the difficulty of the task was manipulated by varying target discriminability, memory load, and presentation rate. Reliable TIDs were found in all conditions, and their magnitude increased with task difficulty. Thus, extrapolating to the present study, dRs can be interpreted as beneficial rather than detrimental for encoding, reflecting a more efficient allocation of resources (i.e., greater deactivation) to R-items and a less efficient allocation of resources (i.e., smaller deactivation) to F-items. Like standard DMs, dRs could account for better subsequent memory for R-items than for F-items. It is still unclear what the relation is between dRs and DMs, including whether their effects are additive or interact.

If one assumes that TIDs reflect the allocation to the task of resources previously used during rest, one may ask what kinds of processes do TID regions normally perform during the resting baseline. Several ideas have been suggested including verbal and visual imagery (Binder et al., 1999), episodic memory processes (Andreasen et al., 1995; Mazoyer et al., 2001), monitoring of the external environment (Raichle et al., 2001), and the internal sensory and emotional state (Gusnard and Raichle, 2001). According to Gusnard and Raichle (2001), TID regions are tonically active during rest, continuously gathering information about the external and internal environment. These processes represent the normal or “default state” of the brain, which is disrupted whenever a person becomes engaged in a demanding cognitive task. Gusnard and Raichle suggest that constant monitoring of the environment probably served an adaptive role in natural settings, where detection of predators was critical for survival. They also suggest hypothetical processes for different TID regions, such as emotional processes for the posterior midline region (posterior cingulate, precuneus) (Maddock, 1999), and

detection of biological motion for the temporoparietal region (Allison et al., 2000).

More concretely, what is clear in the present study is that deactivations in certain brain regions are associated with successful memory encoding. The posterior midline region, for instance, showed a greater deactivation for R-items than for F-items, suggesting that dampening activity in this area is beneficial for learning. Interestingly, a similar conclusion may be reached by comparing not different items within the same group of participants but groups of participants with different levels of memory performance. Lustig et al. (2003) compared groups of young subjects, healthy elderly, and Alzheimer's disease (AD) patients on an incidental encoding task (living–nonliving) that was interleaved with a passive fixation baseline. They found that compared to the fixation baseline, young subjects showed a normal deactivation in the posterior midline region (posterior cingulate and precuneus), the elderly failed to show a deactivation, and AD patients showed a significant activation. Thus, a failure to deactivate the posterior midline region during encoding predicts worse memory performance (the present study) and may signal a pathological alteration of normal memory mechanisms (Lustig et al., 2003). At the same time there is evidence suggesting that pathological aging may be associated with an increase of activations for subsequently remembered items (Bookheimer et al., 2000; Wagner, 2000). This effect may reflect the recruitment of a compensatory mechanism, and it is unclear how it relates to reduced activations in elderly and AD patients (Lustig et al., 2003).

revDMs due to activations for F-items (aFs)

In addition to areas showing dRs, we also identified regions showing aFs. One of these regions was the left insula, which showed greater activity for F-items than for R-items during perceptual encoding. However, no such difference was found for the semantic encoding condition during which both F-items and R-items showed a nonsignificant deactivation (see Fig. 3).

Although some caution in interpreting this finding seems appropriate given that it was beyond our predictions and that we used an uncorrected threshold, the association between the insula and F-items is consistent with evidence linking activity in this region to processes that are detrimental to memory. Cabeza et al. (1997) reported a reverse relation between insular activity and encoding success in a study comparing brain activity in young and older adults. In this study, older adults showed greater insular activity during encoding than young adults. Rather than compensatory, the age-related increase in the insula was associated with poor encoding. The correlation between activity in the insula and subsequent recall performance was negative, indicating that those participants who showed greater activity in the insula encoded items less effectively. Thus, the authors proposed that greater insular activity in older adults reflected a failure to inhibit irrelevant or detrimental neural activity. Interestingly, although the insular activity was greater in older adults, the negative correlation was found in both groups, suggesting that this is not an age-specific phenomenon. Consistent with Cabeza et al.'s suggestion, two recent fMRI studies (Reynolds et al., 2004; Wagner and Davachi, 2001) also associated the insula with detrimental processes.

Thus, these results are consistent with the present finding that greater activity in the insula during encoding predicted subsequent forgetting. Other studies have associated insular activations with

emotional stress and arousal (Chua et al., 1999; Liotti et al., 2000; Paulus et al., 2003; Rauch et al., 1997; Tillfors et al., 2001). Hence, one possible explanation for these findings is that insular activity during encoding reflects excessive arousal, which prevents successful memorization. It is unclear, however, why we found this effect in the perceptual but not in the semantic condition.

Conclusions

In sum, the present study yielded two main findings. The first finding was that dorsolateral PFC, temporoparietal, and posterior midline regions showed reverse Dm effects (revDMs) due to deactivations for R-items (dRs). This finding is consistent with the results of Otten and Rugg (2001), who found revDMs in basically the same regions. However, in contrast with their suggestion that revDMs reflect detrimental processes associated with F-items, the present results indicate that they reflect beneficial processes associated with R-items. This interpretation fits well with evidence that temporoparietal and posterior midline regions tend to show task-induced deactivations (TIDs) during demanding cognitive tasks. TIDs have been attributed to the reallocation of cognitive resources, and hence, the present results suggest that the reallocation of cognitive resources was more efficient for items that were subsequently remembered (R-items) than for items that were subsequently forgotten (F-items). The second finding of the study was that a few regions, including the insula, showed revDMs due to activations for F-items (aFs). The activation of the insula during F-items is consistent with evidence linking activity in this region to processes detrimental to memory. In sum, our results demonstrate that successful memory encoding involves not only activations but also deactivations, and that in some cases less neural activity can mean more learning. More generally, the present findings have direct implications for the interpretation of functional neuroimaging evidence because they directly link decreased neural activity with successful cognitive performance.

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