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REFRESHING: A MINIMAL EXECUTIVE FUNCTION

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Abstract

Executive functions include processes by which important information (e.g., words, objects, task goals, contextual information) generated via perception or thought can be foregrounded and thereby influence current and subsequent processing. One simple executive process that has the effect of foregrounding information is *refreshing* – thinking briefly of a just-activated representation. Previous studies (e.g., Johnson et al., 2005) identified refresh-related activity in several areas of left prefrontal cortex (PFC). To further specify the respective functions of these PFC areas in refreshing, in Experiment 1, healthy young adult participants were randomly cued to think of a just previously seen word (*refresh*) or cued to press a button (*act*). Compared to simply reading a word, refresh and act conditions resulted in similar levels of activity in left lateral anterior PFC but only refreshing resulted in greater activity in left dorsolateral PFC. In Experiment 2, *refreshing* was contrasted with a minimal phonological *rehearsal* condition. Refreshing was associated with activity in left dorsolateral PFC and rehearsing with activity in left ventrolateral PFC. In both experiments, correlations of activity among brain areas suggest different functional connectivity for these processes. Together, these findings provide evidence that (1) left lateral anterior PFC is associated with initiating a non-automatic process, (2) left dorsolateral PFC is associated with foregrounding a specific mental representation, and (3) refreshing and rehearsing are neurally distinguishable processes.

Key words: executive function, refreshing, rehearsing, prefrontal cortex, working memory

Executive cognitive processes serve to foreground, maintain, and manipulate information relevant to an on-going task. There have been a number of characterizations or taxonomies of executive or control mechanisms (e.g., Baddeley, 2000; Duncan, 2001; Johnson, 1992; Miller and Cohen, 2001; Shallice, 1988; Smith and Jonides, 1999; Stuss and Levine, 2002). Here we discuss one simple executive process: *refreshing* – briefly thinking of a just-previously activated thought or percept – is one of the most basic cognitive acts, an instance of reflective attention directed to a target that is no longer externally available (Johnson and Hirst, 1993). For example, one might momentarily refresh the representation of an attractive car that just passed, or momentarily refresh an unfamiliar term a lecturer uses. The result of refreshing presumably is to briefly augment (and foreground) and/or extend (maintain) activity associated with a recently activated representation. Thus, refreshing can be thought of both as a minimal manipulation process, in its effect of foregrounding or selecting a particular representation relative to others, and a minimal maintenance process, in its effect of extending the availability of an active representation. A single refresh is sufficient to improve long-term memory compared to perceiving an item again (Johnson et al., 2002; Raye et al., 2002; see also Ranganath et al., 2005).

Refreshing is proposed to be a component of many more complex tasks (e.g., Johnson et al., 2005). For example, refreshing may help keep agendas (i.e., goals or task contexts) active; keep potentially relevant information active during comprehension or problem solving; and bridge between a thought and its expression, or between intention and action. Thus, refreshing may be a component of much of what we call cognitive control. Disruptions in refreshing associated with aging (Johnson et al., 2002), psychopathology (Grillon et al., 2005), emotion (Johnson et al., 2005, Experiment 6), or other temporary or persisting conditions, could have wide-ranging consequences for cognition. For example, "senior moments" such as beginning to speak and forgetting the thought, or not remembering what you saw in your side mirror a moment before changing lanes on a highway, could reflect deficits in refreshing active representations (Johnson et al., 2002, 2004; McDaniel et al., 2003).

To study the neural correlates of refreshing, Raye et al. (2002) instructed young adults to read words silently as they appeared on a screen and to think of the just-previous word when cued. Trials of three conditions were randomly intermixed. On each trial, participants saw a word that was followed about a half-second later by either the same word (*repeat* condition), a new word (*read* condition), or a dot cue that signaled the participant to think of the just-previous word (*refresh* condition). Compared to the repeat and read conditions, refreshing was associated with activity in left dorsolateral prefrontal cortex (PFC), as well as temporal and parietal cortex. A subsequent study found a deficit in refresh-related activity in left dorsolateral PFC in older compared to young adults (Johnson et al., 2004).

In a meta-analysis of seven functional magnetic resonance imaging (fMRI) studies of the refresh

TABLE I

Trial sequence and timing for Experiment 1

Read	Word	ISI	New Word		<		<		>		
Refresh	Word	ISI	●		<		>		>		Blank
Act	Word	ISI	⧈		>		>		<		
	1450 msec	550	1450	550	1400	600	1400	600	1400	600	2000
	Scan 1		Scan 2		Scan 3		Scan 4		Scan 5		Scan 6

process, Johnson et al. (2005) identified frontal areas associated with refreshing across 13 comparisons that varied in the type of information refreshed (e.g., printed words, spatial locations, auditory words, pictures of people or places). Frontal areas associated with refreshing included left dorsolateral PFC (middle frontal gyrus), and left anterior PFC (superior frontal gyrus). Areas identified in the meta-analysis were then used as regions of interest (ROIs) to examine activity in these regions in each data set in the analysis. Interestingly, across different types of information, refresh-related activity in the anterior PFC area was significantly less variable than refresh-related activity in the dorsolateral PFC area. This pattern is consistent with the idea that left dorsolateral PFC plays a role in maintaining or foregrounding specific information (and therefore varies by type of information), and suggests that left anterior PFC may subserve a more general function, such as initiating the refresh process (and thus varies little with type of information). This raises the question of whether anterior PFC plays a role in initiating processes more generally.

Experiment 1 tested our hypothesis about these possible differential roles of anterior and dorsolateral PFC. We compared cued refreshing with cued button pressing (*act*) – a task that, like refresh, requires initiating a process, but does not involve foregrounding a recently activated representation. If dorsolateral PFC is involved in refreshing a specific representation, activity in this area should be greater in the refresh than act and read conditions. If anterior PFC is involved in initiating processes generally, activity in the refresh and act conditions should be similar in anterior PFC and greater than in the read control condition, because reading is a comparatively automatic response to seeing a word.

EXPERIMENT 1 (REFRESH *VS.* ACT)

Method

Participants for Experiments 1 and 2

The Human Investigation Committee of Yale University Medical School approved protocols for both studies. Participants were healthy, right-handed young adult volunteers from the Yale University community who gave written informed consent. Experiment 1 had 12 participants, all female, mean age 20.2 years (range = 18-24 years); Experiment 2 had 17 participants, 10 female, mean age 21.4 years (range = 18-29 years).

Experimental Procedure and Materials

During scanning, stimuli were projected onto a screen at the foot of the scanner, which participants viewed through a mirror mounted on the head coil. All stimuli appeared in the center of the screen. The refresh procedure followed Experiment 1 of Raye et al. (2002). Stimuli consisted of 160 common 1 to 3 syllable words (e.g., toad, manuscript); mean frequency (42; Kuçera and Francis, 1967) and mean number of syllables (1.66) was equated across conditions. Any particular word was used only once in the experiment for any particular participant. Three trial types (*refresh*, *act*, *read*) were pseudo-randomly intermixed with a different order for each participant. As shown in Table I, trials were 12 sec long. On every trial in all conditions participants first saw a single word (for 1450 msec). The next screen, which followed 550 msec later, implemented the experimental manipulation: Participants saw for 1450 msec either a new word (*read* trial), a black dot (*refresh* trial), or a black square (*act* trial). Participants were told that we were interested in differences in brain activity associated with reading, thinking, and acting and it was important for them to do only what they were instructed for each trial type. They were told whenever they saw a word on the screen to read it silently to themselves, when they saw the black dot to think of the word that just preceded the dot (refresh), and when they saw the square to press a button that they held in their right hand (act). In every case, participants next saw a series of three arrows and thought "right" or "left" according to each arrow's direction. The arrows provided an 8 sec task common to all conditions to separate the trials, allowing time for the hemodynamic response associated with the experimental manipulation, and to decrease variability among participants from uncontrolled mental activity between trials. Each of four runs included 10 trials of each condition (refresh, act, read), for a total of 40 trials per condition for each participant.

Imaging Details for Experiments 1 and 2

T1-weighted anatomical images were acquired for each participant using a 1.5T GE SIGNA (Experiment 1) or Siemens SONATA (Experiment 2) scanner. In both cases, functional scans were acquired with a single-shot echoplanar gradient-echo pulse sequence (TR = 2000 msec, TE = 35 msec, flip angle = 80°, FOV = 24). Twenty-four axial slices were acquired (resolution 3.75 × 3.75 mm in plane, 3.8 mm between planes) aligned with the AC-PC line. Each run began with 12 sec of blank screen to allow tissue to reach steady state magnetization and was followed by a 1-minute rest interval. For each person in both experiments, a total of 240 volumes of data, one volume every 2 sec, or 6 full brain scans for each trial, were collected for each condition.

fMRI Analyses for Experiments 1 and 2

Data were motion-corrected using a 6 parameter automated algorithm (AIR; Woods et al., 1992). A 12 parameter AIR algorithm was used to co-register participants' images to a common reference brain. Data were mean-normalized across time and participants, and spatially smoothed (3D, 8mm FWHM gaussian kernel).

The raw fMRI signal data were analyzed using analysis of variance (ANOVA) with participant as a random factor (NIS software, Laboratory for Clinical Cognitive Neuroscience, University of Pittsburgh, and the Neuroscience of Cognitive Control Laboratory, Princeton University). Run (1-4), condition (read, refresh, act in Experiment 1; read, refresh, rehearse in Experiment 2) and time within trial (volume 1-6) were fixed factors.

Because conditions differed only in the event occurring during the second image in a trial (read, refresh, act in Experiment 1; read, refresh, rehearse in Experiment 2), differences between conditions will appear as differences in the blood oxygen level-dependent (BOLD) signal after the third scan. Thus, we first identified regions that showed a condition × time interaction with a minimum of 6 contiguous voxels, each voxel significant at $p < .00001$ (Experiment 1) or $p < .000001$ (Experiment 2) (Forman et al., 1995). The F-maps were transformed to Talairach space using analysis of functional neuroimaging (AFNI) (Cox, 1996), and areas of activation were localized using Talairach Daemon software (Lancaster et al., 1997), as well as manually checked with the Talairach and Tournoux (1988) or Duvernoy (1999) atlases. For each region identified, we extracted the mean percent signal change from time 1 at time 4 (Experiment 1) or times 4 and 5 (Experiment 2) for each subject for each condition and submitted them to planned subsequent contrasts between conditions. The p-levels for these contrasts are reported in the accompanying *Notes* to the tables.

Correlational Analyses of fMRI Data

Correlational analyses were performed to explore functional connectivity differences between conditions. We used Statistical Parametric Mapping 2 (SPM2) (Wellcome Department of Imaging Neuroscience, University College London) first to model the hemodynamic response function with a temporal derivative and create statistical parametric maps of activation for each condition for each participant. We then entered these contrast maps into a group random-effects analysis separately for each condition. From these random-effects analyses, for each condition, PFC ROIs were selected from those areas with 6 or more contiguous voxels (each voxel significant at $p < .001$). For each individual for each ROI, full time series data were extracted from a 6mm sphere around the peak voxel of the ROI as an index of trial by trial variability. For each individual for each ROI, a correlational analysis was run using the average raw signal in these 6 mm spherical ROIs to model four additional regressors beyond the six (three conditions, each with a temporal derivative) used initially. For each condition, a regressor was created from the raw signal where the values at each of time points 3-6 were retained and all other values within the regressor were set to zero. To covary baseline activity, a fourth regressor contained raw signal from timepoints 1 and 2 (irrespective of condition) with all other values set to zero. Thus, the full time series of data was separated into four regressors representing correlation with the ROI signal for the three covariates of interest and a baseline condition. Individual subject contrast maps were generated to compare the differences in correlations between conditions. These maps were then entered into a group random effects analysis to identify regions where a minimum of six contiguous voxels were each significantly more correlated ($p < .01$) with the area of interest in one condition than another.

Results and Discussion

We hypothesized that dorsolateral PFC, largely middle frontal gyrus, is engaged in the foregrounding of specific information, and that anterior PFC, largely superior frontal gyrus, plays a more general executive role such as initiating processes. As can be seen in Figures 1A and 1B, our results support this hypothesis. Consistent with areas identified in our refresh meta-analysis (Johnson et al., 2005), there was greater activity in the refresh than the read condition in two areas of left PFC: middle frontal gyrus extending into inferior frontal gyrus (Figure 1A) and an anterior area of left lateral superior frontal gyrus (Figure 1B). Importantly, the left anterior PFC area (Figure 1B) was engaged equally when participants were cued to refresh a representation or cued to make a

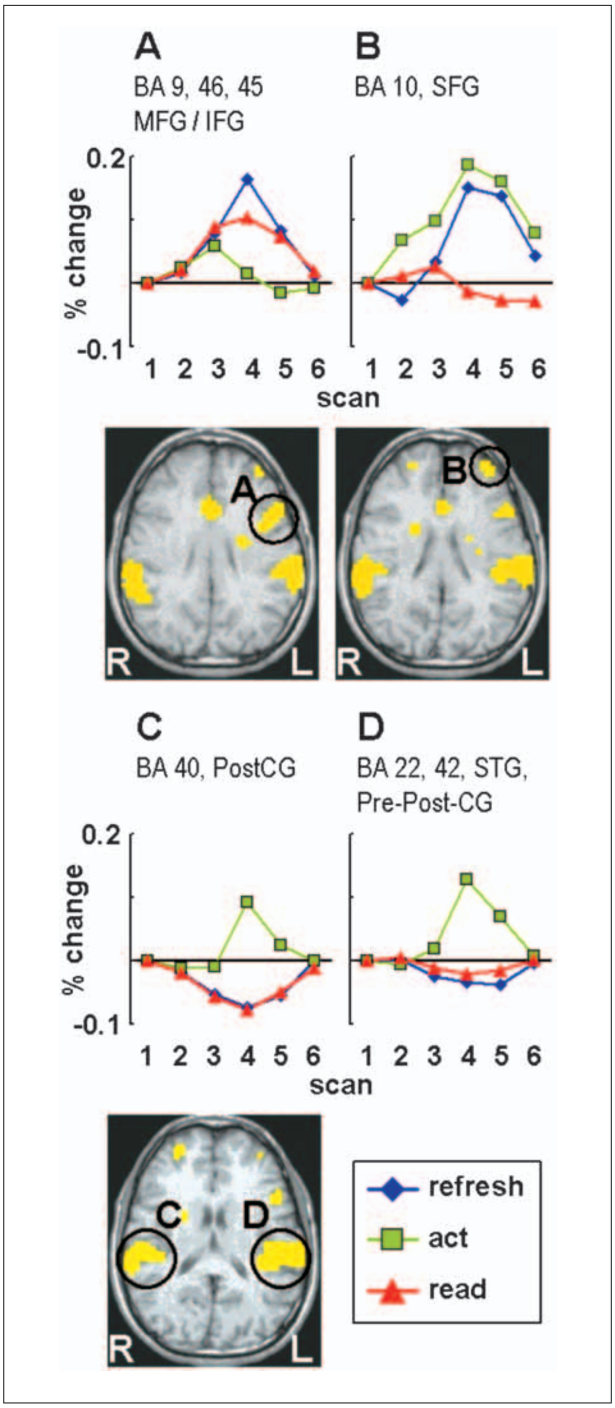

Fig. 1 – *Experiment 1. (A) Left PFC area associated with refresh but not act condition; MFG = middle frontal gyrus, IFG = inferior frontal gyrus. (B) Left anterior PFC area associated with both refresh and act conditions; SFG = superior frontal gyrus. (C, D) Right and left regions along central and lateral sulci associated with act but not refresh condition; Pre-Post-CG = pre-post-central gyrus, STG = superior temporal gyrus. Slices were chosen to show representative areas of activation. In all figures, for the timecourses, the x-axis represents scan within a trial (TR = 2000 msec, thus one scan occurred every 2 sec, each trial was 12 sec), and the y-axis represents mean percent signal change from the first within-trial time point.*

button press, suggesting this area plays a similar role in both the refresh and act conditions such as initiating the relevant process. It was not active during the read task, presumably because reading is a relatively automatic process invoked by the presentation of word stimuli (e.g., MacLeod, 1991). The coordinates for the local maximum of this anterior PFC area are within 2 voxels of the area reported in the meta-analysis of refresh studies in Johnson et al. (2005). In contrast, dorsolateral PFC (Figure 1A) was engaged in the refresh condition but not during the act condition, providing additional evidence that left dorsolateral PFC is engaged when participants refresh a representation and not simply when participants are cued to do something (see also, Raye et al., 2002, Experiments 2 and 3).

As would be expected based on previous studies that involve finger movement (e.g., Khushu et al., 2001; Moritz et al., 2000), act trials showed greater activity than read and refresh trials bilaterally in motor and somatic sensory areas in pre- and postcentral gyri, as shown in Figures 1 C and 1D, as well as in other areas such as thalamus (see Table II for these and additional areas identified).

Consistent with the PFC results discussed above, the first step of the functional connectivity analyses that modeled the hemodynamic response function for each condition separately, identified an area of left anterior PFC (BA 10) for refresh (– 23, 54, 23) and for act (– 30, 50, 27). Both of these areas, including their local maxima, overlapped the area shown in Figure 1B. When these left anterior areas were used as seed areas to identify areas correlated with each seed, activity in left anterior PFC was significantly more correlated with activity in left dorsolateral PFC (– 30, 38, 14) in the refresh than the act condition, and was significantly more correlated with activity in left pre- and postcentral gyri (– 47, – 18, 30) in the act than the refresh condition.

Modeling the refresh response function also identified a region of dorsolateral PFC (– 45, 3, 34) that overlapped the dorsolateral area represented in Figure 1A. Activity in parietal cortex – an area of left precuneus, posterior cingulate (– 15, – 46, 43), medial precuneus (13, – 52, 35) and an area of supramarginal gyrus (– 54, – 47, 22) – was more correlated with this dorsolateral seed area for the refresh than for the act condition. Together, the results of Experiment 1 are consistent with the hypothesis that left lateral anterior PFC is involved in initiating processes and that left dorsolateral PFC is involved in refreshing specific information, perhaps in conjunction with parietal cortex (Raye et al., 2002; Wagner et al., 2005).

EXPERIMENT 2 (REFRESH *VS.* REHEARSE)

Refreshing can be conceptually and operationally distinguished from other reflective mental processes, for example, from *rehearsing*. Whereas *refreshing* is a discrete, briefer act of reflective attention directed toward a current

TABLE II

Brain areas identified in Experiment 1

Anatomical area	H	BA	X	Y	Z	Max F
Refresh > Read > Act						
^{1A}Middle frontal gyrus/Inferior frontal gyrus	L	**9,** (46,45)	– 49	14	26	7.89
Refresh, Act > Read						
^{1B}Superior frontal gyrus	L	**10**,(9)	– 34	50	22	6.84
Precuneus	ML	**7**	– 10	– 72	35	6.73
Act > Refresh, Read						
^{1C}Postcentral gyrus, Posterior insula	R	**40**,13/41	54	– 21	15	13.64
^{1D}Superior temporal gyrus, Pre and Postcentral gyri	L	40,2/**42**,44,6	– 55	– 21	18	20.13
Thalamus	ML		– 12	– 20	6	8.43
Cingulate gyrus, Medial frontal gyrus	M	**24**,6/31,32	– 5	– 6	47	17.28
Medial frontal gyrus, (Superior frontal gyrus)	M	**6**	– 5	– 6	51	13.18
Inferior parietal lobule	R	**40**	51	– 47	44	8.93
Act > Refresh > Read						
Middle frontal gyrus, Superior frontal gyrus	R	**10**,(9)	28	52	19	6.71
Cingulate gyrus	M	**24**,32	– 5	– 3	39	11.67
Inferior parietal lobule	R	**40**	58	– 28	23	9.96
Inferior parietal lobule, Postcentral gryus	L	**40**,1,2,3	– 62	– 29	26	20.51
Inferior parietal lobule, Pre and Postcentral gyri	L	40,2/**4**,1/**3**	– 35	– 24	47	32.00
Precuneus	MR	**7**	5	– 52	43	6.11
Cerebellum	R		21	– 56	– 16	6.23
Refresh, Read > Act						
Lateral orbital gyrus	L	**47**	– 37	30	– 9	7.63
Middle temporal gyrus, (Inferior temporal gyrus)	L	21,**37**	– 42	– 47	– 5	5.43
Middle temporal gyrus	L	**22,21**	– 54	– 40	2	8.20
Read > Refresh > Act						
Precentral, (Middle frontal, Postcentral) gyri	R	**4**,6,(3)	23	– 22	47	9.36
Read > Act > Refresh						
Inferior occipital gyrus	L	18,**19**	– 40	– 84	– 5	6.77

Note. Superscripts in column 1 indicate corresponding figure. All areas showed a condition × time interaction with a minimum of 6 contiguous voxels each significant at $p < .00001$ (Forman et al., 1995). For identified areas, contrasts between conditions were performed on percent signal change at time 4 from time 1, $p < .05$. H: hemisphere, L: left, M: medial, R: right; BA: Brodmann area. For each area of activation, the major anatomical regions and BA numbers are listed in descending order of approximate size, with areas of approximately equal size indicated by a slash (parentheses indicate a small extent relative to other areas listed). Talairach coordinates (x, y, z) are shown for the voxel with the maximum F-value (BA in bold) in each area of activation.

representation, *rehearsing* typically involves one or more items cycled through several times over several seconds (e.g., Baddeley and Hitch, 1974). That is, refreshing is typically engaged and executed over hundreds of millisec rather than continuously over several seconds, as is rehearsing (Johnson et al., 2002).

Given these definitions, one possibility is that rehearsing consists of multiple refreshes. The multiple-entry, modular (MEM) model (Johnson, 1992; Johnson and Hirst, 1993; Johnson and Reeder, 1997), however, proposes that *refreshing* and *rehearsing* are distinct reflective cognitive operations (thus, refreshing could be used to foreground an item from a current rehearsal set). Evidence consistent with this is that rehearsing tends to be associated with activation in ventrolateral PFC in inferior frontal gyrus (Awh et al., 1996; Chein and Fiez, 2001; Ivry and Fiez, 2000; Paulesu et al., 1993; Smith and Jonides, 1999; Wagner et al., 2001), whereas refreshing tends to show activation in middle frontal gyrus (Johnson et al., 2003, 2004, 2005; Raye et al., 2002). The ventrolateral PFC activity in studies of working memory for verbal information is generally interpreted as reflecting a subvocal articulatory rehearsal of phonological information (e.g., Baddeley, 1998). The dorsolateral PFC activity in refresh studies is assumed to reflect attention to various types of activated information (e.g., spatial, visual, auditory). The correlation between activity in dorsolateral PFC and precuneus and supramarginal gyrus in Experiment 1 is consistent with this possibility (Wagner et al., 2005).

To explore these hypothesized differences between refreshing and rehearsing, Experiment 2 contrasted a refresh condition, in which participants were instructed to think back to a word's visual appearance, with a minimal rehearse condition in which they were instructed to subvocally rehearse a word's sound. Based on previous findings from studies of verbal rehearsal, we expected to see greater activity in ventrolateral PFC for rehearsing (e.g., Awh et al., 1996; Chein and Fiez, 2001; Smith and Jonides, 1999) and greater activity in dorsolateral PFC for refreshing (Johnson et al., 2005; Raye et al., 2002).

Rehearsal, by its nature, is useful for retaining several items in memory over a period of seconds, as long as the rehearsal loop is not disrupted. In contrast, the refresh process is more discrete, and more limited in duration and amount of information. To minimize differences in time on task, yet maximize the likelihood that participants would engage different processes in the two conditions, we compared a minimal verbal rehearsal process – one item, subvocally articulated twice – with refreshing the visual aspect of a single item. Thus, in the rehearsal condition we attempted to induce a minimal articulatory/phonological loop (Baddeley and Hitch, 1974), and in the refresh condition we attempted to induce a minimal attentional act to an active representation of a visual stimulus that was no longer perceptually present.

Method

Experimental Procedure and Materials

Stimuli were 160 words from the same pool used in Raye et al. (2002) and in Experiment 1. The trial timing was as in Experiment 1. On each trial, participants read a word presented in the center of the screen, which was followed either by a new word (*read* condition), a "V" signaling participants to think of the visual aspect of the word preceding the V (*refresh* condition), or an "S" signaling participants to say the just-previous word twice subvocally (*rehearse* condition). Each trial ended with the previously described arrow task, and participants pressed left or right buttons to indicate the direction of each arrow.

To compare the effect of refreshing and of rehearsing on long-term memory, participants took a surprise long-term recognition memory test about 5 minutes after exiting the scanner. Old words were intermixed with new words, which were matched with the old words in frequency and length, and participants indicated via button press whether or not they had experienced each word while they were in the scanner. Each word was presented via computer for 2 sec with a 1 sec interstimulus interval.

Results and Discussion

fMRI Results

As predicted, and as shown in Figure 2, there was a dissociation between refresh-related and rehearse-related neural activity. There was greater activity on refresh than rehearse trials in two areas, left BA 9 middle frontal gyrus (Figure 2A), and left BA 6 precentral and middle frontal gyri (Figure 2B). Both of these areas were identified as refresh-related areas in our previous meta-analysis (Johnson et al., 2005). In contrast, an area of ventrolateral PFC, primarily BA 44 left inferior frontal gyrus, tended to show greater activity in the rehearse than the refresh condition ($p < .10$); see Figure 2C. Subsequent analysis of the subset of this ventrolateral PFC area that included Broca's area (Figure 2D; – 45, 4, 22) showed greater activity in the rehearse than refresh condition ($p < .04$), and greater activity in both the rehearse ($p < .001$) and refresh ($p < .04$) condition compared to the read condition. This superior region of Broca's area is very similar to the area (– 43, 7, 26) that

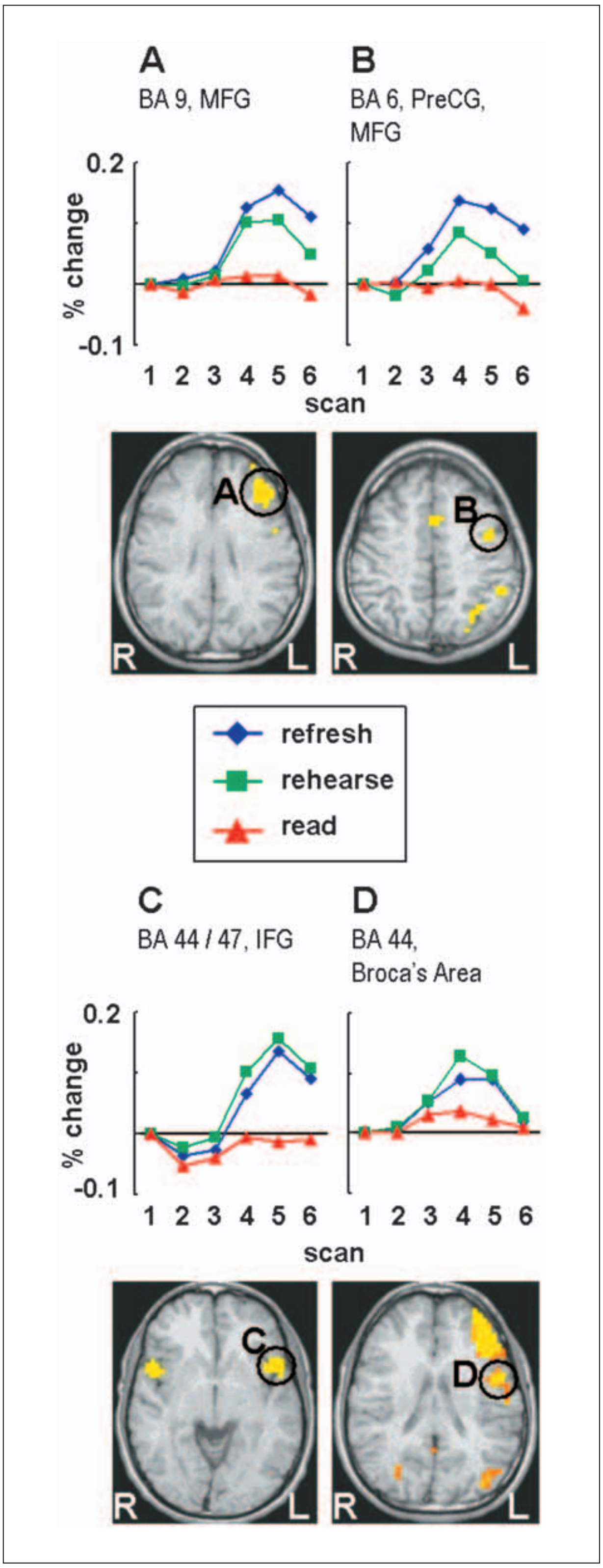

Fig. 2 – *Experiment 2. (A, B) Left prefrontal areas showing greater activity in refresh than rehearse condition; MFG = middle frontal gyrus; PreCG = pre-central gyrus. (C) Left ventrolateral area; IFG = inferior frontal gyrus and (D) Broca's area from same area represented in Fig 2C, showing greater activity in rehearse than refresh condition. Slices were chosen to show representative areas of activation.*

TABLE III

Brain areas identified in Experiment 2

Anatomical area	H	BA	X	Y	Z	Max F
Refresh > Rehearse > Read						
^{2A}Middle frontal gyrus, (Superior frontal gyrus)	L	**9**,46/10	– 38	34	31	11.1
^{2B}Precentral gyrus, Middle frontal gyrus	L	**6**	– 40	– 1	47	6.47
^{3A}Superior parietal lobule, Intraparietal sulcus, Superior occipital gyrus	L	**7**,19	– 30	– 65	51	6.35
Medial frontal gyrus, Anterior cingulate gyrus	M	**6**,(32)	– 1	1	55	9.34
Refresh > Rehearse, Read						
Middle temporal gyrus, (Inferior temporal gyrus)	L	**37**,20	– 53	– 51	– 5	7.08
Rehearse > Refresh > Read						
^{2C}Inferior frontal gyrus, (Precentral/Superior temporal gyri/insula)[a]	L	**44**/47(22,13)	– 48	14	2	8.62
^{2D}Broca's area: Inferior frontal gyrus, (Precentral gyrus)	L	**44**(6)	– 45	4	22	5.72
Refresh, Rehearse > Read						
^{3B}Inferior parietal lobule, Supramarginal gyrus	L	**40**	– 46	– 43	43	6.86
Inferior frontal/precentral, Superior temporal gyri	R	**44**,6,22	49	14	3	8.56
Read > Refresh, Rehearse						
Fusiform, Middle occipital, Lingual gyri	L	**18**(19,17)	– 25	– 84	– 9	7.91
Lingual, Middle occipital/ Fusiform gyri	R	**18**(19,17)	18	– 82	– 8	10.1

Note. Superscripts in column 1 indicate corresponding figure. Listed areas showed a condition × time interaction with a minimum of 6 contiguous voxels (Forman et al., 1995), each voxel significant at $p < .000001$, for an ANOVA including refresh, rehearse, and read. For identified areas, contrasts between conditions were performed on percent signal change from time 1 at times 4 and 5, $p < .05$ ([a]rehearse > refresh, $p < .10$). H: hemisphere, L: left, M: medial, R: right; BA: Brodmann area. For each area of activation, the major anatomical regions and BA numbers are listed in descending order of approximate size, with areas of approximately equal size indicated by a slash (parentheses indicate a small extent relative to other areas listed). Talairach coordinates (x, y, z) are shown for the voxel with the maximum F-value (BA in bold) in each area of activation.

Chein et al. (2002) suggested is related to the setup of an articulatory rehearsal program (i.e., phonological loop).

Table III lists all other areas identified as showing condition × time interactions in Experiment 2 in our primary analysis. In addition to left dorsolateral PFC, there was greater activity in the refresh than the rehearse condition in left superior parietal lobule (see Figure 3A), medial frontal gyrus and middle temporal gyrus. Interestingly, activity for refreshing and rehearsing was equal, and greater than in the read condition, in an area of left inferior parietal lobule (see Figure 3B). The fact that refreshing and rehearsing showed similar activity in one region of parietal cortex, but refreshing showed greater activity in another region of parietal cortex, is consistent with other evidence suggesting differentiation of function in regions of parietal cortex (Wagner et al., 2005).

Because the purpose of this experiment was to investigate the neural differences between refresh and rehearse, we looked more closely at these two conditions by directly comparing refresh and rehearse trials at more liberal thresholds (see Table IV). Areas of right middle occipital gyrus and precuneus showed greater activity in the refresh than rehearse condition, and areas of right and left pre- and postcentral gyrus, left superior temporal gyrus, and right and left parahippocampal and lingual gyri, showed greater activity in the rehearse than refresh condition.

Similar to the correlational analyses in Experiment 1, in separate analyses we modeled the refresh and the rehearse hemodynamic response functions and then used areas identified in each analysis as seeds for correlational analyses. A left dorsolateral PFC seed area (– 41, 22, 26; middle frontal gyrus, BA 46,9) found from modeling the refresh hemodynamic response function was significantly more correlated with activity in left inferior parietal cortex (angular gyrus, – 30, – 54, 35) and middle temporal gyrus (– 54, – 51, 2) in the refresh than the rehearse condition. A seed area of left inferior frontal/precentral gyrus (– 52, 3, 18;

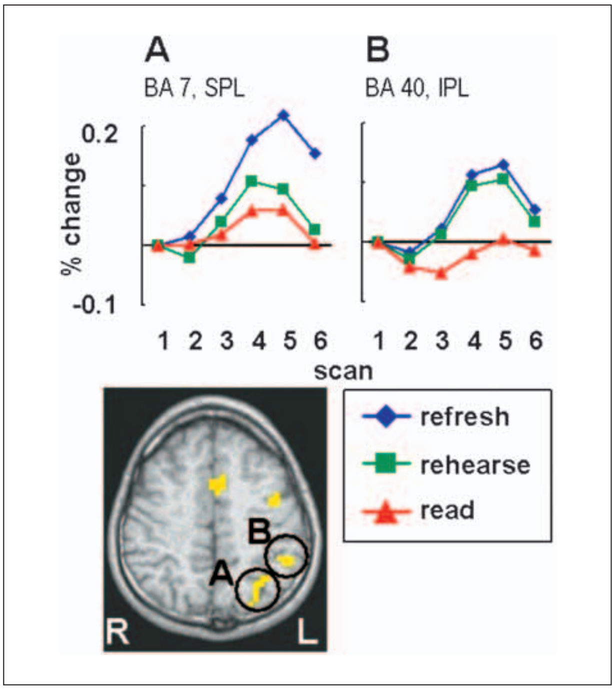

Fig. 3 – *(A) Area of left superior parietal lobule (SPL) showing greater activity in refresh than rehearse condition. (B) Area of left inferior parietal lobule (IPL) showing no difference in activity in refresh and rehearse conditions.*

TABLE IV

Brain areas identified in Experiment 2 in comparison of refresh and rehearse only

Anatomical area	H	BA	X	Y	Z	Max F
		Refresh > Rehearse				
Middle occipital gyrus (Precuneus)[a]	R	**19**(31)	29	–74	23	5.76
Precuneus[a]	ML	**7**	–10	–68	43	7.14
		Rehearse > Refresh				
Postcentral gyrus[a]	L	**43**	–51	–14	18	7.38
Postcentral gyrus[b]	R	**3**	42	–21	44	3.90
Precentral, Postcentral gyrus[b]	R	6,**43**(4)	58	–8	23	5.84
Superior temporal gyrus[b]	L	22,**42**	–50	–36	18	3.96
Parahippocampal gyrus[b]	R	**36**	20	–41	–8	4.54
Lingual gyrus[b]	R	**19**	17	–56	–1	4.54
Parahippocampal/Lingual gyri (Cerebellum)[b]	L	**36/19**	–18	–53	–9	5.24
Calcarine sulcus, Cuneus, Posterior cingulate[b]	R	**17/18**,30	6	–71	11	4.76

Note. Listed regions showed a condition (refresh, rehearse) × time interaction with a minimum of 6 contiguous voxels (Forman et al., 1995) each voxel significant at $p < .001$ (a) or .01 (b). Regions listed in Table III showing differences between refresh and rehearse are not repeated here. H: hemisphere, L: left, M: medial, R: right; BA: Brodmann area. For each area of activation, the major anatomical regions and BA numbers are listed in descending order of approximate size, with areas of approximately equal size indicated by a slash (parentheses indicate a small extent relative to other areas listed). Talairach coordinates (x, y, z) are shown for the voxel with the maximum F-value (BA in bold) in each area of activation.

BA 6/44) found from modeling the hemodynamic response function for rehearse trials was significantly more correlated with activity in left and right lingual gyrus (–6, –72, –2; 14, –75, 2; BA 18) in the rehearse than refresh condition.

The fact that, as predicted, dorsolateral PFC showed greater activation in the refresh condition while ventrolateral PFC showed greater activation in the rehearse condition supports the hypothesis that refreshing and rehearsing are different reflective processes. The greater activity in left middle temporal gyrus, left superior parietal lobule, and left precuneus in the refresh than rehearse condition, when participants were told to refresh the visual characteristics of words, is consistent with other findings suggesting that these areas are involved in the representation of visual information (e.g., Alivisatos and Petrides, 1997; Ishai et al., 2002; Raij, 1999; Wagner et al., 2005). Furthermore, in the rehearse condition, we found activity in inferior frontal gyrus, particularly in a dorsal region of Broca's area, consistent with Chein et al.'s (2002) proposal that this area is involved in setting up a rehearsal loop, and in superior temporal gyrus, which has also been associated with verbal working memory (Chein and Fiez, 2001). The similarities in the activity in the pre- and post-central gyri in the rehearse condition of Experiment 2 and the act condition of Experiment 1 suggest that activity in this area may reflect motor components of subvocal rehearsal (Ivry and Fiez, 2000). We take the activity in Broca's area, superior temporal gyrus, and pre- and post-central gyrus in the present study to reflect the engagement of a minimal phonological loop that could be used to maintain verbal information over longer intervals than investigated here, for example, several seconds (Baddeley and Hitch, 1974; Smith and Jonides, 1999).

Finally, the greater activity in parahippocampal gyrus in the rehearse than refresh condition is interesting. Previous studies have shown activity in parahippocampal gyrus is associated with later long-term memory (e.g., Brewer et al., 1998; Wagner et al., 1998). Our findings suggest that the slightly more extended processing required in the rehearse than refresh condition may increase the probability that parahippocampus is engaged. This is consistent with a common purpose of rehearsal – to increase the probability of later memory (e.g., Rundus, 1971). However, our behavioral results suggest that it may take more than the minimum rehearsal to see a long-term memory benefit over a single refresh.

Behavioral Results

An ANOVA of participants' d-prime scores on the surprise long-term memory test showed a main effect of condition [$F(2, 32) = 4.83$, $MSE = .07$, $p = .01$]. Subsequent planned contrasts indicated that refreshing (mean = 1.38) and rehearsing (mean = 1.41) both improved long term memory compared to reading an item once (mean = 1.15) (p's $< .05$); refresh and rehearse did not differ. These behavioral results, in combination with the fMRI data, illustrate that there can be different processing routes to the same level of memory performance.

GENERAL DISCUSSION

Previously we identified PFC regions associated with refreshing just-activated information (e.g., Johnson et al., 2005; Raye et al., 2002). The present experiments provide new evidence for two main points. First, Experiment 1 indicates a dissociation of function of left anterior and dorsolateral PFC. As Johnson et al. (2005) proposed, anterior PFC appears to have a more general executive role, for example, in initiating processes; it was equally active when participants were cued to press a button as when participants were cued to mentally refresh an item. In addition, on refresh trials anterior PFC was more correlated with an area of dorsolateral PFC previously shown to be refresh-related, while on act trials anterior PFC was more correlated with an area of pre-postcentral gyrus associated with sensory-motor processing (see Sakai and Passingham, 2003, for consistent findings). The similarity in activations in anterior PFC for two quite different processes (initiating a motor response and initiating a mental refresh operation) is consistent with the striking similarity in activation in this region during refreshing for a wide range of different types of information (Johnson et al., 2005, Figure 8D). Overall, these findings suggest a general executive function for this anterior PFC area, such as initiating a process or, perhaps, shifting between processes[1] (e.g., Johnson and Hirst, 1993).

In contrast to the similarity in activity in the refresh and act conditions in anterior PFC, left dorsolateral PFC showed greater activity during the refresh than act condition, consistent with the hypothesis that this region is engaged when the task involves foregrounding a specific representation of recently activated information (e.g., Druzgal and D'Esposito, 2003; Goldman-Rakic, 1987). It is interesting to note that the coordinates for the dorsolateral PFC area in Figure 1A (– 49, 14, 26) are similar to the coordinates (– 41, 18, 28) reported by MacDonald et al. (2000) in a Stroop study that involved saying a word (a color name, e.g. 'red') or naming its print color (blue) depending on the instruction-word (*read* or *color*) that preceded each trial. Because reading words is automatic, it is possible that participants refreshed the *color* instruction but not the *read* instruction, in order to combat the prepotent reading response. Activity in left dorsolateral PFC was associated with trials cued by the immediately preceding instruction *color* but not trials cued by the immediately preceding instruction word *read*. This finding is consistent with the idea that refreshing is a minimal control (executive) mechanism that can be used to foreground relevant representations during cognitive tasks.

The second point supported by the current findings is that *refresh* and *rehearse* are functionally distinct cognitive operations (e.g., Johnson, 1992; Johnson and Hirst, 1993). In Experiment 2, refreshing was associated with greater activity in left dorsolateral PFC (Figure 2A and 2B), left superior parietal lobule, left middle temporal gyrus, and precuneus (Tables III and IV), whereas rehearsing was associated with greater activity in left ventrolateral PFC, especially Broca's area (Figure 2C-D), left and right pre and post-central gyri, left superior temporal gyrus, and parahippocampal gyrus (Table IV). This pattern argues against the idea that rehearsing verbal information is simply multiple refreshes and for the idea that refreshing and rehearsing play distinct roles in cognition (Johnson, 1992).

While we instructed participants in Experiment 2 to refresh the appearance of the words presented, we are not suggesting that the refresh process operates only on visual information. For example, Johnson et al. (2005, Experiment 4) reported a study that compared refreshing words presented auditorily with words presented visually. Notably, dorsolateral PFC activity was associated with refreshing auditory as well as visual words. Nevertheless, given evidence that activity in various areas of parietal cortex is associated with recollection of specific detail (e.g., Wagner et al., 2005), it is interesting that activity in left dorsolateral PFC was more correlated with activity in parietal cortex in the refresh than act condition (Experiment 1) and in the refresh than rehearse condition (Experiment 2).

Although our results are consistent with the idea that refreshing and rehearsing verbal information are distinct processes, the relation between refreshing and rehearsing of *nonverbal* information is an open question. It has been proposed that there is a separate rehearsal mechanism for sustaining nonverbal information over several seconds – a visuospatial sketchpad – analogous to the phonological loop (Baddeley and Hitch, 1974). One possibility is that nonverbal rehearsal consists of multiple refreshes of visual information. On the one hand, findings that show right ventrolateral activity associated with rehearsing spatial information and left or bilateral ventrolateral activity associated with rehearsing object information (D'Esposito et al., 1998; Smith et al., 1995) support the idea that *rehearsing* nonverbal information may be distinct from *refreshing* nonverbal information, which reliably activates left dorsolateral PFC (Johnson et al., 2005). However, refreshing nonverbal items sometimes also shows activity in right dorsal PFC (Johnson et al., 2005) and dorsal areas are sometimes reported in studies of nonverbal rehearsal (e.g., Courtney et al., 1996). Future fMRI studies that directly contrast refreshing and rehearsing nonverbal information are needed to explore the relation between neural activity associated with these processes. In any case, some of the variation in PFC activity associated with working memory for nonverbal as well as verbal information across studies varying in stimulus type, stimulus complexity, number of items to be maintained, retention interval, and amount of interference (e.g., D'Esposito et al., 1998) may, at least in part, reflect a mixture of rehearsing and

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[1] A ROI analysis in Experiment 2, in which we looked at only the slices in which this area had appeared in Experiment 1, showed a left lateral anterior area (-30, 50, 22) in which activity was greater in the refresh than the read ($p < .001$) and rehearse ($p < .04$) conditions but the difference between rehearse and read was not significant. Why this area did not show significant differences between rehearse and read in Experiment 2 is not clear, but one possibility is that, for the specific tasks used here, initiating a minimal rehearsal loop was comparatively more automatic than refreshing or acting.

refreshing as needed to meet the demands of different tasks.

Activity in dorsolateral PFC in more complex tasks than those used here has been proposed to reflect selective attention and task management (Smith and Jonides, 1999), cognitive manipulation (D'Esposito et al., 1999; Petrides, 2000), representing a task context (Courtney, 2004; MacDonald et al., 2000; Miller and Cohen, 2001), or control in the face of interference (e.g., Johnson et al., 2005, Experiments 5 and 6b; MacDonald et al., 2000). These tasks all involve foregrounding some information so that it has (or it conveys to other information) a competitive advantage in ongoing cognition. It also seems likely that, as a basic executive function that momentarily foregrounds, selects, or briefly maintains information (Johnson et al., 2002, 2004), refreshing increases the probability that information will receive further processing (such as rehearsing, binding features, organizing, discovering semantic relations during encoding, evaluating source information during remembering) and can increase the probability that foregrounded/selected information will serve as a context that influences subsequent processing (e.g., Miller and Cohen, 2001).

Investigators have also speculated about the role of lateral anterior PFC (sometimes called frontopolar or rostrolateral PFC), noting that anterior PFC, like dorsolateral PFC, tends to be more likely to be recruited with increasing task complexity (e.g., Christoff and Gabrieli, 2000). Anterior PFC has been proposed to be involved in establishing a task set (e.g., Lepage et al., 2000; Passingham and Sakai, 2004), maintaining information about current contexts and goals (Courtney, 2004), monitoring and integrating subgoals (Braver and Bongiolatti, 2002; or 'branching' Koechlin et al., 1999), reallocation of visual attention (Pollmann, 2001), or evaluation of self-generated information (Christoff and Gabrieli, 2000). A common theme among these ideas, consistent with the present results, is that anterior PFC involves initiating or shifting between agendas, active representations, or stimulus features.

Together, then, this suggests that anterior PFC may play a role in initiating (or shifting between) different agendas, which may be represented elsewhere, and dorsolateral PFC plays a role when the relevant agenda involves refreshing of recently activated representations of specific information (e.g., a word, location, face, category of information) that may be represented elsewhere. This would be consistent with the general idea that PFC operates by influencing (biasing) processing in other regions, and that there may be differences in the types of representations (e.g., perceptual information, agendas, motor programs) that different subregions of PFC typically influence (e.g., Miller and Cohen, 2001).

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