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Electrophysiological correlates of refreshing: Event-related potentials associated with directing reflective attention to face, scene, or word representations

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Abstract

Refreshing is the component cognitive process of directing reflective attention to one of several active mental representations. Previous studies using functional magnetic resonance imaging (fMRI) suggested that refresh tasks involve a component process of *initiating* refreshing as well as the top-down modulation of representational regions central to refreshing. However, those studies were limited by fMRI's low temporal resolution. In the present study, we used electroencephalography (EEG) to examine the timecourse of refreshing on the scale of milliseconds rather than seconds. Event-related potential (ERP) analyses showed that a typical refresh task does have a distinct electrophysiological response as compared to a control condition, and includes at least two main temporal components: an earlier (~400ms) positive peak reminiscent of a P3 response, and a later (~800ms–1400ms) sustained positivity over several sites reminiscent of the late directing attention positivity (LDAP). Overall, the evoked potentials for refreshing representations from three different visual categories (faces, scenes, words) were similar, but multivariate pattern analysis (MVPA) showed that some category information was nonetheless present in the EEG signal. When related to previous fMRI studies, these results are consistent with a two-phase model, with the first phase dominated by frontal control signals involved in *initiating* refreshing and the second by the top-down modulation of posterior perceptual cortical areas that constitutes refreshing a representation. This study also lays the foundation for future studies of the neural correlates of reflective attention at a finer temporal resolution than is possible using fMRI.

Introduction

Recently, interest has grown in studying the similarities and differences between two types of attention: externally directed or *perceptual* attention, and internally directed or *reflective* attention (M. K. Johnson et al., 2005; for review: Chun, Golomb, & Turk-Browne, 2011; Chun & M. K. Johnson, 2011). These two types of attention involve activity in highly overlapping networks of brain regions related to executive function and have similar modulatory effects on posterior areas of cortex related to perceptual processing (e.g., M. R. Johnson & M. K. Johnson, 2009a; M. R. Johnson, Mitchell, Raye, D'Esposito, & M. K.

Johnson, 2007; Lepsien & Nobre, 2007; Wojciulik, Kanwisher, & Driver, 1998). Although reflective attention, as a means of limiting and shaping information flow, is as central to the study of thought as perceptual attention is to the study of the senses, difficulties controlling or even ascertaining the target of reflective attention in the lab — versus the relative ease of providing a controlled perceptual environment — pose special challenges for reflective attention research.

One way of addressing such challenges is to focus on relatively simple, constrained reflective processes such as *refreshing*: the act of thinking of, or foregrounding, one of several active mental representations via reflective attention, similar to highlighting one of several present sensory stimuli via perceptual attention (M. K. Johnson, Reeder, Raye, & Mitchell, 2002). Refreshing is thought to be a key process for selecting, maintaining, and manipulating information within working memory (Chun & M. K. Johnson, 2011). It is proposed to be different from *rehearsing* in that rehearsing typically involves recycling multiple items over several seconds or minutes via a phonological looping processes (Baddeley, 2012). A typical task for studying refreshing might begin by displaying 1–3 items (e.g., words, pictures, or other stimuli), followed by a short delay (e.g., 400–1500ms) and then a cue indicating that the participant should think back to one item (e.g., verbalize a cued word, visualize a cued picture, etc., depending on modality). Neuroimaging investigations have shown that refreshing reliably activates left dorsolateral prefrontal cortex (DLPFC; M. K. Johnson et al., 2005) and parietal cortex (Raye, M. K. Johnson, Mitchell, Reeder, & Greene, 2002; Raye, Mitchell, Reeder, Greene, & M. K. Johnson, 2008) and is capable of both enhancing and suppressing activity in high-level representational areas in visual cortex (M. R. Johnson & M. K. Johnson, 2009a). Baddeley (2012, p. 23) has suggested that refreshing may underlie the visual-spatial sketch-pad and/or maintenance in the episodic buffer in his model of working memory. This would be consistent with evidence that refreshing is not specific to modality of input (e.g., can occur for either visual or auditory information; M. K. Johnson et al., 2005, Experiment 4), and the suggestion that refreshing could operate not only on information that has just been perceived, but also on information that is being reflectively rehearsed; thus refreshing may be a critical component in tasks that require manipulation such as updating (e.g., n-back, Cohen et al., 1997) or alphabetizing (D'Esposito, Postle, Ballard, & Lease, 1999). Refreshing has been referred to as a "minimal" executive process (Raye, M. K. Johnson, Mitchell, Greene, & M. R. Johnson, 2007), but the brain activity associated with refreshing can vary depending on task demands. For example, increasing the number of potential candidates for refreshing increases activity in anterior cingulate cortex (M. K. Johnson et al., 2005; Raye et al., 2008).

Although refreshing — a single, brief instance of directing reflective attention — is one of the simplest executive functions a participant might be asked to perform, its operationalization in experimental task paradigms may invoke additional reflective component processes (M. K. Johnson, 1992). For example, in addition to the theoretical component process of refreshing (the mental foregrounding of a particular representation, with concomitant enhancement of appropriate brain activity patterns), a refresh *task* procedure may require participants to *initiate* (i.e., switch between) tasks. Comparisons with other task conditions can help distinguish these processes: In one fMRI experiment, Raye and colleagues (2007, Experiment 1) compared a *Refresh* task condition to two control conditions, one in which participants read a novel word (*Read*) and one in which participants saw a square onscreen that cued them to press a button (*Act*). As in previous studies, Raye and colleagues found greater activity in DLPFC associated with refreshing than either control condition. In addition, an area of anterior prefrontal cortex (PFC) was equally active for the *Act* and *Refresh* conditions but exhibited little activity for the *Read* condition (Figure 1). The authors concluded that the anterior PFC area was likely responsible for *initiating* a non-automatic action based on a cue, as this was the major commonality between *Refresh* and *Act*, whereas *Reading* the word was mostly automatic. This interpretation dovetails with the proposed role of anterior PFC (also known as frontopolar cortex) in subgoal management and cognitive branching (e.g., Braver & Bongiolatti, 2002; Koechlin & Hyafil, 2007), and in task initiation (Koshino et al., 2011).

As noted above, refreshing a stimulus such as a face or scene also modulates activity in extrastriate cortical regions selective for the category in question (M. R. Johnson & M. K. Johnson, 2009a; M. R. Johnson et al., 2007), in agreement with the idea that memory representations of sensory percepts are maintained by re-instantiating activity patterns from when they were originally perceived (Curtis & D’Esposito, 2003; Pasternak & Greenlee, 2005; Postle, Druzgal, & D’Esposito, 2003; Ranganath & D’Esposito, 2005; Ruchkin, Grafman, Cameron, & Berndt, 2003). These results, coupled with the refresh-related activity observed in anterior PFC, DLFPC, and other areas, suggest a two-phase model of refresh tasks in which a frontal (and/or parietal) control signal first *initiates* the component cognitive process *refreshing*, which subsequently manifests as modulated activity in posterior representational areas. This hypothesized sequence of neural and cognitive events within a short (< 2sec) act of refreshing occurs too quickly to be detected easily with fMRI, but electroencephalography (EEG) measures neural activity on the scale of milliseconds. Thus, we probed a refresh task using EEG to determine whether event-related potentials (ERPs) associated with *refresh* events might indeed be further broken down into two (or more) distinct, temporally defined subcomponents.

We presented participants with pairs of face, scene, or word stimuli, followed by a cue to either refresh one of the stimuli, press a button, or do nothing. Our primary aims were to determine 1) whether refreshing had an ERP signature that could be distinguished from control conditions, 2) whether refresh-related ERPs could be divided into temporal subcomponents, and 3) whether the refresh response was significantly modulated by, or contained measurable information about, the category of the refreshed item, as had previously been shown using fMRI.

Methods — Experiment 1

Participants

Twenty-one right-handed, self-reported healthy young adults (9 male, mean age 21.9 ± 2.5 SD) with normal or corrected-to-normal vision participated in exchange for compensation. Procedures were approved by the Yale University institutional review board. Six additional participants also took part in the study, but their datasets were rejected due to either poor fixation, excessive sleepiness, or greater than 50% of their trials meeting rejection criteria due to movements or blinking (see below).

Task

On each trial (Figure 2), a white central fixation point against a black background (750ms) first signaled the start of the trial. Participants were asked to maintain fixation on this point throughout each trial without blinking. Then, two stimuli of the same category (either two faces, two scenes, or two words) appeared above and below fixation (1500ms). Next, a 500ms delay (with only the fixation point shown) was followed by a 1500ms cue that could be 1) a *Refresh* cue: a white arrow pointing up or down, indicating that participants should briefly refresh (think back to, visualize) the stimulus just presented in the upper or lower position; 2) a *NoAct* cue: the white central fixation dot turning bright green, indicating that participants need not do anything at all; or 3) an *Act* cue: the white central fixation dot both turning green and growing larger, indicating that participants should press a button with their right index fingers. Lastly, the central fixation point was presented alone again (750ms), indicating that the trial was nearly over. After that, the screen went entirely black for an inter-trial interval of 2500ms, during which participants could blink freely, before the next trial began.

The *Refresh* condition was similar to tasks and instructions used in previous fMRI studies of refreshing (M. R. Johnson & M. K. Johnson, 2009a; M. R. Johnson et al., 2007). Post-experimental surveys after these types of studies typically indicate that participants understand the instructions, comply, and do not report engaging in additional processes beyond refreshing. Participants did not complete such a survey for Experiments 1 and 2 of this study, but for a similar, contemporaneous EEG study involving a *Refresh* condition for scene stimuli, participants (N=19) responded to a post-experiment survey as follows. “How easy did you find it to think back to each scene picture when you saw the arrow?”: M = 4.3 ± 2.2 SD on a 0–10 scale (10 = very difficult). “Rate how vivid your mental image was when you saw the arrow and had to think back to a scene”: M = 5.8 ± 1.7 SD on a 0–10 scale (10 = incredibly vivid). “… what percentage of each scene picture would you say you were able to mentally revisualize?”: M = 57% ± 18% SD. For the free response question, “Do you recall using any strategies to think back to the scenes when you saw the arrow?”, most participants did not report a specific strategy (e.g., “Not really – not enough time to strategize,” “Not really. Just tried to concentrate,” “Just tried to ‘see’ the image again”), aside from several noting that they tended to focus on the most salient or striking elements of the stimulus, and some others reporting that they sometimes automatically associated stimuli with a verbal label (e.g., “college apartment,” “red mountain”) or a feeling/memory from their past.

There were 240 trials, divided into 4 runs of 60 trials each. There were equal numbers of trials using face, scene, and word stimuli. 50% of all trials ended with a *Refresh* cue, 40% with a *NoAct* cue, and 10% with an *Act* cue. Thus, participants received a total of 120 *Refresh* trials (40 each of faces, scenes, and words), 24 *Act* trials, and 96 *NoAct* trials, pseudorandomly intermixed. Whereas Raye et al. (2007; see Figure 1) had used an *Act* condition as a primary comparison to a *Refresh* condition, we were concerned that large potentials from preparing and executing the button press would dominate the *Act* ERPs, making it a poor comparison condition. (This was not a concern in fMRI studies, as the spatial dispersion of fMRI activity is much lower than that of scalp potentials; thus button-press-related activity during *Act* would not spread to other brain regions during fMRI in the same way that motor-related potentials can be recorded from many distant scalp sites during EEG.) However, we did not use *NoAct* as the sole comparison condition because this may have given participants too little to do on *NoAct* trials, potentially leading to mind-wandering or unintentional refreshing. Thus, we included both *Act* and *NoAct* trials to introduce some ambiguity to the meaning of the *NoAct* cue and induce participants to process the *Act* and *NoAct* cues more fully than if there were only a single "non-*Refresh*" condition. Fewer *Act* trials were included because the primary purpose of the *Act* condition was to facilitate this ambiguity; our primary comparison was between the *Refresh* and *NoAct* conditions.

Stimuli

All face and scene stimuli were color pictures measuring 300 × 300 pixels. Faces were forward-facing complete head shots of young and older men and women (in equal proportions) with neutral or pleasant facial expressions, drawn from a database developed by Minear and Park (2004). Scenes were indoor and outdoor (in equal proportions) pictures of landscapes, buildings, and interior rooms in a wide variety of settings, drawn from a number of sources (mostly freely available images from the Internet). Words were chosen from a set of everyday, neutrally-valenced, one-to-three-syllable nouns, presented in a bold white font that could be easily read even while maintaining central fixation. Stimuli were counterbalanced across participants with regard to the condition and run in which they appeared, and on *Refresh* trials, the stimulus to be refreshed occurred equally often on the top and bottom for each category. Every face, scene, and word stimulus was used exactly once per participant.

Data acquisition and analysis

Scalp potentials were recorded from a 32-channel EEG cap using a nose reference. Channels for horizontal and vertical electrooculography (EOG) were also included to monitor eye movements and blinks. Signals were recorded with a gain of 10,000 and a bandpass filter (−3dB) of 0.01–100Hz, and continuously digitized and stored with 14-bit precision and a 250Hz sampling rate. Electrodes included a 31-channel subset of the international 10/20 and 10/10 systems, and were positioned and labeled according to the conventions of those systems. Electrode impedances were kept below 5 kΩ.

Analyses were focused on the final cue period when either a *Refresh*, *NoAct*, or *Act* cue was presented. For each trial, a 2100ms signal epoch was extracted for each channel (the 1500ms that the cue was onscreen, as well as a 100ms pre-onset baseline period and a 500ms post-offset period). After each epoch was extracted, all channels were linearly detrended, and artifact rejection was performed. Trials were rejected if the peak-to-peak amplitude of any EEG channel exceeded 150μV after linear detrending or if any EEG channel contained a flat period of more than 75ms, which generally indicated amplifier clipping caused by excessive movement. Next, signal correlated with each of the EOG channels was regressed out of all

EEG channels, in order to remove any residual influence from small eye movements that may have occurred on trials that survived blink artifact rejection. As noted above, participants who had more than 50% of their trials rejected due to these criteria were not included in later analyses. The mean voltage from the 100ms preceding the cue period was treated as a baseline and subtracted from the entire epoch, to ensure that the signal at each cue onset began at approximately 0μV.

For standard ERP analyses, the non-rejected trials for each condition/participant/channel were collapsed to create a participant average. These were, in turn, smoothed slightly using a 5-point moving average and then collapsed across participants to create a grand average. (These grand averages were then smoothed again with a 5-point moving average for display purposes in Figures 3, 5, and 7, but this did not affect data analysis.) Standard parametric statistics (e.g., repeated-measures ANOVAs) were conducted to determine timepoints where the ERPs from each condition significantly differed from one another. A false discovery rate (FDR) correction was used to adjust for multiple comparisons (Benjamini & Hochberg, 1995; Genovese, Lazar, & Nichols, 2002). See Results for further details.

We also fed trial-by-trial ERP data from refreshing faces, scenes, and words into a multivariate pattern analysis (MVPA; Haxby et al., 2001; Norman, Polyn, Detre, & Haxby, 2006) to see if it could reliably classify the category being refreshed. The same analysis was performed for the *NoAct* condition (attempting to classify the stimulus category that was initially presented on *NoAct* trials, even though participants were not refreshing during those trials), to determine whether successful classification was specific to refreshing. We used values that were pre-processed as detailed above, but also binned them into 40ms bins to reduce the total number of features fed into the classifier. Only ERP data from the 1500ms period that the *Refresh* (or *NoAct*) cue was actually onscreen were used for MVPA. To perform the classification, for a given participant, we first determined which sub-condition (initial presentation of faces, scenes, or words for either the *Refresh* or *NoAct* condition) had the smallest number of acceptable trials. That number was rounded down to the nearest multiple of 5. That number of trials was then randomly selected from each condition and divided into training and test sets, with 4/5 of the trials being used for training and 1/5 for testing. This process was iterated 500 times for each analysis, with a different random sampling of trials used in each iteration.

For classification, we used sparse multinomial logistic regression (SMLR; Krishnapuram, Figueiredo, Carin, & Hartemink, 2005), which attempts to obtain a sparse classifier during training. This removes the need for a separate feature-selection step and is useful in exploratory analyses where it is not known *a priori* which features (i.e., EEG channels/timepoints) are likely to be most informative. After classification, the SMLR algorithm yielded a matrix of scores indicating, for each trial, the classifier's confidence that the trial belonged to each of the three conditions. These scores were used to calculate receiver operating characteristic (ROC) curves and the area under the ROC curve (AUC) for each condition and each participant. Finally, AUCs were collapsed across condition and classifier iteration to yield a single AUC value for each participant, indicating the classifier's overall accuracy at distinguishing among the three conditions for that participant. These AUC values could range from 0–1, with chance = 0.5; even though there were three conditions being classified, the final AUC was calculated from an average of per-condition ROC curves, hence chance equaling 0.5 rather than 0.33. These AUC scores were then subjected to traditional group statistics (e.g., t-tests against chance).

The MVPA classifications described above were initially performed for both the *Refresh* and *NoAct* conditions for the full time (1500ms) that the corresponding cue was onscreen, and then separately for the initial time period that the cue was onscreen (0–800ms post-cue) and a later portion of the cue period (800–1400ms post-cue). They were also performed separately at each 40ms time bin to examine the timecourse of classification performance for *Refresh* and *NoAct*. See Results for further details.

Results — Experiment 1

ERPs for Refresh, Act, and NoAct

ERPs for representative EEG electrodes are shown in Figure 3 collapsed across the category (faces, scenes, or words) initially presented. As noted in the Methods, a separate repeated-measures ANOVA was run at each timepoint (526 timepoints, for a 2100ms epoch acquired at 250Hz) and channel (31 channels of EEG data), yielding a total of 16,306 p-values. These were subjected to an FDR correction at q = 0.05, and those channels/timepoints that survived the correction are shown in bold in the ERP plots of Figure 3.

Only Figures 3A–B show ERPs in the *Act* condition, for illustrative purposes; in general, *Act* ERPs progressed similarly to the *NoAct* condition for the first ~400ms post-cue but then continued to grow in amplitude to reach a substantially higher positive peak at ~600ms post-cue, likely due to the button-press response, the substantially lower frequency of *Act* trials (making it an “oddball” in some sense), and/or greater temporal synchrony in neural responses to *Act* trials. This confirmed our expectation that *Act* is a less appropriate condition for comparison to *Refresh* in ERP than in fMRI analyses. Thus, because the numbers of *Refresh* and *NoAct* trials were more nearly equal and neither required a motor response, the analyses reported below (and illustrated in Figures 3C–F) compare only the *Refresh* and *NoAct* conditions.

At a number of electrodes, both the *Refresh* and *NoAct* conditions showed a large positive peak at approximately 400–500ms after cue onset, but with the *Refresh* response peaking earlier than the *NoAct* response. These effects are illustrated for Fz and Pz in Figures 3A and 3B; similar patterns were found at F3, F7, FCz, FC3, FT7, Cz, T3, and CPz (not shown). These central and left-lateralized frontal sites showed positive peak responses that were similar in amplitude (but different in latency) in the *Refresh* and *NoAct* conditions, perhaps associated with *initiating* the appropriate response to the onscreen cue in the two conditions.

The response at several other electrodes exhibited a similar positive peak for both *Refresh* and *NoAct,* but in addition to a faster latency for *Refresh* trials, there was also a higher amplitude peak for *Refresh* versus *NoAct*. This pattern is shown for the F4, CP4, T6, and O2 electrodes in Figures 3C–F; similar patterns were found at F8, FC4, FT8, C4, T4, TP7, TP8, T5, P3, P4, O1, and Oz (see also Figure 4C). One possible hypothesis arising from this finding is that the greater amplitude in these right frontal and bilateral parietal, temporal and occipital electrodes could reflect the onset of top-down modulation signals that are unique to the *Refresh* condition.

Consistent with previous fMRI findings that refreshing modulates activity in posterior representational regions, we observed another set of differences between *Refresh* and *NoAct* ERPs, primarily in more posterior electrodes on the right side, arising later during the cue period. The T6 electrode in Figure 3E and the O2 electrode in Figure 3F show this effect most clearly: a sustained positivity for *Refresh* (relative to *NoAct*, which hovered around the 0μV baseline) that reached multiple-comparisons-corrected significance at several points between approximately 800ms and 1400ms after the onset of the cue. Other electrodes showing similar, but somewhat weaker, patterns were FC4, TP8, and O1 (see also Figure 4D).

Figures 4A–B summarize the electrodes and timepoints that showed significant differences between the *Refresh* and *NoAct* conditions (after FDR multiple-comparisons correction). Many electrodes showed significant differences at the earlier (~400ms post-cue) large peak of the *Refresh* response, and then again (~600–800ms post-cue) as that response returned to baseline faster than the *NoAct* response. Fewer significant differences were found in the later period (~800ms–1400ms post-cue) of sustained *Refresh* positivity observed at the electrodes noted above, but some additional significant differences, all showing greater positivity for *Refresh* than *NoAct*, did appear at electrodes Oz, C4, and FT8 for at least two consecutive timepoints within that window. All in all, 3356 timepoint-electrode combinations (out of 16,306), or about 20.6%, showed a significant difference between the *Refresh* and *NoAct* conditions at the FDR-corrected threshold ($q = 0.05$). Figures 4C–D also show scalp distributions for the subtraction *Refresh – NoAct* at the periods of interest discussed above: Figure 4C shows the distribution of the amplitude difference at the early positive peak (adjusted for the latency difference between *Refresh* and *NoAct*, by taking each condition’s peak voltage anywhere in the period 300–600ms post-cue at each electrode), and Figure 4D shows the distribution of the overall difference during the later period of sustained *Refresh* positivity (by taking each condition’s mean voltage over the period 800–1400ms post-cue at each electrode).

In addition to the ~400ms positive peak and ~800–1400ms later period, differences between the *Refresh* and *NoAct* conditions were also observed in the very early or very late portions of the time window (i.e., less than 250ms post-cue-onset, or after the offset of the cue at 1500ms post-cue-onset). Namely, in several electrodes there was a more pronounced and/or earlier-latency negative peak at ~200ms post-cue for the *Refresh* condition compared to *NoAct*, and an earlier-latency cue-offset response for *Refresh* than *NoAct*. Given the timing of these ERPs, it is likely that they were primarily sensory responses related to the onset and offset of the cue stimuli, and were not directly related to the cognitive process of refreshing per se. However, to confirm that our primary effects of interest were not driven by low-level sensory differences between the *Refresh* and *NoAct* cues, we conducted Experiment 2 (see below), focusing on replicating the primary effects of interest at ~400ms and between 800–1400ms, while using more similar cues for the *Refresh* and *NoAct* conditions to better equate low-level sensory responses.

ERPs for refreshing faces, scenes, and words

To determine if refresh ERPs differed by stimulus category, we split all *Refresh* epochs based on whether the refreshed stimuli were faces, scenes, or words. Figure 5 shows ERPs for a set of representative electrodes. Qualitatively, it is clear that the three categories of *Refresh* responses track together much more closely than the *Refresh* and *NoAct* responses, with no obvious pattern of differences among the three *Refresh* sub-conditions. In fact, no timepoint-electrode combinations survived an FDR correction, so timepoints plotted in bold in Figure 5 only differed at an uncorrected threshold of $p < 0.05$.

However, based on fMRI findings of differences in brain activity patterns depending on what is being refreshed (M. K. Johnson, Raye, Mitchell, Greene, & Anderson, 2003; M. K. Johnson et al., 2005; M. R. Johnson & M. K. Johnson, 2009b) we hypothesized that the entire pattern of scalp activity might contain enough information to afford above-chance category decoding. Thus, we conducted the MVPA described in the Methods. Across participants, the mean AUC for decoding the category refreshed during the full 1500ms cue period (Figure 6A, left pair of bars, in blue) was 0.540. Although not numerically far above chance (0.5), the difference was statistically significant ($t_{20} = 3.48$, $p = .0024$, two-tailed t-test against chance) and the effect size (Cohen's $d = 0.76$) indicated a medium-to-large effect. To confirm that this result was not due to bias in our algorithm, we ran the same analysis, but shuffled the labels of the conditions randomly before classifying, which should yield chance performance. Indeed, the shuffled classification did not differ from chance (mean AUC = 0.499, $t_{20} = 0.82$, $p = 0.42$) but did differ from the non-shuffled analysis ($t_{20} = 3.60$, $p = 0.0018$, two-tailed paired t-test).

We also performed the same analysis for *NoAct*, to determine whether successful category decoding was specific to refreshing. *NoAct* classification was also significantly above chance (mean AUC = 0.526, $t_{20} = 2.21$, $p = 0.039$; Figure 6A, left pair of bars, in green). Although this was numerically worse than *Refresh*, the difference between *Refresh* and *NoAct* classification during the full 1500ms cue period was not significant ($t_{20} = 0.88$, $p = 0.39$).

However, given that our ERP analyses (Figure 3) had shown differences between *Refresh* and *NoAct* at two separate periods (early and late) within the overall cue period, we hypothesized that *NoAct* category classification might be driven exclusively by activity in the earlier period (e.g., by lingering perceptual activity from the initial two-stimulus display and/or participants' inadvertently beginning to refresh on some *NoAct* trials before processing the *NoAct* cue and realizing that they did not have to). Thus, we repeated the *Refresh* and *NoAct* MVPA separately for the earlier (0–800ms post-cue) and later (800–1400ms post-cue) periods. As predicted, during the earlier period (Figure 6A, middle pair of bars) both *Refresh* category classification (mean AUC = 0.534, $t_{20} = 3.81$, $p = 0.0011$) and *NoAct* category classification (mean AUC = 0.531, $t_{20} = 2.49$, $p = 0.022$) differed from chance, but not from each other ($t_{20} = 0.28$, $p = 0.78$). However, during the later period (Figure 6A, right pair of bars), *Refresh* category classification remained above chance (mean AUC = 0.536, $t_{20} = 3.40$, $p = 0.0028$), but *NoAct* category classification dropped to chance (mean AUC = 0.502, $t_{20} = 0.14$, $p = 0.89$), and *Refresh* classification was significantly better than that of *NoAct* ($t_{20} = 2.31$, $p = 0.032$).

We also ran the same MVPA for both *Refresh* and *NoAct* separately at each 40ms time bin, to plot the timecourse of category classification performance. As shown in Figure 6B, at individual timepoints early in the cue period, category classification for both conditions was somewhat above chance, with no separation between *Refresh* and *NoAct* performance. However, at ~700ms post-cue, *NoAct* classification dropped to near chance while *Refresh* classification remained high. When we tested for significant differences in performance (paired t-tests at each time bin), no timepoints survived an FDR correction; however, *Refresh* category classification was significantly better than *NoAct* category classification at an uncorrected p-threshold of 0.05 at 5 timepoints (out of 37 in the entire cue period), all between 700ms and 1200ms post-cue.

Methods — Experiment 2

As noted above, Experiment 2 was conducted to replicate the major effects observed in Experiment 1, but using more similar cues for the *Refresh* and *NoAct* conditions, to eliminate the possibility that low-level sensory differences might be driving our effects. All methods were the same as in Experiment 1, except where stated below.

Participants

Sixteen right-handed, self-reported healthy young adults (8 male, mean age 22.4 ± 2.9 SD) with normal or corrected-to-normal vision participated in the study. Four additional participants were excluded according to the same criteria as in Experiment 1.

Task

The task was identical to that used in Experiment 1, except that we changed the *NoAct* condition’s cue stimulus. Whereas the *NoAct* cue was a small green dot in Experiment 1, in Experiment 2 it was a white arrow — identical to the arrow used in *Refresh* trials, except that the arrow pointed left or right instead of up or down. Given that the faces, scenes, and words presented initially on each trial were above and below fixation, participants were instructed to refresh the indicated item if the arrow pointed up or down, and do nothing if the arrow pointed left or right (i.e., not toward the previous location of a stimulus). The presentation of the *Refresh* and *Act* cues, as well as the proportion of different trial types, the face/scene/word stimuli used, and the order in which stimuli/conditions were presented, were all the same as in Experiment 1.

Results — Experiment 2

ERPs for Refresh versus NoAct

For this replication, we focused on differences between the *Refresh* and *NoAct* conditions at the electrodes/timepoints where the most notable differences were found in Experiment 1. Figures 7A–D show the *Refresh* and *NoAct* ERPs for the same electrodes illustrated in Figures 3C–F from Experiment 1, with a similar pattern of results; in fact, all four electrodes in Figures 7A–D (F4, CP4, T6, O2) exhibited differences between *Refresh* and *NoAct* at both the earlier ~400ms positive peak (driven primarily by a faster-latency *Refresh* response) and during the later 800–1400ms period. In contrast, only T6 and O2 showed a difference between *Refresh* and *NoAct* during the later period in Experiment 1. Although these differences did not pass the FDR-corrected threshold of $q = 0.05$ used in Experiment 1 (timepoints shown in bold in Figures 7A–D are at an uncorrected $p < 0.05$ threshold), they did emerge at the same timepoints with the same qualitative characteristics (faster latency for *Refresh* during the earlier positive peak, greater sustained positivity for *Refresh* during the later period), suggesting that the overall pattern of results from Experiment 2 did replicate that of Experiment 1. For further quantification, we used the enhanced FDR procedure introduced by Storey (2002). After feeding the p-values for the *Refresh* – *NoAct* comparisons at all electrodes and timepoints into this procedure, it returned a π_0 parameter of 0.771, suggesting that approximately $(1 - \pi_0)$ or 22.9% of measurements in Experiment 2 contain true differences between conditions, even if they do not pass a conventional FDR threshold. When considering only the electrodes/timepoints of maximum interest that 1) occurred between 300ms post-cue and cue offset, and 2) passed the FDR threshold in Experiment 1, the expected percentage of true differences rose to 40.0%. This suggests a fair rate of replication that is relatively specific to the effects of maximum interest, despite the changes to the *Refresh* and *NoAct* cue stimuli.

In addition to the electrodes in Figures 7A–D, similar patterns of differences ($p < 0.05$, uncorrected, at multiple consecutive timepoints) between *Refresh* and *NoAct* at both the earlier peak and the later period were found at F8, FC4, FT8, C4, T3, T4, TP7, TP8, P3, P4, T5, O1, and Oz. A related but somewhat different pattern was also seen at Fz, FCz, Cz, CPz, Pz, F3, FC3, C3, and CP3. Those electrodes showed the same greater sustained *Refresh* positivity during the later 800–1400ms period, but with no significant difference between conditions at the *Refresh* peak timepoint of ~400ms post-cue; instead, early-period differences between *Refresh* and *NoAct* were driven by a greater positive peak for *NoAct* (though still at a slower latency than *Refresh*), occurring ~500–600ms post-cue. See Figure 7E for the scalp distribution of the magnitude difference of the initial peak between *Refresh* and *NoAct*, irrespective of latency, and Figure 7F for the scalp distribution of the difference in mean voltage during the 800–1400ms later period. Note that although Figures 4C/7E and 4D/7F exhibit some clear visual dissimilarities from each other, these are largely due to overall baseline voltage shifts. Figure 7E reflects a global negative shift relative to 4C, and 7F reflects a global positive shift relative to 4D, but the relative distributions of voltages independent of these baseline shifts are largely similar between Figures 4C/7E and between Figures 4D/7F.

Critically, the very early (~200ms post-cue-onset) and very late (after cue offset, >1500ms post-cue-onset) differences between *Refresh* and *NoAct*, observed in Experiment 1 and which served as the motivation for Experiment 2, were eliminated in Experiment 2 (see Figures 7A–D). This suggests that the differences found in Experiment 1 at these timepoints were indeed due to low-level sensory differences between the *Refresh* and *NoAct* cues. However, as the effects at ~400ms post-cue and between 800–1400ms post-cue remained (although at an uncorrected significance threshold), Experiment 2 also suggests that those effects of primary interest were *not* driven by low-level sensory differences between cues.

ERPs for refreshing faces, scenes, and words

MVPA results were also similar between Experiments 1 and 2. Over the full 1500ms cue period, decoding for the category refreshed (Figure 8A, left pair of bars, in blue) was significantly better than chance (mean AUC = 0.566, $t_{15} = 4.35$, $p = 0.00057$, two-tailed t-test). Classification of the initially presented category from *NoAct* trials (Figure 8A, left pair of bars, in green) was not different from chance (mean AUC = 0.516, $t_{15} = 1.61$, $p = 0.13$). Unlike Experiment 1, the difference between *Refresh* and *NoAct* classification during the full cue period was significant ($t_{15} = 3.79$, $p = 0.0018$).

We then split the data into earlier (0–800ms post-cue) and later (800–1400ms post-cue) periods and ran the MVPA again, as in Experiment 1. During the earlier period (Figure 8A, middle pair of bars), *Refresh* category classification was significantly better than chance (mean AUC = 0.560, $t_{15} = 4.03$, $p = 0.0011$) whereas *NoAct* classification showed only a trend toward better-than-chance performance (mean AUC = 0.524, $t_{15} = 1.88$, $p = 0.080$); the difference between *Refresh* and *NoAct* performance during the earlier period was significant ($t_{15} = 2.20$, $p = 0.044$). During the later period (Figure 8A, right pair of bars), *Refresh* category classification, as in Experiment 1, remained above chance (mean AUC = 0.534, $t_{15} = 2.18$, $p = 0.045$) whereas *NoAct* was at chance (mean AUC = 0.493, $t_{15} = 0.54$, $p = 0.59$), and *Refresh* performance was again significantly better than that of *NoAct* ($t_{15} = 3.74$, $p = 0.0020$).

Finally, we performed the MVPA separately at each 40ms time bin and plotted the timecourse of category classification in Figure 8B. As in Experiment 1, performance was more similar between *Refresh* and *NoAct* during the early cue period; *Refresh* classification was only significantly better than *NoAct* at one early timepoint (time bin centered at 420ms post-cue). However, *NoAct* performance dropped to near-chance later in the cue period while *Refresh* remained high, as in Experiment 1. Eleven timepoints between 700ms and 1420ms post-cue showed a significant difference between *Refresh* and *NoAct* performance (paired t-tests, $p < 0.05$, uncorrected); the differences at 420ms, 980ms, and 1220ms post-cue survived FDR correction.

Discussion

Summary of results

To our knowledge, this is the first EEG study of the cognitive processes engaged during refresh tasks. The results supported our two main hypotheses: Refresh ERPs (relative to a control condition) can be broken down into temporal subcomponents, and the refresh response is significantly modulated by the category refreshed. There were two major ERP differences between refreshing and our control *NoAct* condition; one a positive peak relatively early in the cue period, and one a span of more sustained positivity later in the cue period. Both *Refresh* and *NoAct* had early peaks at multiple electrodes, with the *Refresh* peak occurring sooner (~400ms post-cue) than the *NoAct* peak (~500ms post-cue). This latency difference was not due to sensory differences between the *Refresh* and *NoAct* cues (or difficulty distinguishing the *NoAct* and *Act* cues), as it occurred not only in Experiment 1 but also in Experiment 2, in which the *Refresh* and *NoAct* cues were visually similar and the *NoAct* and *Act* cues were visually dissimilar.

However, in Experiment 2, the amplitudes of *Refresh* peaks compared to *NoAct* peaks were somewhat reduced (or, conversely, *NoAct* peaks were relatively larger). This could either have been due to purely sensory effects (i.e., the *NoAct* cues were larger and more visually salient, thus producing amplitudes more similar to those of *Refresh*) or cognitive effects relating to the cue change (i.e., the greater similarity of the cues made it more challenging to interpret the cue and initiate the appropriate response, leading to more similar amplitudes between conditions). Regardless, in both experiments, we observed somewhat different scalp distributions in the *Refresh* versus *NoAct* peak responses. In central and left-lateralized frontal sites (Fz, FCz, Cz, CPz, Pz, F3, FC3), the *Refresh* peak amplitude was approximately equal to (Experiment 1) or somewhat smaller than (Experiment 2) the *NoAct* peak, whereas in right frontal and bilateral parietal, temporal, and occipital electrodes (F4, CP4, F8, FC4, FT8, C4, T4, TP7, TP8, T5, T6, P3, P4, O1, O2, Oz), the *Refresh* peak amplitude was somewhat greater than (Experiment 1) or approximately equal to (Experiment 2) the *NoAct* peak (see Figures 4C and 7E).

The *Refresh* and *NoAct* responses also differed later in the cue period, in the form of a more sustained positivity, rather than a distinct peak, that was greater for *Refresh* than *NoAct* from ~800ms post-cue onward. In Experiment 1, this was seen at several posterior sites, most notably T6 and O2, as well as at a number of additional sites in Experiment 2. At several sites, the *Refresh* and *NoAct* ERPs converged to similar amplitudes after their initial peaks before separating for the later period, suggesting that the later positivity is a distinct ERP subcomponent of refreshing, separate from that initial peak. This is further supported by our MVPA results; although category information could be decoded during *Refresh* trials throughout the cue period, it could only be decoded during *NoAct* trials in the earlier period, and thus the MVPA primarily differentiated *Refresh* from *NoAct* during the later period. Classifiable category information during the early cue period may have been more related to persisting activity from the initial stimulus presentation in both the *Refresh* and *NoAct* conditions, or spontaneous (anticipatory) refreshing in *NoAct*. Thus, for future studies examining the relationship between top-down modulation of sensory cortex and category-specific EEG patterns evoked by refreshing, it may be most useful to focus on the later cue period, which is presumably carrying the clearest signal of the top-down modulation of representations that is a defining function of the refresh process.

Relation to previous work

The distinct refresh-related ERP components we observed here bear some resemblance to ERP effects previously found in other contexts. In particular, our earlier positive peak is reminiscent of the large, well-characterized ERP component known as the P3 or P300. Although our refresh task was quite different from the infrequent target-detection or “oddball” tasks classically used to elicit the P3, the positivity, latency, and magnitude of the responses are similar enough to suggest that our early refresh-related peak and the classical P3 might share some degree of underlying neural activity. The P3 has been linked to attention and working memory updating, and is presumed to arise from activity in a broad frontoparietal network (for review: Polich, 2007; Polich & Kok, 1995; Soltani & Knight, 2000). Given that refreshing is thought to constitute a fundamental component of many executive functions and shows some overlap in brain activity with perceptual attention processes (e.g. Roth, M. K. Johnson, Raye, & Constable, 2009; for review, see Chun & Johnson, 2011), including both frontal and parietal regions of activation (M. K. Johnson et al., 2005), it seems reasonable to draw some relation between the peaks we observed here and the P3 family of responses.

More specifically, the P3 is typically subdivided into two subcomponents, the P3a — associated with irrelevant, novel, or distractor stimuli, a fronto-central scalp distribution, frontal source generators, and an earlier latency – and the P3b, which is associated with voluntary target detection, a more posterior scalp distribution, parietal and inferior temporal source generators, and a later latency (Bledowski et al., 2004; Knight, 1997; Polich, 2007). Given that our *Refresh* cue might be thought of as a type of target and our *NoAct* cue a type of distractor, the scalp distributions we observed are broadly consistent with these divisions: a less *Refresh*-associated (more *NoAct*-associated) fronto-central distribution with the P3a, and a more *Refresh*-associated (less *NoAct*-associated) posterior distribution with the P3b.

Thus, although our initial *Refresh*- and *NoAct*-related peaks likely both reflect some weighted combination of P3a-like and P3b-like processing, our results could be interpreted in terms of (and may shed new light on) theoretical models of the P3a and P3b. The details of such models are still debated, but it appears that the P3a is related to the initial orienting to and evaluation of a stimulus, driven primarily by prefrontal cortex (Bledowski et al., 2004; Friedman, Cycowicz, & Gaeta, 2001; Polich, 2007), whereas the P3b seems to be more related to the resolution of uncertainty about stimuli and the concomitant updating of expectancies or context, potentially engaging additional attentional or memory processes, and driven primarily by temporo-parietal activity (Bledowski et al., 2004; Knight, 1997; Polich, 2007; Sutton, Tueting, Zubin, & John, 1967; Verleger, 1988). Both our *Refresh* and *NoAct* conditions are likely to involve P3a-like processing in the need to initially orient to and evaluate a cue in order to make an action (or inaction) decision, but P3b-like processing should be more *Refresh*-specific, given that only *Refresh* involves subsequent deployment of reflective attention to an active representation. The earlier latency for *Refresh* is consistent with the sensitivity of the P3 latency to the time required to evaluate/resolve a stimulus, driven primarily by the later and more temporally variable P3b. In our study, given the greater salience of the *Refresh* cue, participants likely held a refresh-specific attentional set that may have facilitated faster evaluation of that cue.

Previous ERP studies of orienting internally directed attention to items held in working memory, a task that likely entails refreshing, have also reported enhanced P3-like responses (e.g., Griffin & Nobre, 2003); however, those tasks have typically also involved a subsequent memory probe for the attended item. Thus, the less complex nature of the refresh task used here helps to establish with greater certainty that this P3-like enhancement is due to the act of reflective attention itself, rather than the preparation of a response based on the representation selected.

The later sustained positivity we associated with refreshing also has some analogue in previous work, the closest of which may be the late directing attention positivity (LDAP; Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000). The LDAP is a late positive potential associated with perceptual attention, lasting up to several hundred milliseconds. It has been interpreted as arising from the anticipatory top-down modulation of visual regions in response to an attentional pre-cue. Given the known top-down modulation effect of refreshing on activity in extrastriate category-selective visual regions of cortex (e.g., M. R. Johnson & M. K. Johnson, 2009a; M. R. Johnson et al., 2007), this interpretation is broadly consistent with our later refresh-related sustained positivity. If the LDAP and our refresh-related late positivity were indeed determined to stem from similar sources, it would suggest 1) that although the LDAP has previously been observed in terms of greater contralateral than ipsilateral positivity for visual attention directed to one hemifield, similar positivity can also be observed from directing reflective attention to representations of stimuli presented centrally and thus not explicitly lateralized; and 2) that LDAP-like positivity is not limited to simply a gain increase from attending to an empty visual field, but can also be evoked by top-down modulatory signals to visual regions that carry meaningful information about currently active mental representations (after the offset of the corresponding perceptual stimulus). These task differences (lateralized versus central stimulus presentation, spatial/perceptual versus reflective attention) limit how directly we might compare the traditional LDAP to our LDAP-like positivity, although they also may help explain differences in timing (the traditional LDAP arises ~500ms post-cue whereas our positivity began ~800ms post-cue, but reflective attention may reasonably be expected to take longer to initiate than spatial/perceptual attention) and create opportunities for future studies more specifically designed to assess the similarities and differences between ERPs associated with perceptual versus reflective attention.

Consistent with the above interpretation is our finding of *Refresh*-specific category decoding during the later part of the cue period that contained this LDAP-like positivity. At least one previous EEG study (LaRocque, Lewis-Peacock, Drysdale, Oberauer, & Postle, 2013) has successfully decoded the general category of information (visual, phonological, or semantic) maintained in working memory over several seconds; the present study extends this result to demonstrate above-chance decoding for a shorter time span and a more similar set of categories. Although classifier performance in both cases was modest, this is to be expected with EEG; even during perception, category-specific ERP effects are not as pronounced as in fMRI. For example, although the fusiform face area in fMRI studies and the N170 potential in ERP both respond selectively to faces (Bentin, McCarthy, Perez, Puce, & Allison, 1996; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997), there is no similarly diagnostic ERP component for visual scenes, despite the existence of several scene-preferring areas that are readily observed using fMRI (e.g., Epstein, 2008; Epstein & Kanwisher, 1998). Thus, both our study and that of LaRocque et al. highlight the utility of applying MVPA to reveal information about reflective processing that would not be recoverable from traditional ERP analysis (and with finer temporal resolution than is possible with fMRI); however, relatively large differences between stimulus categories may be necessary to achieve satisfactory decoding.

Conclusions

These EEG results support hypotheses formed as a result of previous fMRI investigations, thus fleshing out a dynamic cognitive and neural model of reflective attention and executive function more generally. Those fMRI studies found that refreshing was associated with activity in DLPFC, anterior PFC, and parietal regions, particularly the supramarginal gyrus (M. K. Johnson et al., 2005; Raye et al., 2007), as well as category-specific modulation of extrastriate visual areas (M. R. Johnson & M. K. Johnson, 2009a; M. R. Johnson et al., 2007). The short timescale of the refresh process (typically < 2sec) and the low temporal resolution of fMRI make it difficult to resolve the order in which those regions become active, but comparisons among task conditions suggested a basic model of how these areas interact: Anterior PFC, associated in previous studies with subgoal management, cognitive branching, and task initiation (Braver & Bongiolatti, 2002; Koechlin & Hyafil, 2007; Koshino et al., 2011), and activated for both *Refresh* and *Act* conditions (Raye et al., 2007), is primarily responsible for *initiating* an appropriate non-automatic cognitive or motor action based on the interpretation of a cue. DLPFC, which is relatively specific to the *Refresh* condition in most studies of refreshing, and which is thought to generate signals that bias the flow of activity in other brain regions (Miller & Cohen, 2001), produces a control signal to direct reflective attention to a representation. Subsequently, and potentially mediated by parietal regions, activity patterns associated with that representation's initial perception are sustained, enhanced, or partially revived in representational cortical regions (e.g., visual areas, for visual stimuli).

Although our present findings do not allow us to map ERP phenomena directly onto specific cortical areas, they do suggest that refresh *tasks* contain at least two distinct component cognitive processes of reflection, which is generally consistent with the two-phase model predicted from fMRI: One with a peak at ~400ms post-cue (*initiating*), and another that is more distributed between ~800–1400ms post-cue (*refreshing*). The latter potential, its similarity to the LDAP, and the refresh-specific category decoding we found during its temporal window imply that this interval represents the period during which top-down modulation of representational regions occurs and patterns associated with the attended representation are most enhanced.

The earlier P3-like peak also integrates well with existing fMRI data, suggesting that disambiguation of the cue and initiation of the appropriate action occurs by 400–500ms post-cue. The scalp distributions we observed for *Refresh* versus *NoAct* suggested both P3a-like (relatively less specific to refreshing) and P3b-like (more specific to refreshing) aspects. The known role of the P3a in initial stimulus orienting and evaluation, coupled with frontal source generators and an earlier latency than the P3b, may map onto the posited function of anterior PFC in *initiating* the appropriate cue-based response in both conditions. By contrast, the more refresh-specific P3b-like activity may reflect the slightly later recruitment of DLPFC and/or parietal regions to bias reflective attention to one representation, consistent with the P3b's later latency and role in context updating or recruitment of further attention/memory processes. Although the P3b is generally associated with temporo-parietal source generators (Bledowski et al., 2004; Polich & Criado, 2006), frontal sources have also been found (Volpe et al., 2007); it is also true that our task is quite different from traditional P3-

elicitation paradigms, and thus interpretations of our P3-like peak may not map onto a “canonical” P3 response in every respect. Another alternative is that since the temporal onset of DLPFC activity in refreshing is thought to occur between that of anterior PFC and more posterior regions, any DLPFC-associated ERPs may overlap too heavily with the earlier and later aspects of the P3-like peak to be easily dissociated from either.

Although the present study did not record any behavioral data for the *Refresh* or *NoAct* conditions, there are clear implications for behavior. The *refresh* process has been proposed to be a key component of many more complex mental tasks (Chun & M. K. Johnson, 2011; M. K. Johnson et al., 2005; M. R. Johnson & M. K. Johnson, 2009a) and a critical element in conceptual (Baddeley, 2012) and quantitative (Barrouillet, Portrat, & Camos, 2011) models of working memory performance. Indeed, we have found that refreshing can have both immediate and long-term behavioral consequences. Refreshing can inhibit immediate perceptual access to a refreshed item (M. R. Johnson et al, 2013) but produce perceptual priming after a delay (Yi, Turk-Browne, Chun, & M. K. Johnson, 2008) and increase long-term recognition memory of the refreshed item (M. K. Johnson et al., 2002). The current findings provide some new tools for later studies to investigate such behavioral phenomena in a more fine-grained manner; for example, the latencies of the temporal subcomponents of the refresh task could be used as a more precise measure of when reflective attention is deployed on each trial, or classifier performance could be used as a measure of representation strength. Either or both of those variables could then be used to predict behavioral effects such as long-term recognition performance or response times for overtly refreshing (e.g., speaking aloud) an item or identifying a later re-presentation of a previously refreshed item.

All in all, these results contribute to a more complete understanding of the *refresh* component process specifically, its potential relation to another component process (*initiating*), and more generally of the spatio-temporal neural dynamics of the building blocks of more complex reflective thought processes. Additionally, the successful isolation of refresh-related ERP responses paves the way for future studies that may manipulate the refresh task to obtain a more thorough understanding of the refresh process itself, the downstream consequences of refreshing upon memory representations, or the role of reflective attention in more complex cognitive operations (e.g., the relation between *refreshing* and *rehearsing*, or *retrieving*). Future studies may also benefit from employing combined fMRI and EEG analyses in designs specifically targeted towards integrating the spatial and temporal features of the model described above.

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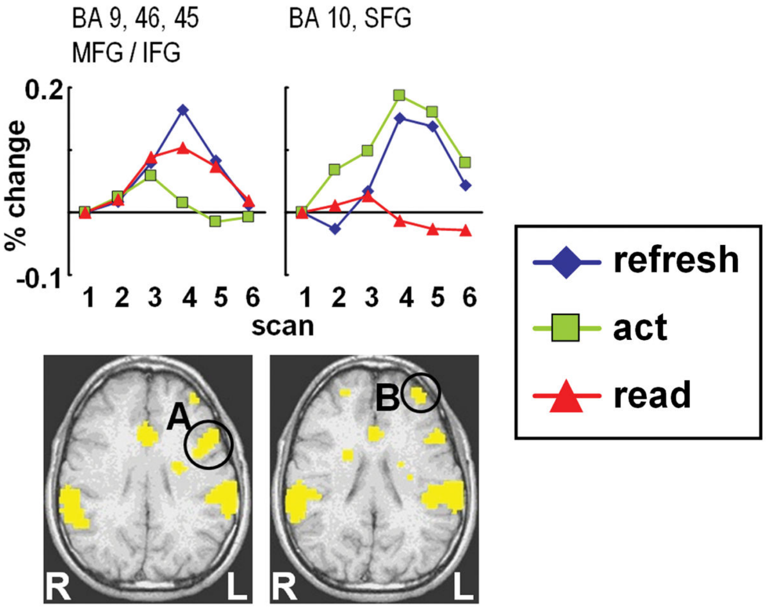

Raye et al., 2007

Figure 1. Previous results by Raye et al. (2007)

This previous study of refreshing found two frontal areas activated by refreshing, one in DLPFC (A) and one in anterior PFC (B). Both the *Refresh* and *Act* conditions activated anterior PFC more than the control *Read* condition, but *Refresh* activated DLPFC significantly more than *Act*.

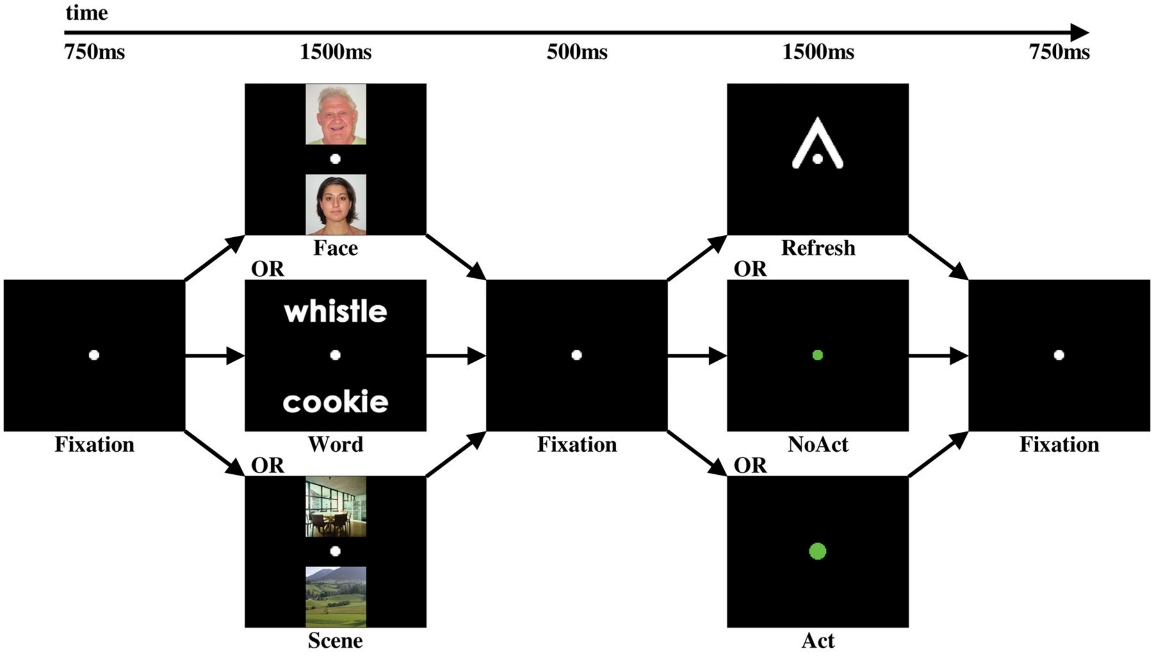

Figure 2. Task design (Experiment 1)

Participants first saw either two faces, two scenes, or two words (1500ms), followed by a brief delay (500ms) and a cue (1500ms) to either *Refresh* one of the two stimuli, press a button (*Act*) or do nothing (*NoAct*). Each trial began and ended with a fixation point; participants were instructed to keep their eyes still and not to blink for the entire time that the fixation point or other stimuli were onscreen. Experiment 2 used an identical design, except that the *NoAct* cue was replaced by a leftward- or rightward-pointing arrow similar to those shown for *Refresh*; see text for details.

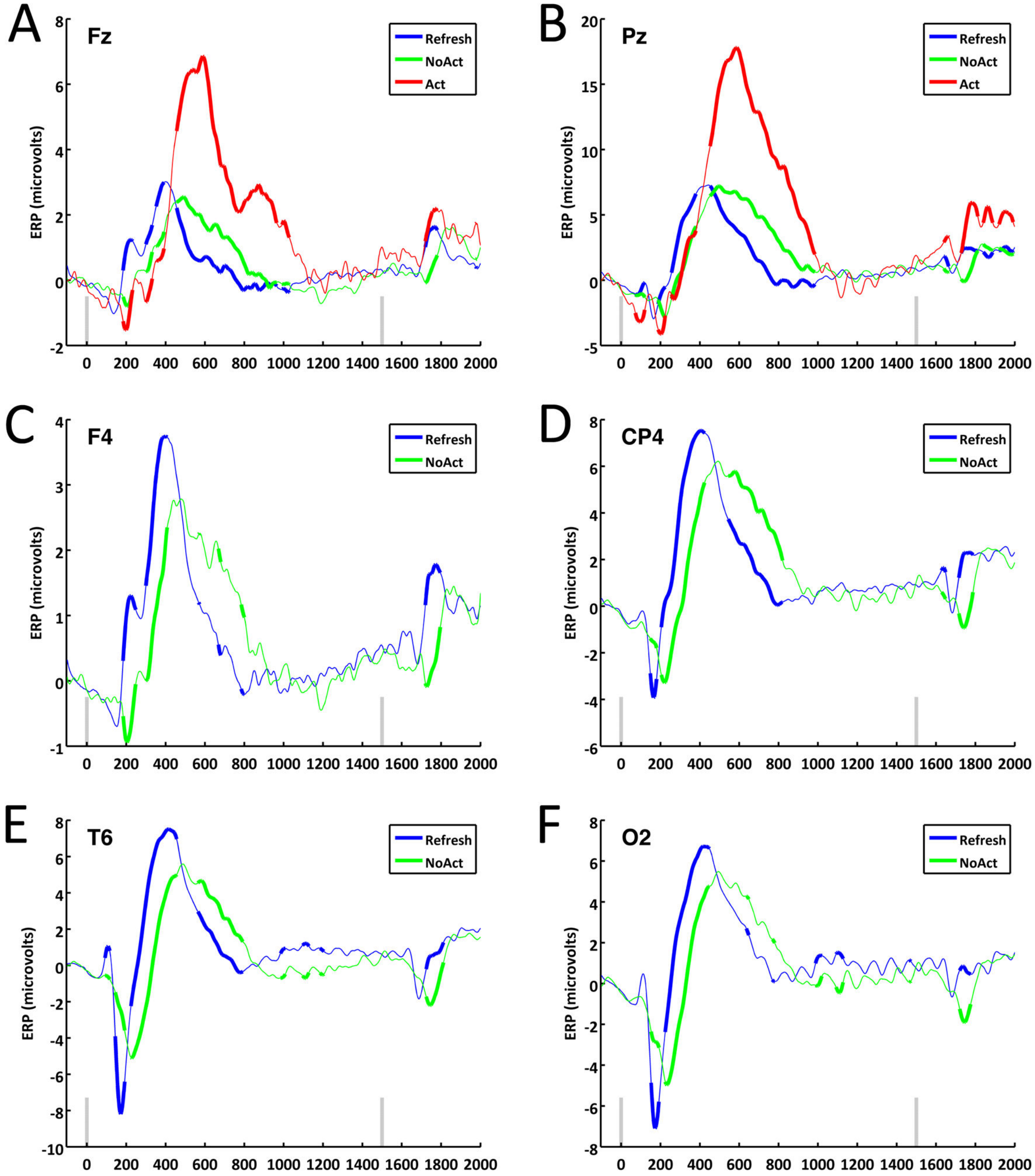

Figure 3. Refresh-related responses at selected electrodes (Experiment 1)

The *Act* condition is only shown for reference in panels A and B, as it tended to dwarf the *Refresh* and *NoAct* conditions, making it a poor comparison condition for refreshing. In multiple electrodes, the *Refresh* condition had a more positive and/or earlier-latency peak than *NoAct* in the early part of the cue period (~400ms post-cue). Some electrodes also showed a sustained positive response that was greater for *Refresh* than *NoAct* later in the cue period (between ~800–1400ms post-cue). Timepoints plotted in bold are those that significantly differed between conditions at an FDR-corrected threshold of q = 0.05. The lines at 0ms and 1500ms indicate the onset and offset of the *Refresh*/*NoAct*/*Act* cue.

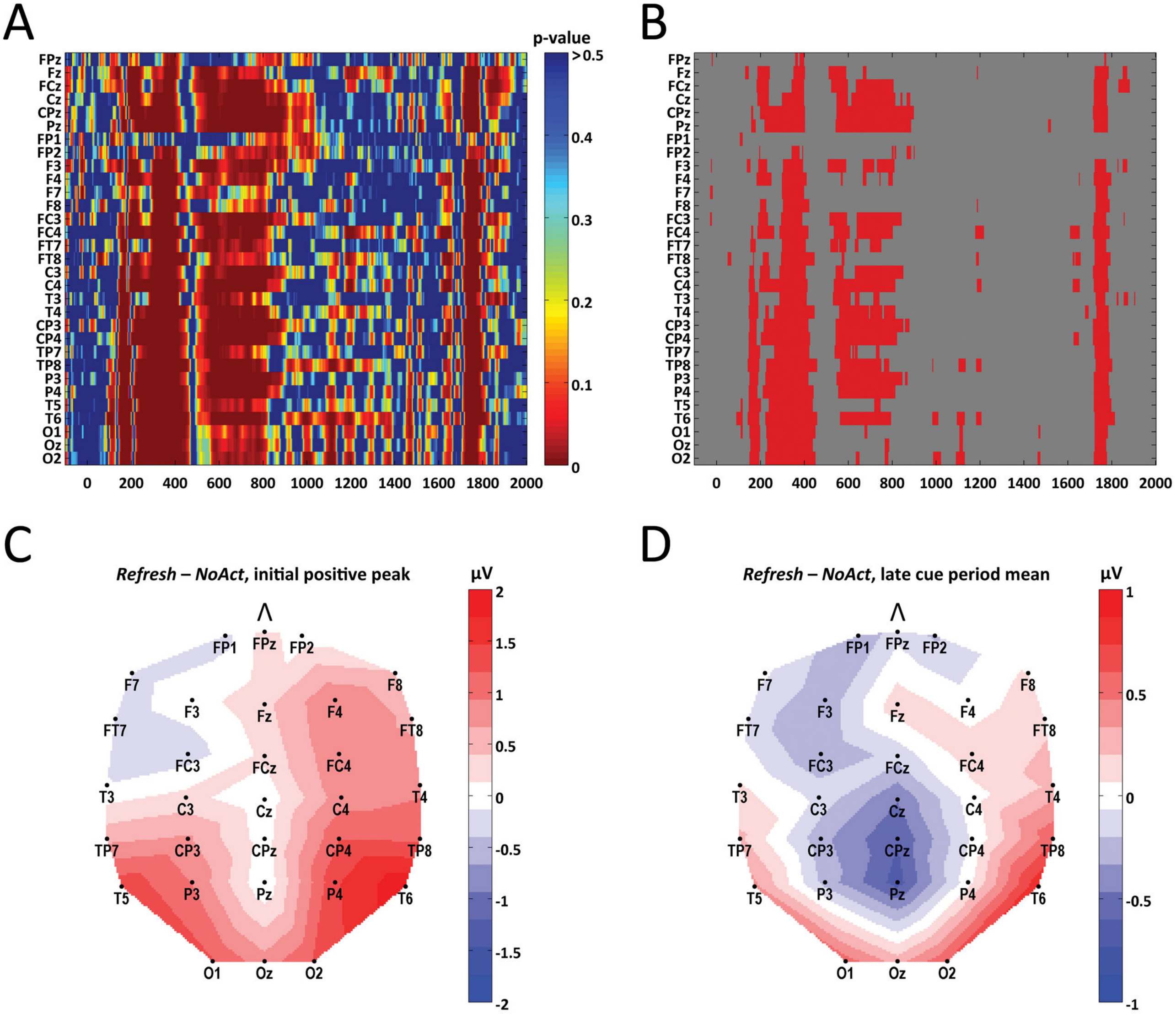

Figure 4. Statistical representation of differences between *Refresh* and *NoAct* and scalp distributions (Experiment 1)

Graphs in panels A–B are arranged with time (relative to the onset of the *Refresh*/*NoAct* cue) on the x-axis and electrode site on the y-axis. **A.** The graph displays uncorrected p-values for paired t-tests between *Refresh* and *NoAct* across electrodes and timepoints, with warmer colors representing lower numbers (greater significance). **B.** The graph indicates, in a binary fashion, electrodes/timepoints from the graph in panel A that did (red) or did not (gray) show a significant difference between *Refresh* and *NoAct* at a false discovery rate (FDR)-corrected threshold of q = 0.05. Most electrodes showed significant differences at an initial P3-like peak occurring approximately 400ms after the onset of the cue (and again at the peak's offset 200–300ms later). Several electrodes also showed significant differences at a later time period, representing the sustained positivity for *Refresh* between approximately 800ms and 1400ms post-cue, as shown in Figures 3E and 3F. **C.** Scalp distribution of the difference between *Refresh* and *NoAct* at the initial P3-like peak, irrespective of latency, defined as each condition’s maximum voltage in the period 300–600ms post-cue. **D.** Scalp distribution of the difference between *Refresh* and *NoAct* during the later period, defined as each condition’s mean voltage in the period 800–1400ms post-cue.

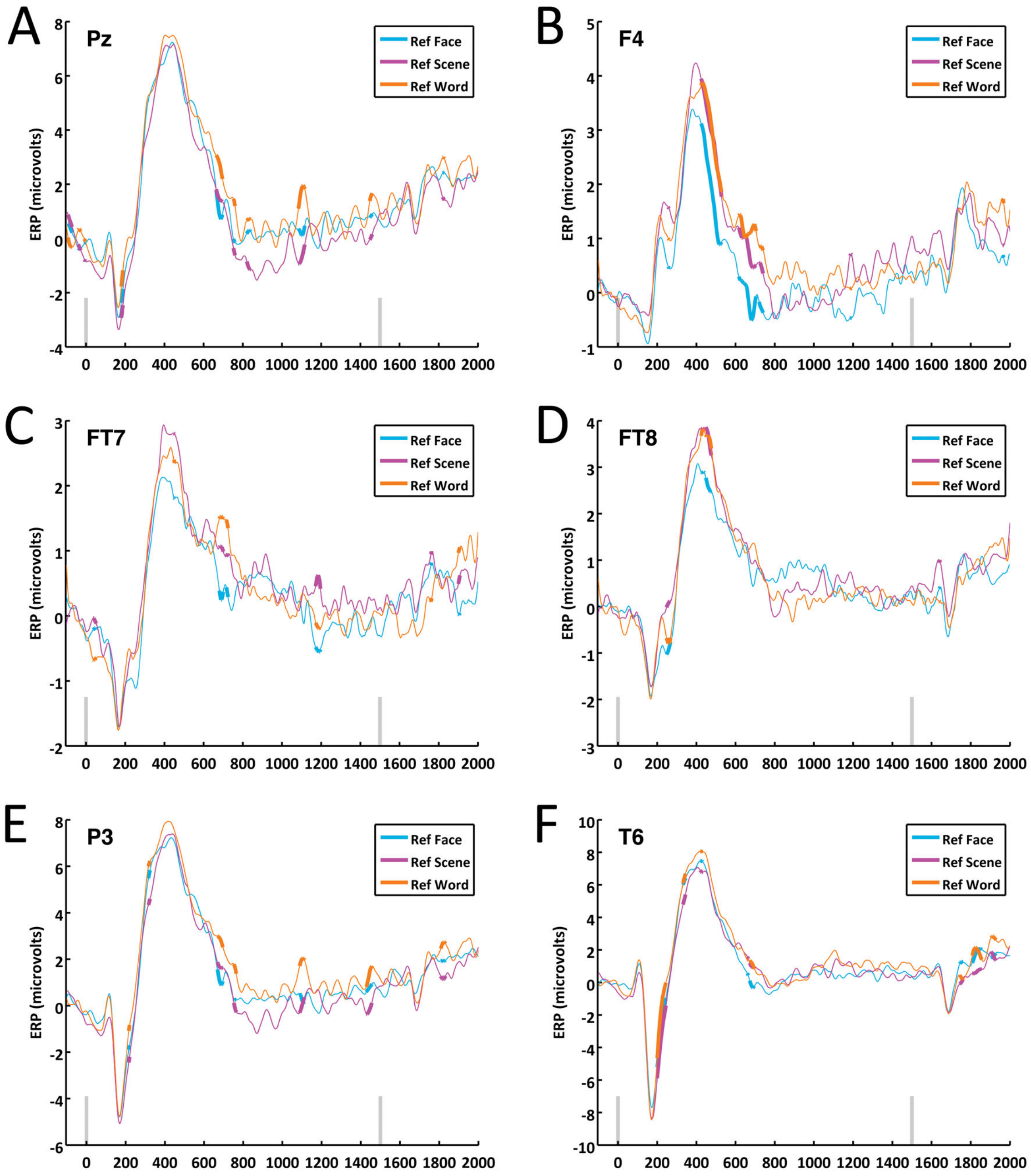

Figure 5. Refresh-related responses by category at selected electrodes (Experiment 1)

The *Refresh* responses for different categories are shown at several representative electrodes. Responses for refreshing different stimulus categories tracked fairly closely together; although modest differences appeared at some electrodes, none passed an FDR-corrected threshold of $q = 0.05$. Timepoints plotted in bold are those that differed between conditions at an uncorrected threshold of $p < 0.05$. The lines at 0ms and 1500ms indicate the onset and offset of the *Refresh* cue.

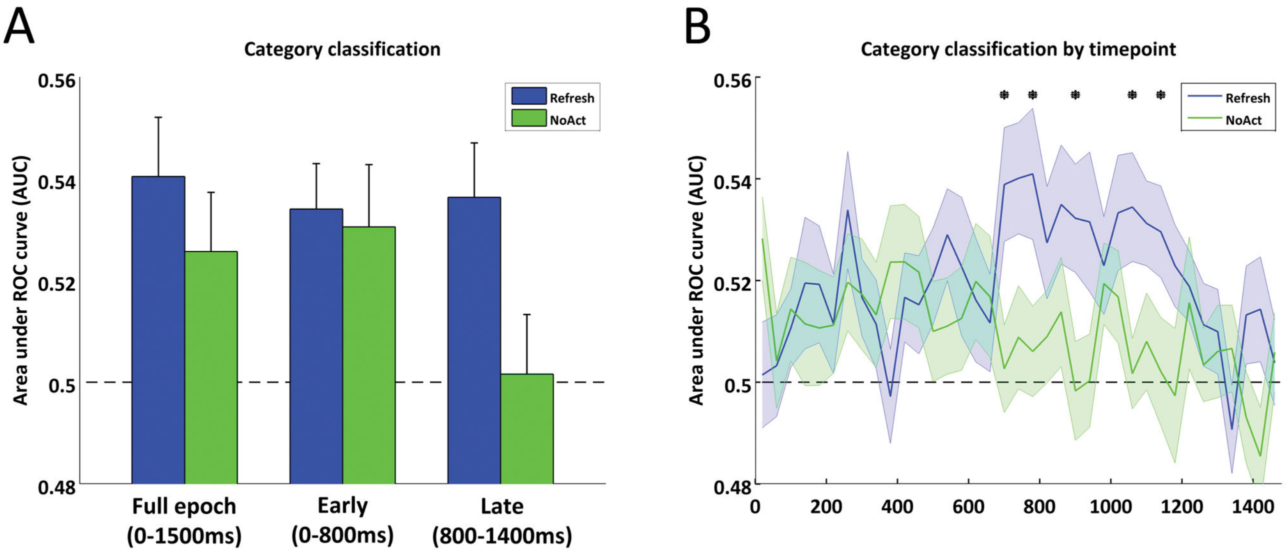

Figure 6. Multivariate pattern analysis of category information (Experiment 1)

A. Classification analyses of the initially presented stimulus category were significantly above chance (= 0.5) during both the *Refresh* and *NoAct* conditions when considering the full time period that the *Refresh* or *NoAct* cue was onscreen (left pair of bars) and during only the early portion of the cue period (0–800ms post-cue; middle pair of bars). During those time periods, classification performance between *Refresh* and *NoAct* did not differ. However, during the later portion of the cue period (800–1400ms; right pair of bars), category classification for *Refresh* was significantly greater than both chance and *NoAct* classification; *NoAct* classification did not differ from chance. **B.** The same category classification analysis is shown across individual timepoints (collapsed into 40ms bins) for the *Refresh* and *NoAct* conditions. At approximately 700–800ms post-cue, *NoAct* classification performance dropped to near chance while *Refresh* classification performance remained higher. Asterisks indicate significant differences in classification performance between *Refresh* and *NoAct* at an uncorrected threshold of $p < 0.05$ (paired t-tests). Error bars (**A**) and shaded regions (**B**) indicate standard error of the mean.

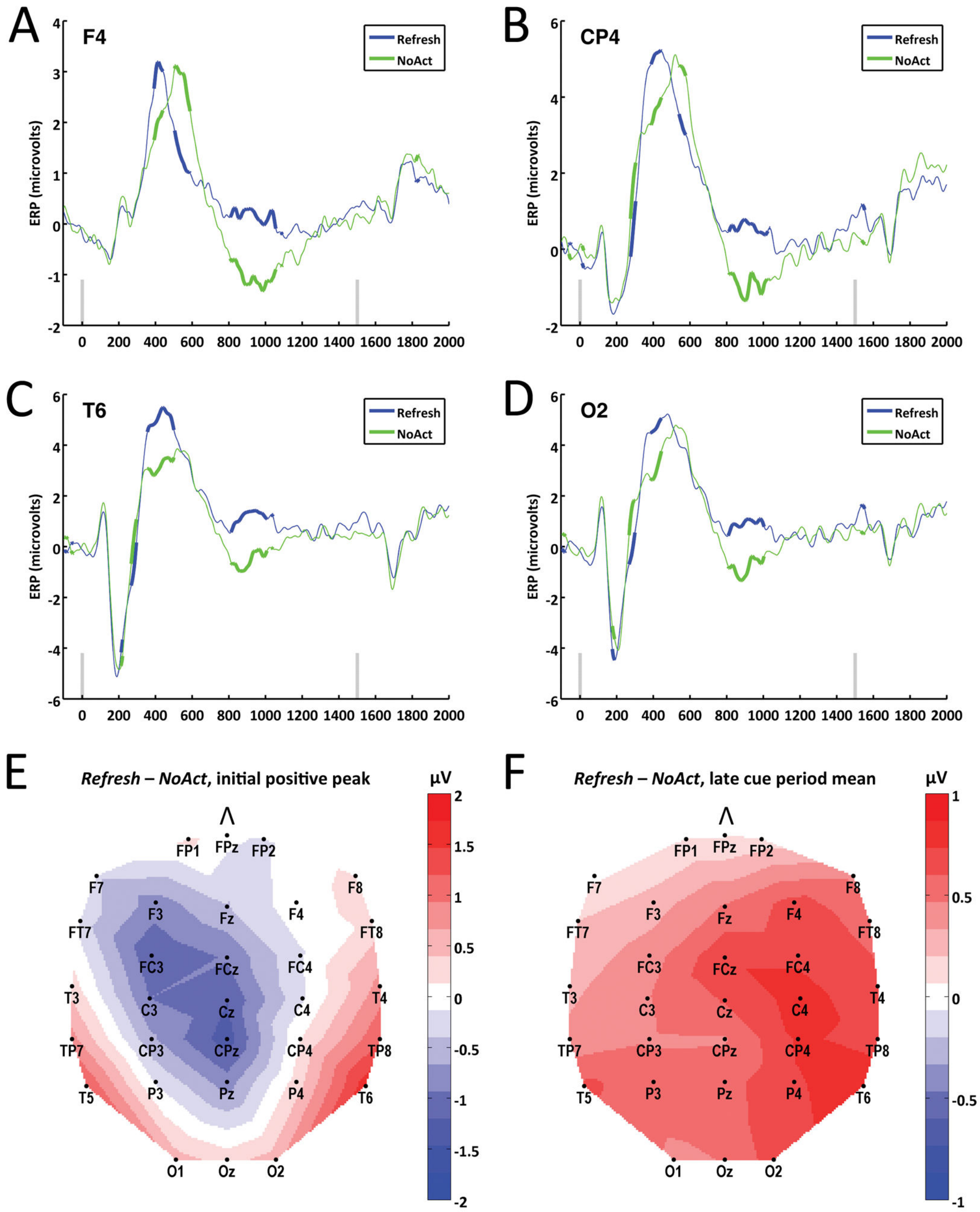

Figure 7. Refresh-related responses at selected electrodes and scalp distributions (Experiment 2)

A–D. Panels show post-cue ERPs for the *Refresh* and *NoAct* conditions at the same electrodes shown in Figure 3C–F. At multiple electrodes, the *Refresh* condition had a more positive and/or earlier-latency peak than *NoAct* in the early part of the cue period (~400ms post-cue), as well as a sustained positive response that was greater for *Refresh* than *NoAct* later in the cue period (between ~800–1400ms post-cue). Timepoints plotted in bold are those that significantly differed between conditions at an uncorrected threshold of $p < 0.05$. The lines at 0ms and 1500ms indicate the onset and offset of the *Refresh*/*NoAct*/*Act* cue. **E.** Scalp distribution of the difference between *Refresh* and *NoAct* at the initial P3-like peak, irrespective of latency, defined as each condition’s maximum voltage in the period 300–600ms post-cue. **F.** Scalp distribution of the difference between *Refresh* and *NoAct* during the later period, defined as each condition’s mean voltage in the period 800–1400ms post-cue.

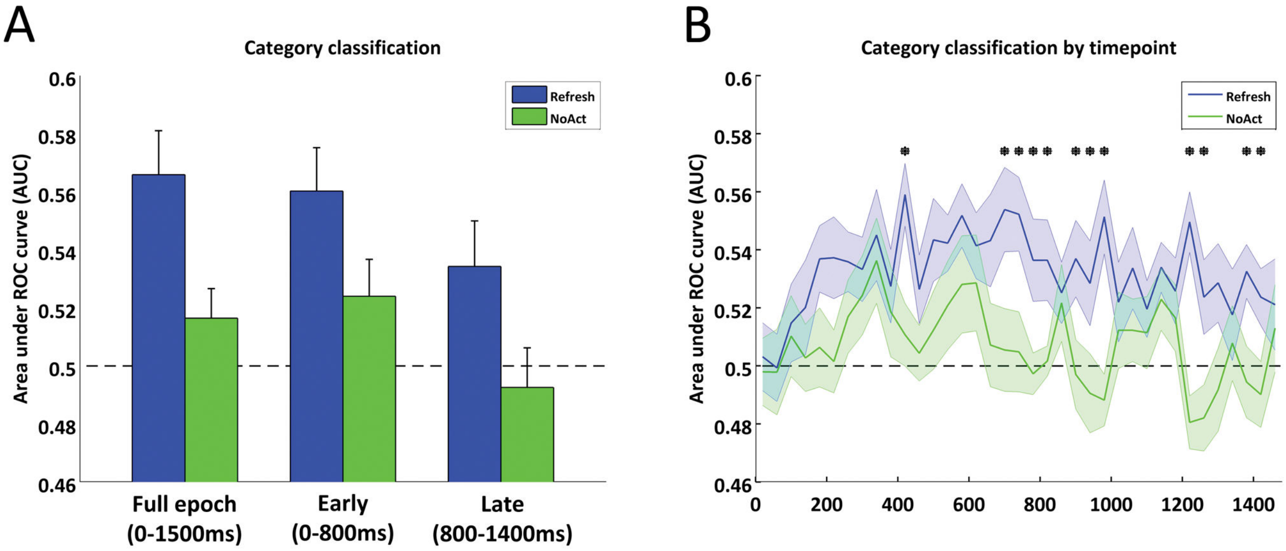

Figure 8. Multivariate pattern analysis of category information (Experiment 2)

A. Classification analyses of the initially presented stimulus category were significantly above chance (= 0.5) during the *Refresh* condition when considering the full time period that the cue was onscreen (left pair of bars), during only the early portion of the cue period (0–800ms post-cue; middle pair of bars), and during the later portion of the cue period (800–1400ms; right pair of bars). In contrast, *NoAct* classification was not significantly greater than chance during the full cue period, or during either the early or late portions alone. Category classification for *Refresh* was significantly greater than *NoAct* classification in all cases. **B.** The same category classification analysis is shown across individual timepoints (collapsed into 40ms bins) for the *Refresh* and *NoAct* conditions. *NoAct* classification performance generally remained near chance throughout the cue period while *Refresh* classification performance remained higher. Asterisks indicate significant differences in classification performance between *Refresh* and *NoAct* at an uncorrected threshold of $p < 0.05$ (paired t-tests); differences between conditions appeared primarily during the late portion of the cue period. Error bars (**A**) and shaded regions (**B**) indicate standard error of the mean.