Similar and dissociable mechanisms for attention to internal versus external information

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ABSTRACT

We compared two attentional executive processes: *updating*, which involved attending to a perceptually present stimulus, and *refreshing*, which involved attending to a mentally active representation of a stimulus no longer perceptually present. In separate blocks, participants either replaced a word being held in working memory with a different word (update), or they thought back to a just previously seen word that was no longer perceptually present (refresh). Bilateral areas of frontal cortex, supplementary motor area, and parietal cortex were similarly active for both updating and refreshing, suggesting that a common network of areas is recruited to bring information to the current focus of attention. In a direct comparison of update and refresh, regions more active for update than refresh included regions primarily in right frontal cortex, as well as bilateral posterior visual processing regions. Regions more active for refresh than update included regions primarily in left dorsolateral frontal and left temporal cortex and bilateral inferior frontal cortex. These findings help account for the similarity in areas activated across different cognitive tasks and may help specify the particular executive processes engaged in more complex tasks.

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Introduction

A common fronto-parietal network of areas (lateral prefrontal cortex, parietal cortex and supplementary motor area) is active in many cognitive tasks (Cabeza and Nyberg, 2000; Duncan and Owen, 2000) including working memory (WM), visual attention (Kelley et al., 2007; Serences et al., 2005; Serences and Yantis, 2007; Marois et al., 2004), and encoding (Blumenfeld and Ranganath, 2007) and retrieval from long term memory (Cabeza et al., 2008). This similarity of activity is consistent with the idea that common component processes are recruited for diverse cognitive tasks (Duncan and Owen, 2000; Cabeza and Nyberg, 2000; Johnson and Hirst, 1993; see also Awh and Jonides, 2001, Awh et al., 2006). Characterizing these components more specifically is a major challenge for cognitive science.

Two component executive processes that might, in part, account for this common activation across experiments are *updating* (Roth et al., 2006) and *refreshing* (Johnson et al., 2005). Updating, the replacement of an item actively being maintained in working memory with a different item, produces activity in a network including left inferior frontal junction (IFJ, the junction of inferior frontal sulcus and

inferior precentral sulcus), dorsolateral prefrontal cortex (DLPFC), supplementary motor area (SMA), and bilateral parietal cortex including intraparietal sulcus (IPS). This network becomes active during updating of different types of visual stimuli (Roth et al., 2006), updating from a sensory stimulus or an item from long term memory (Roth and Courtney, 2007), and when the rule operating on a stimulus is updated (Montojo and Courtney, 2008). Refreshing is the process of attending to information that is not perceptually present but is momentarily active from either recent perception or thought (e.g., thinking back to a just-seen stimulus no longer on the screen; Raye et al., 2002; Johnson et al., 2005). Refreshing produces activity in a network including DLPFC, anterior cingulate cortex (ACC), supramarginal gyrus (SMG), IPS, and middle temporal gyrus, for a variety of types of stimuli (Johnson et al., 2005; Raye et al., 2002, 2007).

Similarities in activation for updating and refreshing across experiments have been noted before (Courtney et al., 2007), but this is the first experiment to directly compare them. One possibility is that updating and refreshing are the same process investigated in the context of different experimental paradigms and under different names. If so, we would expect refreshing and updating to produce the same patterns of activation in the same participants in procedures using the same materials. On the other hand, updating has been proposed as a specific mechanism for changing the contents of what is being actively maintained in working memory by prioritizing new information that is concurrently perceived or retrieved. Refreshing has

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been proposed as a general mechanism for briefly bringing information that is currently active but not perceptually present to the foreground of attention. Update and refresh may involve different areas of cortex. For example, updating should show relatively greater activity in posterior visual processing regions as a new target is perceptually attended, and refreshing should show relatively greater activity in frontal regions (e.g., left DLPFC) associated with modulating representations of no longer present perceptual stimuli (M.R. Johnson et al., 2007).

Assuming that there is a distinction between the cognitive operations and neural activity involved in perceptual vs. reflective attention (e.g., Dobbins and Han, 2006; Gilbert, Frith and Burgess, 2005; Johnson et al., 2005; Johnson and Johnson, in press), directly comparing the neural correlates of updating working memory from a perceptually present stimulus with refreshing an active representation of a stimulus that is no longer perceptually present should help clarify similarities and differences in neural activity observed in more complex cognitive tasks that recruit these processes.

Methods

Participants

Participants were 22 (12 females) healthy adult ($M = 24$ yrs, range 19–44) non-smokers, with no history of head injury, psychiatric illness, drug or alcohol abuse, and no current medications that would affect the function of the brain, heart or blood circulation. Participants were compensated and all gave written informed consent. The experiments were undertaken with the approval of Yale University School of Medicine Human Investigation Committee, and in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association.

Procedure

Immediately before the fMRI scan, participants had a practice session. They read task instructions, listened to verbal instructions, and performed one practice block of each condition (update, refresh) with experimenter feedback. They then performed, in random order, three blocks of each condition without feedback (performance was monitored to determine that they were doing the task correctly). Each practice block was 64.5 s.

There were 6 fMRI experimental runs. Within each run there were 4 blocks of each type (update and refresh), presented pseudorandomly and counterbalanced within run and across scan session.

Task blocks were nearly identical in task set-up. Different geometric shapes were used as cues for update (triangles), refresh (circles) and control (squares) conditions. Otherwise the stimulus presentation was the same. In both update and refresh blocks, words appeared on the screen one at a time and participants were instructed to read them silently.

Update blocks

In update blocks, there were four event types: *read* (words that did not match the word currently maintained in WM), *update* WM, *match*, and *control*. Participants were given a word to maintain in WM and sometimes were cued (with a row of triangles) to replace the word currently being held in WM with the next word to appear on the screen (update; see Fig. 1). Thus, in update blocks, participants always maintained one word as the sample stimulus in WM while reading other words, and their task was to determine whether each word they read matched or did not match the word being maintained. If the word on the screen matched the item in WM, participants responded with a button press (match). Occasionally they saw a row of squares, a "null"
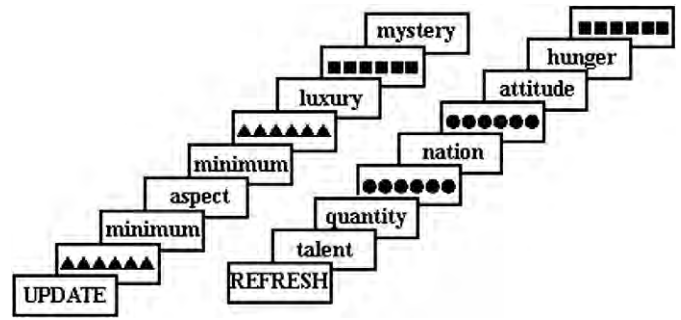

Fig. 1. Task design. First participants were cued with the block type, update or refresh. In each block they read each word. In update blocks they were to maintain one word in working memory at all times while reading the stream of words. A row of triangles cued them to update working memory by replacing the current contents of working memory with the subsequent word in the stream. (In update blocks, when they saw a word in the stream that matched the contents of working memory they pressed a button.) All update blocks began with the update cue so that participants immediately maintained an item in working memory. In refresh blocks, a row of dots cued them to think back to the just-previous word. In both block types the control event was a row of squares. Participants were instructed to look at the squares and wait for the next word. Within each block, events occurred pseudorandomly with an update, refresh or control cue every 3–20 s (mean time between cues was 10.5 s). Each word or cue appeared on the screen for 1 s with a 500 ms interstimulus interval containing a visual mask (row of plus signs not shown).

cue acting as a sensory control event (control), and they were instructed to look at the squares, but continue to maintain the current sample in WM and wait for the next word. Participants were to press a button only when the item on the screen matched the contents of working memory (match).

Refresh blocks

As in update blocks, single words appeared on the screen one at a time and participants were instructed to read them. Within refresh blocks, there were four event types: *read*, *refresh*, *control*, and *match*. During refresh blocks participants performed a modified version of a refresh task (see Fig. 1; Raye et al., 2002). Occasionally, instead of a word, they saw a row of dots which cued participants to think back to the word that preceded the refresh cue (refresh event). They were instructed to think back to that word once, and not continue to think of it. Occasionally they saw a row of squares that cued them to look at the squares and wait for the next word; this served as a sensory control event in which they saw a row of geometric stimuli, as in refresh trials, but were not asked to refresh. Occasionally participants read a word they had recently refreshed; these 'match' events were included to parallel match events in update trials. Read events corresponded to read trials from the non-match (read) trials in update blocks. Participants were not required to make any button press responses during the refresh blocks.

Stimulus presentation

Before each block, a cue ("UPDATE" or "REFRESH") appeared for 1 s (Fig. 1). Within each block, events occurred pseudorandomly with an update (or refresh) cue every 3–20 s (mean time between cues was 10.5 s). All events were counterbalanced such that each event type preceded and followed every other event type equally often. Each word or cue appeared on the screen for 1 s with a 500 ms interstimulus interval containing a visual mask (row of plus signs). The row of plus signs subtended the same visual angle as the longest word. During the practice session stimuli were presented on a Dell Inspiron 640 m laptop running EPrime software Version 1.1 (Psychology Software Tools), which also collected key press responses for match events in the update blocks. During the fMRI session, stimuli were projected onto a screen located behind the participant's head inside the bore of

the scanner. Participants viewed the stimuli via an angled mirror mounted on the head coil. Responses were collected via an MRI-compatible button box.

Stimuli were 24 repeated, 2- and 3-syllable abstract nouns (e.g., *method*, *concept*, *quality*, *miracle*). Each word appeared in 28-point Arial font centered on the screen in black lower-case font on a white background. In a pilot experiment, 23 participants evaluated words for imageability and emotionality on a 10 point rating scale. Words were eliminated whose scores on either rating were more than two standard deviations from the mean on either measure.

The 6 fMRI experimental runs each lasted 9 min 18 s, for a total of 55 min, 48 s of functional data collection. Each block lasted 64.5 s with a temporally jittered interblock interval where a row of pluses remained on the screen for 3–7.5 s. Across all scans there were 144 events of each type (update, refresh, read during the update task, read during the refresh task, match in the update task, match in the refresh task).

fMRI data acquisition

All scans were collected on a Siemens 3 T Trio scanner at the Magnetic Resonance Research Center, Yale University School of Medicine. Functional data were collected as T2*-weighted gradient echo, echo planar images (TR = 2000 ms, TE = 25 ms, flip angle = 80°, voxel size 3.438 × 3.438 mm, 3 mm axial slice, 1 mm gap, FOV = 22 cm, matrix = 64 × 64) during the experimental task. A high-resolution T1-weighted anatomical scan was collected between the 3rd and 4th functional scan runs (TR = 2530 ms, TE = 3.34, flip angle = 7°; FOV = 256 × 256).

fMRI analysis

Data were slicetime corrected and motion corrected with SPM5 as a standard lab preprocessing step. SPM software was not utilized after this point. Functional data were filtered with a 3rd order polynomial orthogonal function to correct for mean, linear drift and any third order nuisance variable. The frequency of change between block types is more frequent than the periodicity of a third order polynomial function, therefore this filter should not reduce statistical power. Anatomical and functional images were coregistered then morphed into MNI space using BioimageSuite software (Lacadie et al, 2008; Papademetris et al.; http://www.bioimagesuite.org). After preprocessing, fMRI data were analyzed using Analysis of Functional NeuroImages (AFNI) software (Cox, 1996). Data were normalized to have a mean of 100. Data for each voxel were analyzed via a simultaneous regression for all critical and control events (update, read in update, match in update, errors detecting match events, control in update, refresh, read in refresh, match in refresh, control in refresh, update and refresh block cues) as well as block regressors for each block type (update block and refresh block). This was a mixed block/event-related design. Each event included two stimuli. For example, an update event included the cue to update and the subsequent word to be maintained in working memory. For each event, the convolution of event regressors began with the onset of the first stimulus. Event regressors and block regressors both were convolved with a standard hemodynamic response function using the AFNI software waver program (delay time = 2 s, rise time = 3 s, fall time = 5 s, no undershoot; Cox, 1996). Block regressors modeled sustained activity within the two block types. Simultaneous regression with the block regressors and the event regressors allows for both sustained and transient components of the activity to be identified (Visscher et al., 2003). Given the temporal jitter of events within blocks, the correlation between block and each event regressor did not exceed .3, allowing for an efficient estimation of sustained and event-related activity. Interblock intervals were not modeled and contributed to the baseline.

For the purpose of creating regressors for the different event types, all events modeled in the fMRI analysis included two successive stimuli. An update event included the update cue and the subsequent word to be encoded into memory. Refresh events included the word to be refreshed (the just-previous item) and the refresh cue. Control events were modeled separately within update and refresh blocks. In each case, an "event" included two stimuli. In the update blocks control events consisted of the control cue and subsequent word to be read, and in refresh blocks, control events consisted of the control cue and the word preceding it. Read events, modeled separately within update and refresh blocks, included two words in a row to be read, that neither matched the contents of WM, each other, nor the word recently refreshed. Match events included the item that matched the contents of WM and the subsequent word to be read. Each of these events included two successive stimuli for the purpose of making particular direct comparisons. Within the update blocks direct comparisons were made between update events and control events. An update event included the cue to update and the subsequent word, which was to be brought to the current focus of attention and maintained in working memory; the control event included a null cue and a word to be read. The refresh event included a word to be read followed by the cue to refresh; thus, its control event included a word to be read followed by a "null" cue. For direct comparisons between update and refresh, in both cases, the item to be brought into the current focus of attention was the second stimulus of a two stimulus event. Block cue events included the instructional cue marking the beginning of the block and the subsequent fixation cue. The block cue event only included one stimulus and was included simply to account for the variance in signal associated with this cue.

Individual participant data were smoothed with a three dimensional 4 mm Gaussian kernel, then entered into a series of t-tests to compare events of interest, with participant as a random factor. To find regions of the brain differentially active for each condition, t-tests compared the following events: update versus control event within the update blocks, refresh versus control event within the refresh blocks, update versus refresh events, and update block versus refresh block. This last comparison of activity for the update block versus refresh block identified areas associated with sustained activity associated with WM maintenance since maintenance was required in update, but not refresh, blocks.

For each resulting t-map, individual voxel thresholds were set at p < 0.01. Voxelwise data were corrected for multiple comparisons by spatial extent of contiguous suprathreshold individual voxels (experiment-wise p < 0.01 for a cluster). A Monte Carlo simulation was run in the AFNI software package on a brain mask with 4 × 4 × 4 mm voxels, a smoothing kernel of 4 mm, connection radius of 5.2 mm, to determine that a 704 µl cluster satisfied a threshold of p < 0.01 (Forman et al., 1995).

To find regions of the brain similarly active in update events, refresh events, and sustained maintenance, we performed an overlap analysis of three Voxelwise t-maps: update versus control events, refresh versus control events, and update blocks versus refresh blocks. An overlap map was generated using AFNI software by weighting equally the active voxels from each input map and summing the inputs to yield a map where different sums corresponded to different combinations of active conditions from the input maps. The threshold for each of the three t-maps contributing to this overlap map was p < 0.01. Therefore, this is a conservative method for determining areas of overlap as each region of overlap must pass the threshold of two or more t-tests.

Results

Behavioral results

The percent correct (87.3%, standard error 2.5%) for the response to match to sample, and false alarm rate (0.17%, standard error 0.03%), in the update task indicated that participants effectively updated WM.

fMRI results

Overlap in executive function areas

Fig. 2 shows areas of activation associated with transient activity associated with update and refresh, sustained activity associated with working memory maintenance (identified with a sustained block regressor for the update blocks) and their overlap. As is clear from Fig. 2, update and refresh both (red areas) showed activity in bilateral areas of precentral gyrus and superior frontal junction (SFJ) including left IFJ, right middle frontal gyrus, SMA, bilateral inferior parietal lobule (IPL) and intraparietal sulcus (IPS), and an area of left posterior fusiform gyrus. Regions of left superior parietal cortex and right SMA were active for both update and maintenance (green areas). (See

Table 1; Supplementary Table 1 includes a complete list of regions for different combinations of overlap.)

Direct comparison of update and refresh

Areas more active for update than refresh events included right SFJ and superior frontal sulcus, right superior and middle frontal gyrus, and bilateral primary and secondary visual cortex, and cuneus (see Fig. 3, orange areas, and Table 1).

Regions more active for refresh than update events included left DLPFC (superior and middle frontal gyrus), bilateral inferior frontal gyrus (including left IFJ), anterior insula, SMA, and ACC, left IPL and left supramarginal gyrus, and left middle and superior temporal gyrus (see Fig. 3, purple areas, and Table 1).
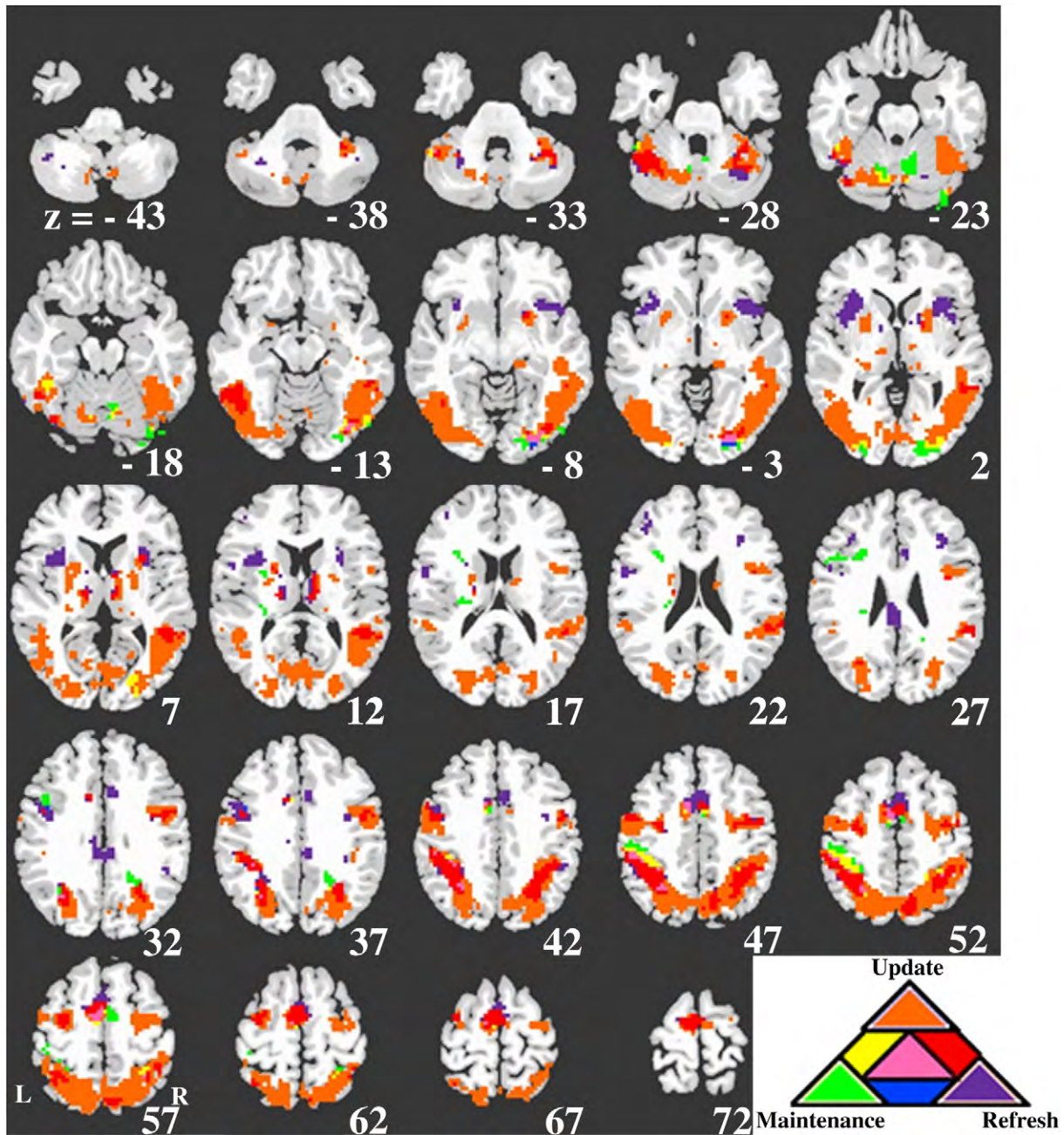

Fig. 2. Overlap analysis of update, refresh, and maintenance (see text). Regions significantly responsive to update are shown in orange, refresh in purple and maintenance in green. Regions responsive both to update and refresh are shown in red. Regions responsive both to update and maintenance are shown in yellow. Regions responsive to refresh and maintenance are shown in blue. Regions responsive to update, refresh and maintenance are shown in pink. The left side of the image represents the left side of the brain.

Table 1
Regions of overlap for update and refresh and regions active in the direct comparison of update and refresh.

Region	BA	Volume (μl)	MNI center of mass (mm)		
			X	Y	Z
Overlap of update and refresh					
Prefrontal					
L precentral gyrus/IFJ	6	1216	−50	−2	42
R MFG/precentral gyrus/SFJ	6	1730	44	−3	39
L SFJ	6	1568	−32	−8	55
Medial					
Bilateral SMA	6	3757	−4	−4	62
Parietal					
L inferior parietal/intraparietal sulcus	40	7838	−38	−48	44
R inferior parietal/intraparietal sulcus	40	5514	33	−52	44
R precuneus	7	1568	10	−70	52
Temporal					
L posterior fusiform/IT	19, 37	4811	−44	−57	−22
Update>refresh					
Prefrontal					
R SFJ/superior frontal sulcus	6	1000	32	−1	56
R SFG/MFG	10	568	27	42	−5
Occipital					
Bilateral primary and secondary visual cortex, cuneus	7, 17, 18, 19	42,379	2	−72	9
Refresh>update					
Prefrontal					
L SFG/superior frontal sulcus	8, 9, 10	**	−22	21	54
L MFG	8, 9, 46	**	−30	16	39
L SFG	6	**	−15	4	56
L IFG	47	**	−46	37	−8
R STG/IFG	38, 47	757	24	22	−23
R precentral gyrus, precentral sulcus, IFG	4, 6, 44	757	63	−3	19
L IFJ/IFG	44, 45	**	−55	12	27
L anterior insula	13	**	−45	9	−2
R anterior insula	13	**	41	4	−2
Medial					
Bilateral SMA	6, 8	**	−7	18	57
Bilateral preSMA	6, 8	3027	−2	−8	69
Bilateral ACC	32	**	−3	18	38
L ACC	24, 32	**	−7	43	1
Parietal					
L inferior parietal, postcentral gyrus	2, 40	**	−51	−29	47
L supramarginal gyrus	40	**	−55	−40	28
Temporal					
L MTG/STG	21, 22	3703	−60	−36	−8

Notes. R = right; L = left; ACC = anterior cingulate cortex; IFG = inferior frontal gyrus; IFJ = inferior frontal junction (junction of the precentral sulcus and inferior frontal sulcus); IT = inferior temporal gyrus; MFG = middle frontal gyrus; MTG = middle temporal gyrus; SFG = superior frontal gyrus; SFJ = superior frontal junction (junction of the precentral sulcus and superior frontal sulcus); SMA = supplementary motor area; STG = superior temporal gyrus. Brodmann areas are reported not only for the peak active voxel but for the entire active region. Only areas of overlap with volumes of 200 μl or greater are included in this table. For additional regions active in this contrast see Supplementary Table 1. **For the refresh>update contrast, there was a large cluster (85,191 μl) and coordinates for local maxima for subregions of this large cluster are reported instead of centers of mass.

Discussion

This study investigated two types of executive function: attending to a perceptual stimulus in order to replace a representation in WM (update) and attending to an active representation that is no longer perceptually present (refresh). We identified areas that were commonly active across these two types of executive function and areas that differed between these two executive functions.

Common regions of activation across types of executive function

In the present experiment, both updating and refreshing brought information into the focus of attention, either perceptually (update) or reflectively (refresh). For both processes, we found anatomical areas similar to those found in other experiments involving attending to information in various ways. For example, some areas in the current study that showed activity in both update and refresh, including left precentral gyrus, IFJ, SMA, and bilateral IPS and IPL, are similar to those involved in visual attention switching (Serences et al., 2004), task switching (Derrfuss et al., 2005), episodic and semantic long term memory retrieval (Shannon and Buckner, 2004; Nyberg et al., 2003), and to cues signaling the start of a task block (Dosenbach et al., 2006).

A recent study also examined regions of activation common across tasks involving bringing information into the focus of attention (Marklund et al., 2007). They directly compared transient activity during episodic and semantic long term memory and working memory to the transient activity during an attention task. Aside from ACC/preSMA (SMA in the current study), the regions common to update and refresh in our study, as would be expected, were not differentially active across the memory and attention conditions in the Marklund et al. study. If, as we argue, update and refresh are both involved in bringing information to the focus of attention, then we might expect that these common regions will be absent from comparisons where both conditions include such attentional processes.

Distinguishing elements of executive function

Although the commonality of activity across refreshing and updating was striking, equally important are the differences we observed. First, Fig. 2 shows that some areas exhibit a functional topography where immediately adjacent regions were responsive to different processes. For example in left superior parietal cortex, a region with diverse cell types, functional activity, and extensive connectivity to diverse regions (Rushworth et al., 2006; Nickel and Seitz, 2005; Scheperjans et al. 2008), there were adjacent regions showing activity for maintenance, both update and maintenance, update and refresh, and update. Similarly, different subregions were responsive to different elements of executive function in left IFJ and SMA.

A recent study by Dosenbach et al. (2006) also was directed at identifying common and distinct regions associated with executive functions. They compared 10 studies all conducted on the same scanner, and all using a mixed blocked/event-related design, and various types of cognitive tasks and materials. Comparing activations across studies, Dosenbach et al. (2006) identified regions of dorsal anterior cingulate cortex/medial superior frontal cortex (Talairach coordinates −1, 10, 46), and bilateral anterior insula (−35, 14, 5; 36, 16, 4) common across tasks and phases within tasks. They suggested that these regions form a core task set system. Consistent with this idea of a general purpose task set system, we found an area of SMA activation (see Supplementary Table 1) in the overlap of update, refresh, and maintenance within 2.5 voxels of their dorsal anterior cingulate cortex/medial superior frontal cortex area. Interestingly, in the refresh condition, three areas (bilateral SMA/ACC, and left and right anterior insula, see Supplementary Table 1) were within 7.3, 3 and 4.6 mm, respectively, of the three regions in Dosenbach et al.'s proposed core task set system. These findings suggest that refreshing may be a component of the kind of core task set system suggested by Dosenbach et al. In addition, both studies suggest that there may be more functional specificity within areas commonly reported in meta-analyses across diverse tasks (Cabeza and Nyberg, 2000; Duncan and Owen, 2000), and finer-grained information about such functional specificity should improve the accuracy of "reverse inferences" (Poldrack, 2006) about executive processes.

In the present study, the best evidence for differences in the neural substrates of the executive functions of updating and refreshing comes from a direct contrast between them under conditions where we held other factors (e.g., type of stimuli, control conditions, cue conditions) as similar as possible (Fig. 3). It is not surprising that
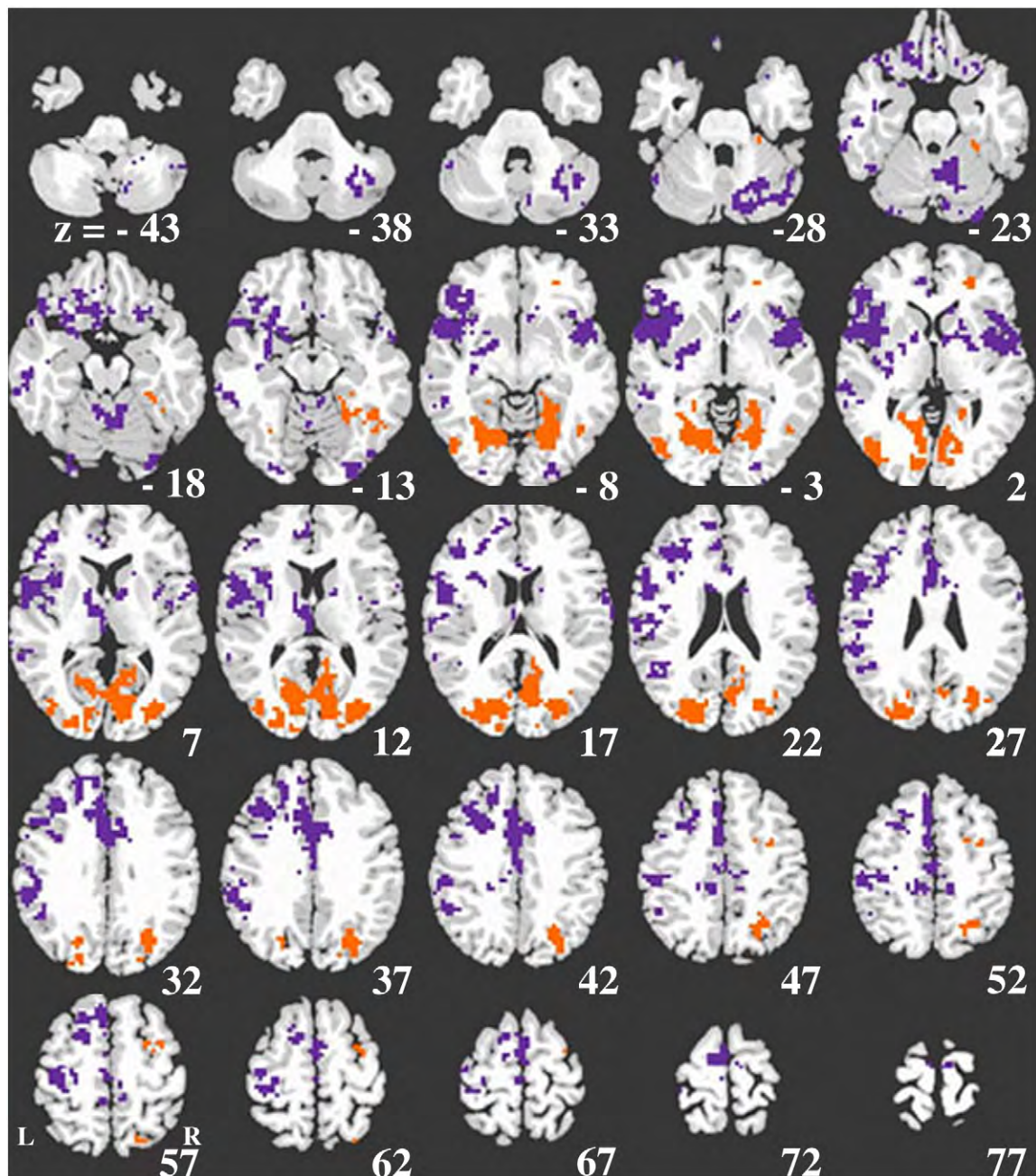
Fig. 3. Direct comparison of update and refresh. Refresh activity greater than update activity is shown in purple. Update activity greater than refresh activity is shown in orange. The left side of the image represents the left side of the brain.

regions more active for updating than refreshing included SFJ (often called the frontal eye fields), and areas of bilateral primary and secondary visual cortex and cuneus. These are regions commonly active in studies of perception and perceptual attention, and a primary difference between update and refresh conditions was that the critical item was perceptually present at the time of update and not refresh. Furthermore, SFJ has been associated with maintenance in WM (Courtney et al., 1998; Roth et al., 2006), further supporting the notion that SFJ activity in the update condition in the present study reflects a change in the state of the WM maintenance network (Roth et al., 2006). In addition, a region of right anterior frontal cortex (BA 10) was more active in update than refresh. It has been suggested that anterior frontal cortex (sometimes called frontopolar cortex) is recruited for complex tasks such as those involving monitoring and integrating subgoals (Braver and Bongiolatti, 2002), or contingent task switching or "branching" (Koechlin et al., 1999; Koechlin and Hyafil, 2007).

Compared to refresh, the update task likely involved more coordination of subgoals given that the task has several components — reading words while maintaining an item in working memory, assessing whether a word matches the maintained item, and occasionally replacing the maintained item. Greater activity in right BA 10 could reflect the simultaneous engagement of multiple, non-superordinate operations, and/or suspending one operation while another is performed (see Koechlin and Hyafil, 2007).

In the refresh task participants must reflectively attend to a representation of a word just seen but no longer present. Prior refresh studies found a network that includes regions similar to those in the present study that were significantly more active in refresh than update: left MFG, left SFG, ACC/MdPFC, and left SMG (Raye et al., 2002; Johnson et al., 2003, 2004, 2005; Raye et al., 2007, 2008). Furthermore, studies suggest that DLPFC is involved in modulating posterior representational areas (e.g., Johnson et al., 2007), while

anterior PFC (BA 10/SFG) is involved in initiating the refresh process (Raye et al., 2007, Experiment 1). We found an area of left superior frontal sulcus (largely BA 8, extending into BA 10) in the refresh>update contrast. This area was somewhat posterior and superior to the right BA 10 area where update was greater than refresh. Although these are not exactly homologous areas, these findings may suggest some lateralization of perceptual attention (right PFC) and reflective attention (left PFC). Activity in BA 10 has been hypothesized to be involved in the evaluation of internally generated information (Christoff et al., 2003) relative to the evaluation of information in the perceptual environment, and switching between stimulus-oriented and stimulus-independent thought (Gilbert et al., 2005). In a refresh event in the present experiment the participant first sees a cue (stimulus-oriented thought) then must reactivate a representation of information no longer present (stimulus-independent thought).

Although our focus is on update and refresh, we should note that there were regions of left ventrolateral PFC that were active for *maintenance* (i.e., maintaining an item in working memory in the update task), as would be expected (Smith and Jonides, 1999; see green regions in Fig. 2 and Supplementary Table 1). There were very few regions where update, refresh, or both overlapped with areas associated with maintenance, as noted (see Supplementary Table 1). These findings are consistent with the idea that refresh and update are involved in brief attentional processes that are different from process (es) typically involved in *sustaining* information over intervals of several seconds (see Raye et al. (2007), Exp 2, for additional evidence differentiating refreshing and rehearsing and Roth et al. (2006), for additional evidence differentiating updating from maintenance). Similarly there is a dissociation of regions involved in the sustained vs. transient control of task switching (Braver et al., 2003). Only a few small regions were responsive to update, refresh and maintenance. Interestingly, these areas (SMA, middle occipital, and parietal, see Fig. 2 and Supplementary Table 1) were located directly adjacent to regions active for both update and maintenance, providing further support that updating involves a change in the state of the maintenance system.

Additional studies involving direct comparison of putatively different executive functions are necessary to identify the common and distinct regions involved when information enters the current focus of attention, as in studies of perceptual attention (Yantis and Serences, 2003), selection of information via priority changes (Courtney et al., 2007), task updating (Derrfuss et al., 2005), component processes of executive function (e.g., *initiating*, *noting*, Johnson et al., 2003; Raye et al., 2007), or shifts in context (Miller and Cohen, 2001; MacDonald et al., 2000). Such studies would help disambiguate the functional relevance of similarity and differences in areas activated across experiments, which reflect unspecified combinations of perceptual and reflective attentional demands of complex tasks. That is, such studies would clarify the component processes of executive function as discussed in several models (Cowan, 2008; Johnson and Hirst, 1993; Kane and Engle, 2000; Miyake et al., 2001).

Conclusions

The current results indicate that it is possible to separate executive functioning into regions commonly active across different executive functions and regions more specific to particular functions such as attending to an incoming stimulus to replace a maintained stimulus (update) or attending to an already active representation (refresh). Updating and refreshing are two mechanisms for bringing information into the focus of conscious attention. We would expect the network of commonly active regions found for updating and refreshing to be found also in within-participant comparisons of update or refresh with other tasks requiring changes in which information is currently attended (e.g., visual attention switching,

monitoring information in short term memory or retrieved from long term memory), providing further evidence of a similarity of function across diverse executive processes. Such studies would also clarify differences in executive functions by identifying differences in their neural signatures.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.07.002.

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