Using Event-Related Brain Potentials to Help Explain Posterior-Parietal Repetition Effects in Functional Magnetic Resonance Imaging

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Abstract

Background: A major distinction in cognitive psychology is that two different forms of memory exist, explicit and implicit memory. Explicit memory is the effortful, deliberate recollection of past experiences (e.g., remembering a specific event in one's past). Unlike explicit memory, implicit memory does not require effortful, deliberate recollection of past experiences to influence behavior, yet memory is still expressed (e.g., stimulus processing is facilitated for repeated relative to a non-repeated stimulus, an effect labeled repetition priming,). Each of these forms of memory has been extensively researched and different cortical regions appear to underlie explicit and implicit memory. Recently, however, functional magnetic resonance imaging (fMRI) experiments have indicated that repetition effects in posterior-parietal regions that are usually associated with explicit memory have been measured in implicit memory experiments.

Question: Why are repetition effects in posterior-parietal regions observed during an implicit memory task when intentional (or explicit) memory retrieval is not necessary for task performance?

Possible Interpretations: Three possible interpretations of these effects were put forward and tested in this experiment using event-related potentials (ERP). Previous studies of posterior-parietal activity suggest that repetition effects in these areas could be attributable to (1) involuntary contamination of explicit memory for previously presented stimuli during putative implicit memory tests, (2) changes in the default mode network (DMN), which is a general network in the brain most active when the participant is not taxed with a cognitive task, and (3) priming in the action pathway of vision.

Method: These interpretations were tested using time domain (TD) ERPs collected during a putatively implicit memory experiment that paralleled the procedure used in a preceding fMRI experiment. Time-frequency (TF) analysis also was performed on these ERP data and two frequency bands were extracted (alpha, 8-12 Hz; theta, 2.5-8 Hz). Using TD ERPs and TF analysis allows for arbitrating between the three potential interpretations.

Predictions: The explicit memory contamination hypothesis posits that primed (repeated) stimuli should not differ from unprimed (new) stimuli in the TD until 500 ms or later, but afterward there should be a positive deflection (primarily anterior in topography) for primed stimuli compared to unprimed stimuli. Also, the explicit memory contamination posits that anterior alpha or theta power should be greater for primed stimuli than for unprimed stimuli. The change in DMN hypothesis posits that posterior alpha power should be greater for primed stimuli than for unprimed stimuli or anterior theta power should be lesser for primed stimuli than for unprimed stimuli. The priming in the action pathway hypothesis posits that a difference in activity between primed and unprimed conditions should be observed in an early P1 component in occipital temporal locations, and this effect should be greater for highly actionable objects than for non-actionable objects.

Results: Primed stimuli elicited a more positive deflection (beginning between 300 and 400 ms) in the TD ERP measures relative to unprimed stimuli, replicating many previous implicit memory ERP studies. One of the three possible interpretations to explain posterior-parietal activation was supported with the ERP and TF analysis. In line with the change in DMN hypothesis, lesser anterior theta power was measured for the primed stimuli relative to the unprimed stimuli.

Conclusion: In conclusion, the current ERP experiment offers insight into posterior-parietal repetition effects measured with fMRI during putatively implicit memory experiments. Results supported the hypothesis that the DMN is engaged by primed and unprimed stimuli to different degrees. This will allow researchers to interpret posterior-parietal repetition effects measured with fMRI in a putatively implicit memory experiment as potentially reflecting a change in DMN processing.

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Introduction

A major distinction in cognitive psychology is that two different forms of memory exist, explicit and implicit memory (Graf & Schacter, 1985; Tulving, 1985; Tulving, Schacter, & Stark, 1982). Explicit memory is the effortful, deliberate recollection of past experiences. Remembering a specific event in one's past is an example of explicit memory. Unlike explicit memory, implicit memory does not require effortful, deliberate recollection of past experiences to influence behavior, yet memory is still expressed. An example of implicit memory is repetition priming, in which performance of a task is facilitated when processing a repeated stimulus compared with processing a non-repeated stimulus. For example, repetition priming can be observed as faster and more accurate object identification when processing a repeated object relative to a non-repeated object (Bartram, 1974; Cave & Squire, 1992).

While the distinction between explicit and implicit memory has been investigated, much has been learned about the neural regions underlying vision and memory in the last three decades. Replicating previous neuroscientific work with non-human primates (Ungerleider & Mishkin, 1982), an important finding in human visual cortex is that ventral and dorsal visual pathways diverge after lower-level visual processing in occipital cortex (Haxby et al., 1991). Information travels ventrally into temporal cortices in the ventral visual pathway, and information travels dorsally into parietal regions in the dorsal visual pathway. The ventral visual pathway has been named the 'what' pathway because areas that make up this pathway (e.g., occipital, occipitotemporal, and temporal) have been associated with processing visual-form information. The dorsal visual pathway has been named the 'where' pathway

(Ungerleider & Mishkin, 1982) or 'action' pathway (Goodale & Milner, 1992) because areas that make up this pathway (e.g., parietal and into motor cortex) have been associated with processing spatial information, especially information relevant to guiding motor actions.

Specific and separable regions have been implicated in visual-form repetition priming (Henson, 2003) and episodic memory retrieval (Cavanna, & Trimble, 2006; Wagner, Shannon, Kahn, & Buckner, 2005). Visual-form repetition priming has been implicated in ventral regions (e.g., ventral visual pathway) and episodic memory retrieval has been implicated in dorsal regions (e.g., dorsal visual pathway) as well as prefrontal regions (Shimamura, 1995; Struss & Benson, 1984) and medial temporal regions including the hippocampus (Cohen & Eichenbaum, 1993; Squire, 1992).

Recently and somewhat unexpectedly, repetition effects have been reported in the posterior-parietal cortex (part of the dorsal visual pathway) during visual-form repetition priming experiments (Blondin & Lapage, 2005; Chao, Weisberg, & Martin, 2002; Fiebach, Gruber, & Supp, 2005; Habeck, Hilton, Zarahn, Brown, & Stern, 2006; Korsnes, Wright, & Gabrieli, 2008; Koutstaal, Wagner, Rotte, Maril, Buckner, & Schacter, 2001; Lin & Ryan, 2007; Poldrack, Desmond, Glover, & Gabrieli, 1998; Poldrack & Gabrieli, 2001; Soldan, Zarahn, Hilton, & Stern, 2008; Turk-Browne, Yi, Leber, & Chun, 2007; Vuilleumeir, Schartz, Duhoux, Dolan, & Driver, 2005; Wheatley, Weisberg, Beauchamp, & Martin, 2005; Zago, Fenske, Aminoff & Bar, 2005). This is somewhat surprising because damage restricted to posterior parietal areas in humans (Ally, Simons, McKeever, Peers, & Budson, 2008; Simons et al., 2008) and in non-human primates (Ungerleider & Mishkin, 1982) tends not to impair visual object perception. What do posterior parietal repetition effects reflect when measured during visual-form repetition priming experiments? In this paper, I seek to answer this question by reviewing the relevant neuro-cognitive (functional magnetic resonance imaging [fMRI] and event-related potentials [ERPs]) literature and directly testing neural repetition effects with ERPs.

Potential Difficulties in Measuring Priming

In a putatively implicit memory experiment, there is a possibility that not just implicit memory has been measured. Explicit memory contamination during a putatively implicit memory task is possible because completely extinguishing explicit processing during an implicit memory experiment is difficult. Differentiating between explicit and implicit memory contributions during the performance of an implicit memory task is important in order to understand priming effects. Separable neural substrates have been proposed for implicit and explicit memory (Henson, 2003; Rugg et al., 1998) but confidently distinguishing between these has proven difficult. Measuring topographical differences between activation due to incidental or spontaneous processing (implicit) and deliberate retrieval of memory (explicit) could be a way to differentiate between substrates. A frontal topographical distribution of activity has been measured for explicit retrieval and a posterior topographical distribution of activity has been measured for implicit memory, using ERPs (Rugg et al., 1998; Voss & Paller 2008) and fMRI (for review, see Schacter, Wig & Stevens, 2007; Henson, 2003). Although topographical differences between implicit processing and explicit retrieval are apparent, several other factors could affect measurement.

Certain variables increase the likelihood that participants will use implicit processes instead of explicit processes. For example, allowing only superficial processing of the prime stimuli (e.g., via pattern masking; Dehaene et al., 1998) decreases explicit memory contamination. Also, using different encoding and test tasks reduces possible response learning that can lead to explicit memory contamination (Dobbins, Schnyer, Verfaellie, & Schacter, 2004; Horner & Henson, 2008; Schnyer, Dobbins, Nicholls, Schacter, & Verfaellie, 2006). When different tasks are used, the likelihood of measuring true implicit processing may be increased and explicit memory contamination may be reduced.

Additional evidence indicates that increasing perceptual difficulty during the test task increases the likelihood of explicit memory contamination (James, Humphrey, Gati, Menon, & Goodale, 2000; Osftergaard, 1998). By presenting repeated and new stimuli at test in a slow, gradual fading-in manner, a greater behavioral priming effect (Ostergaarrd, 1998) and a greater repetition enhancement (RE; discussed below) effect in fMRI (James et al., 2000) have been measured, relative to un-degraded stimulus presentation conditions. More important, the increase in priming for items in the degraded conditions was accompanied by increased likelihood of remembering those items in a subsequent explicit memory test. Thus, one interpretation is that greater behavioral priming and RE in these reports reflect explicit memory contamination. That is, speeded responding and greater BOLD signal may be measures of increased explicit retrieval, which could be useful for helping to process the perceptually degraded stimuli. These potential issues were taken into account when setting up the current experiment.

Neuroimaging Techniques and Typical Measurements of Repetition Priming

Neural correlates of repetition priming have been measured using both fMRI ERPs. Precise spatial resolution but poor temporal resolution can be achieved with fMRI and precise temporal resolution but poor spatial resolution can be achieved with ERPs. Converging evidence of repetition priming measured in fMRI and ERP allows for a better understanding of where and when these processes occur. An important next step in understanding neural correlates of repetition priming is distinguishing which brain area is activated when.

Functional Magnetic Resonance Imaging. The neuroimaging technique of fMRI has the advantage of high spatial resolution in localizing brain activity. Measurement of deoxygenated hemoglobin (blood-oxygenation-level dependent or BOLD signal) is of greatest interest here (see Huettel, Sond & McCarthy, 2003 for in-depth description of fMRI techniques and quantification). The BOLD signal has been linked to dendritic activity that makes up local field potentials (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). Often in fMRI research, the BOLD signal elicited by a baseline condition is subtracted from the BOLD signal elicited by an experimental condition. The relative increase or decrease in activation is then (broadly speaking, assuming the use of an appropriately tight control condition) interpreted to reflect activity associated with processing the experimental stimulus (specific examples of relative activation differences are presented below). The advantage of using this technique to explore cognitive processes is the spatial resolution. However, the temporal resolution of this technique is quite low (normal activation is measured in the brain over a long period of time, such as 2 seconds). Another neuroimaging technique is required to increase temporal resolution.

One of the most replicated neural measures associated with priming is a decrease in BOLD signal elicited by repeated stimuli relative to non-repeated stimuli (Eddy, Schnyer, Schmid, & Holcomb, 2007; Eger, Henson, Driver, & Dolan, 2004; Fiebach et al., 2005; Grill-Spector & Malach, 2001; Habeck et al., 2006; Henson, 2003; Henson, Rugg, & Shallice, 2000; James & Gauthier 2006; Klaven et al., 2007; Koutstaal et al., 2001; Lin & Ryan, 2007; Poldrack et al., 1998; Poldrack & Gabrieli, 2001; Sayres, & Grill-Spector, 2006; Turk-Browne et al., 2007; Vuilleumeir et al., 2005; Wheatly et al., 2005; Xu, Turk-Browne, & Chun, 2007; Yi, & Chun., 2005; Zago et al., 2005). These "repetition suppression" (RS) effects have been measured in the inferior temporal (IT; e.g., Buckner, Koutstaal, Schacter, & Rosen, 2000) cortex, the lateral occipital complex (LOC; e.g., Grill-Spector & Malach, 2001), the fusiform cortex (FS; e.g., Koutstaal et al., 2001), the parahippocampal place area (PPA; e.g., Yi, & Chun, 2005), and the inferior prefrontal cortex (IPFC; Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000; Wig, Grafton, Demos, & Kelley, 2005). RS generally has been understood as reflecting a reduction, ease, or facilitation in processing repeated stimuli because of recent exposure to them (Henson, 2003). Three different theories have been proposed to explain reduced BOLD signal as a measure of facilitated processing of repeated stimuli, the sharpening model (Desimone, 1996; Wiggs & Martin, 1998), the fatigue/adaptation model (Grill-Spector, Henson, & Martin, 2006; Grill-Spector & Malach, 2001), and the accumulation model (Henson & Rugg, 2003;

James & Gauthier, 2006; James et al., 2000). Though RS is very prevalent, additional patterns of results have been measured with fMRI.

In some cases, repeated stimuli do not elicit decreased BOLD signal relative to non-repeated stimuli (Eger et al., 2004; Yi & Chun, 2005) and in certain situations repeated stimuli elicit increased BOLD signal relative to non-repeated stimuli (Henson et al., 2000; Turk-Browne et al., 2007; Vuilleuimier et al., 2005). In the latter cases, "repetition enhancement" (RE) was observed. Therefore, both RS and RE have been measured during repetition priming experiments. RE in the ventral visual pathway has been elicited by repeated unattended stimuli (Yi & Chun, 2005), novel (Fiebach et al., 2005; Hensons et al., 2000) and degraded stimuli (Turk-Browne et al., 2007) in particular. One model, the accumulation model (Henson & Rugg, 2003; James & Gauthier, 2006; James et al., 2000) can account for RE, though only in certain situations (i.e., when stimuli are unidentified). Another interpretation is that RE could be related to the engagement of a new process during test that was not engaged during encoding for repeated stimuli, although it is unclear what such an additional process may be or what purpose it may serve (Henson, 2003). An alternative interpretation of RE effects measured during an implicit memory experiment could be that explicit memory processes have contaminated the priming effect (Schacter & Badgaiyah, 2001).

Electroencephalography and Event-Related Potentials. Unlike fMRI, the neuroimaging technique of ERP has the advantage of high temporal resolution. With electroencephalography (EEG) as a tool to measure electrical activity associated with brain functions, researchers are able to measure neural processing during the performance of cognitive tasks. Of primary interest is scalp recorded EEG which is a measure of postsynaptic electrical activity occurring primarily in the dendrites of neurons (see Luck, 2005 for in-depth description of EEG and ERP techniques and quantification). By averaging portions of the continuous EEG recording, using stimulus onset (i.e., an event) as a zero time point, ERPs can be extracted (i.e., the average electrical potential elicited by events in one condition). With information from stimulus-locked ERPs, researchers are able to measure differences in activity between experimental conditions in a way that can lead to further understanding of the underlying neural processes.

Researchers using ERPs have been successful in delineating explicit and implicit memory processes both temporally and spatially. An early positive deflection in the ERP waveform (e.g., ~250 ms), with a posterior distribution of electrode sites, elicited by repeated stimuli relative to non-repeated stimuli has been attributed to implicit memory processing (Bentin, Moscovitch, & Heth, 1992; Doyle, Rugg, & Wells, 1996; Paller & Gross 1998; Rugg, 1995; Rugg et al., 1998). A late positive deflection (e.g., > 500 ms), with an anterior distribution of electrodes, elicited by repeated stimuli relative to new stimuli has been attributed to explicit memory processing (Rugg et al., 1998; Voss & Paller, 2008). This distinction is important because it allows researchers to better isolate specific memory processes of interest when using this neuroimaging technique.

Each of these techniques has an advantage (fMRI his high spatial resolution; ERP has high temporal resolution) and disadvantage (fMRI has low temporal resolution; ERP has low spatial resolution). By combining measurements in fMRI and

ERP using the same task, both high spatial resolution and high temporal resolution can be obtained.

***Unexpected Neural Correlate of Priming in fMRI*.**

Traditionally, neural correlates of priming of visual objects have been found in the LOC (e.g., Grill-Spector & Malach, 2001), the FS (e.g., Koutstaal et al., 2001), the IT (e.g., Desimone, 1996), the PPA (e.g., Yi. & Chun, 2005), and IPFC (Wagner et al., 2000; Wig et al., 2005). LOC, FS, and IT are ventral visual pathway areas that operate downstream of primary visual cortices and are thought to process visual stimuli at higher levels than primary visual cortices. That is, low-level visual information from the primary visual cortex feeds to the LOC, FS, and IT where higher level visual processing of objects occurs, as necessary to identify objects. Specific cortical areas in which RE and RS effects have been measured during repetition priming tasks are partially determined by stimulus type. For example, the LOC and the FS have been implicated in processing objects (e.g., Grill-Spector, Kushnir, Hendler, & Malach, 2000), the PPA has been implicated in processing scenes (e.g., Yi, & Chun, 2005), and the FS has been implicated in processing faces (e.g., Henson et al. [2000], but see also Haxby et al. [2001] and Gauthier, Skudlarski, Gore, & Anderson [2000] for evidence against face-specific processing in the putative fusiform face area).

In addition to these traditional brain regions, initially unexpected repetition effects have been reported in posterior-parietal regions (including the precuneus) in recent priming experiments (e.g., Korsnes et al., 2008). Given that object repetition effects typically have been found in relevant visual-form processing areas (LOC, FS, IT, PPA, and IPFC) repetition effects in posterior-parietal regions are of particular interest in the present project. Such effects are surprising because damage to posterior parietal areas does not impair visual object recognition (Ally et al., 2008; Simons et al., 2008; Ungerleider & Mishkin, 1982).

Deason, Steele, Marsolek, and Koutstaal (2008) carried out an fMRI repetition priming experiment in which posterior-parietal (i.e., precuneus) activation was measured in a putatively implicit memory experiment. This experiment was designed with the hope of eliciting repetition effects in ventral visual stream areas that are most commonly associated with neural repetition effects for objects (see Figure 1). Using typical univariate fMRI analyses, little differentiation between experimental conditions was found in the ventral stream (however, differentiation was observed using multivariate techniques; McMenamin, Deason, Steele, Koutstaal, & Marsolek, 2009; 2011). Surprisingly, the strongest effects indicated that repeated stimuli elicited less neural deactivation than new stimuli (a repetition effect) in the dorsal stream (i.e., posterior-parietal region; see Figure 2). During the encoding phase of this experiment, familiar objects and concrete nouns were individually presented to participants who made a likeability rating for each stimulus. At test, four types of familiar objects were presented: same-exemplar primed (objects repeated from encoding); different-exemplar primed (objects that were different exemplars within the same categories as objects presented at encoding); word primed (objects for which a corresponding object name was presented at encoding); and unprimed objects (new objects unrelated in any way to stimuli presented at encoding). During the test phase, participants performed a perceptual identification task (i.e., press one button if they could identify the briefly presented stimulus and another button if they could not). Repetition effects (differential activity between the primed and unprimed conditions) were measured in two separate posterior-parietal regions (see Figure 2).

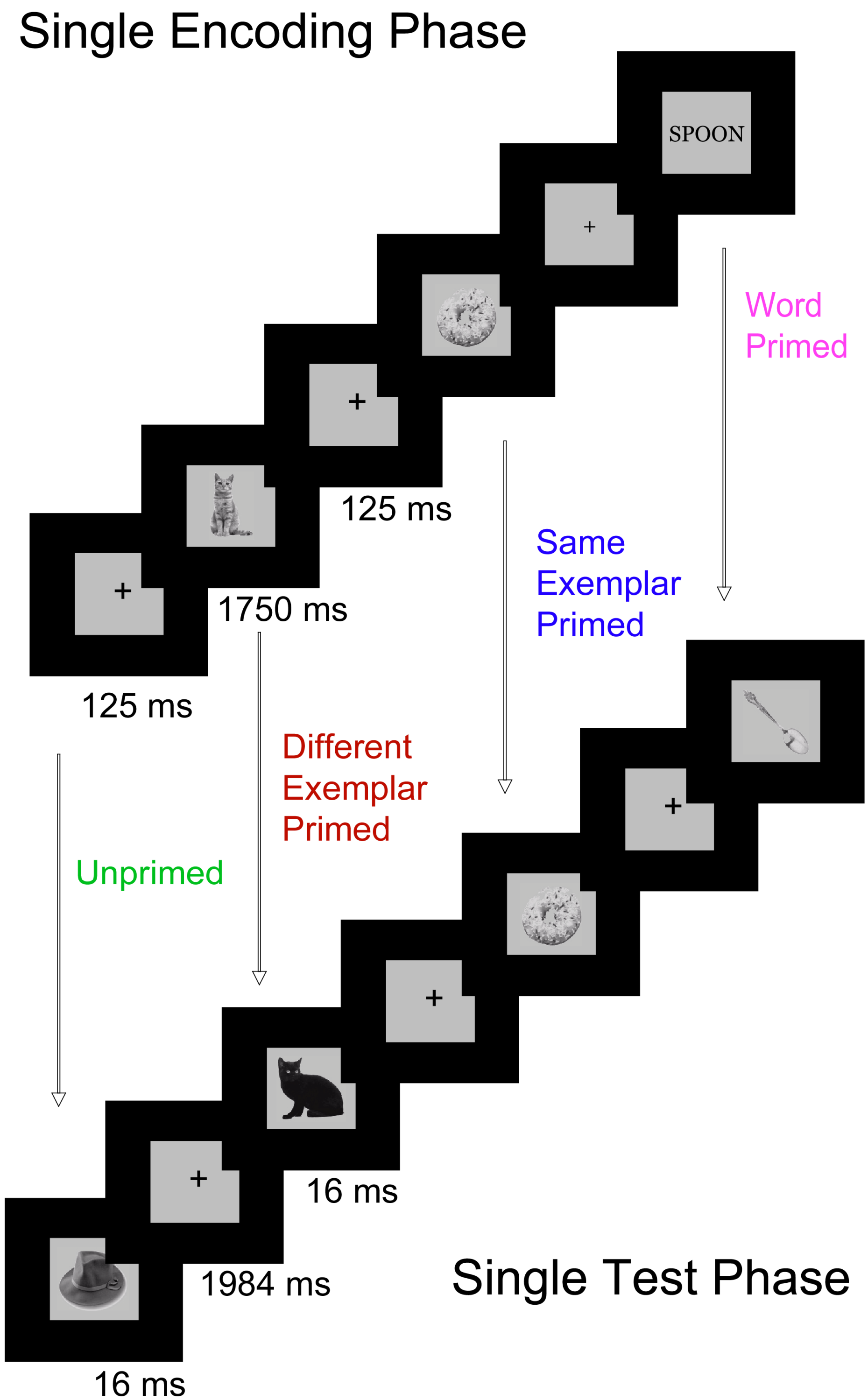

Figure 1. Experimental method from a preliminary fMRI repetition priming experiment (Deason et al., 2008) depicting examples of experimental conditions (same-exemplar primed, different-exemplar primed, word primed, and unprimed).

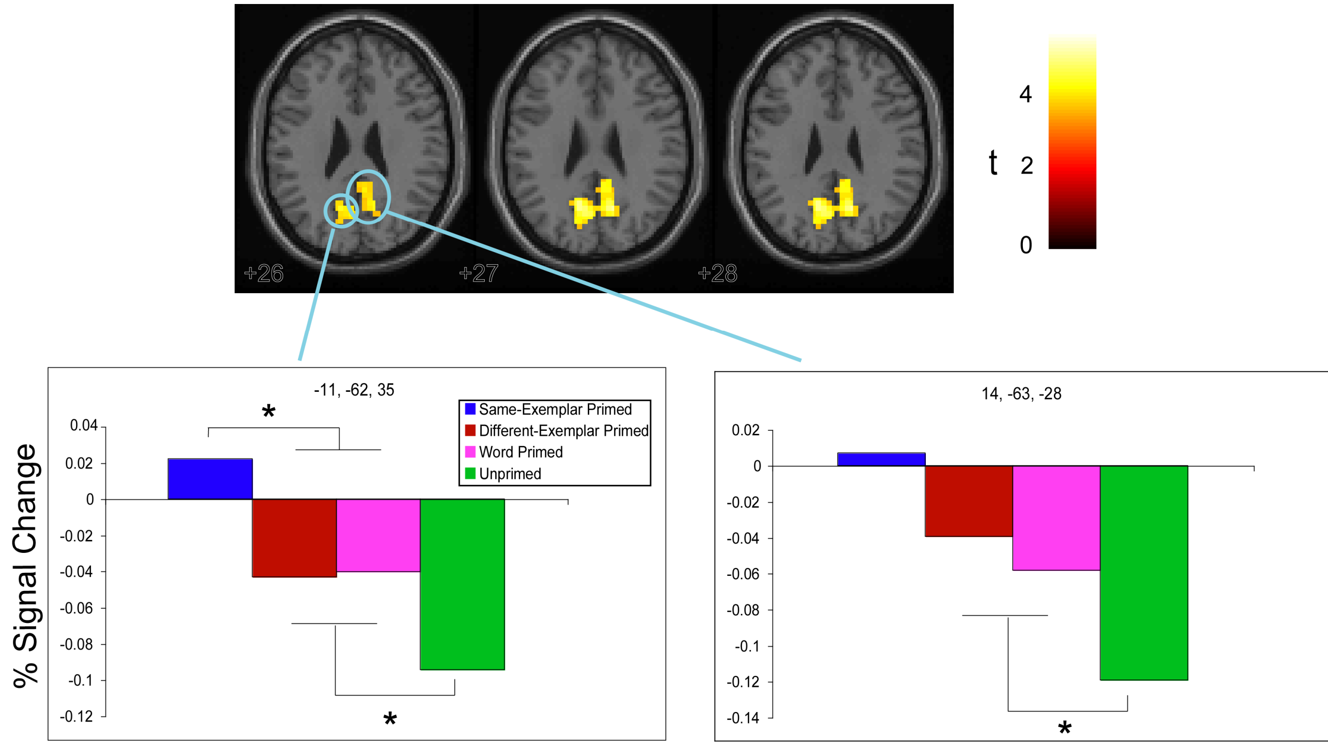

Figure 2. BOLD results from a preliminary fMRI repetition priming experiment (Deason et al., 2008) indicating neural repetition effects in posterior-parietal cortical areas.

The difference in fMRI BOLD signal for primed objects compared with unprimed stimuli was interpreted to reflect involuntary explicit memory retrieval for the primed stimuli (Deason et al., 2008). Although this posterior-parietal region has been implicated in explicit memory processing, possible alternative explanations for the posterior-parietal effects can be offered, and these were tested in the present study.

Many different functions have been attributed to precuneus activation. Few focal lesions of the precuneus occur and localization is difficult because it lies between two distinct Brodmann areas (BA). The precuneus lies between BA 7 and 31, dorsal to the intraparietal sulcus (IPS) and posterior to the central sulcus (see Cavenna, 2007; Cavanna, & Trimble, 2006; Zilles, & Palomero-Gallagher, 2001). The precuneus is interconnected to several anterior and posterior cortical regions. Anterior regions include dorsal pre-motor areas, supplementary motor areas, and the anterior cingulate (Cavada & Goldman-Rakic, 1989; Leichnetz, 2001). The precuneus is also involved in reciprocal parietal-frontal communication with regions involved with oculomotor function (Leichnetz, 2001; Leichnetz & Gonzalo-Ruiz, 1996). Guided hand movements and hand-eye coordination in humans requires processing in the precuneus (Ferraina et al., 1997). Finally, because of the great numbers of connections with cortical and subcortical structures, the precuneus has been suggested to play an integral role in what is called the default mode network (DMN; Fransson & Marrelec, 2008; Raichle et al., 2001). The DMN is identified as having increased activation during resting state periods (eyes open or closed) relative to non-resting state periods (performing a cognitive task). Four main categories of processing have been attributed to the precuneus: consciousness (for review, see Shulman et al., 1997; Mazoyer et al., 2001; Gusnard & Raichle, 2001; Fransson & Marrelec, 2008; Laureys et al., 1999; Maquet et al., 1997; Raichle et al., 2001;), self-processing (Lou et al. 2004; Ruby & Decety, 2001; Vogeley et al., 2001), visuo-spatial imagery (Astafiev et al., 2003; Berryhill, & Olson, 2008; Fink et al., 1997; Kawashima, Roland, & O'Sullivan, 1995; Nagahama et al., 1999), and episodic memory retrieval (Berryhill, & Olson, 2008; Buckner et al., 1995; Fletcher, Shallice, Frith, Frackowiak, & Dollan, 1996; Halsband et al., 1998; Henson, Rugg, Shallice, Josephs, & Dollan, 1999; Henson, Shallice, Gorno-Tempini, & Dollam, 2002; Valenstein et al., 1987; for reviews see Cavanna, 2007; Cavanna & Trimble, 2006; Wagner et al., 2005).

Repetition effects measured in posterior-parietal regions are commonly reported during implicit memory experiments (for review, see Steele, 2009; Blondin & Lapage, 2005; Chao et al., 2002; Fiebach et al., 2005; Habeck et al., 2006; Korsnes et al., 2008; Koutstaal et al., 2001; Lin & Ryan, 2007; Poldrack et al., 1998; Poldrack & Gabrieli, 2001; Soldan et al., 2008; Turk-Browne et al., 2007; Vuilleumeir et al., 2005; Wheatley et al., 2005; Zago et al., 2005). Two interpretations of these repetition effects are most prevalent. First, they are usually interpreted as reflecting involuntary explicit memory processes during putative implicit memory tests (Blondin & Lapage, 2005; Chao et al., 2002; Korsnes et al., 2008; Poldrack & Gabrieli, 2001; Poldrack et al., 1998; Vuilleumeir et al., 2005; Wheatley et al., 2005; Zago et al., 2005). This interpretation had been put forward because posterior-parietal activation has been linked to explicit memory (Cavanna, & Trimble, 2006; Wagner et al., 2005) and repetition effects in areas other than parietal cortex were the primary focus of implicit memory effects in most of those reports.

Second, repetition effects in the posterior-parietal cortex have been interpreted as reflecting DMN processing, because posterior-parietal areas are one part of the larger interconnected DMN (Habck et al., 2006; Koutstaal et al., 2001; Turke-Browne et al., 2007). Increases and decreases in fMRI BOLD signal are almost always measured relative to a baseline measure, and conceptualizing activation increases and decreases in the DMN is dependent on the specific baseline measure. Often, the baseline measure is a resting state (e.g., eyes open/closed) or a null trial (e.g., a blank or fixation-point trial that requires no response). In these instances, BOLD signal is decreased during experimental trials relative to the resting state or null trials (Shulman et al., 1997; see

Singh & Fawcett, 2008 for discussion). Therefore, the negative BOLD signal presented in Figure 2 may be interpreted as a decrease in DMN processing (DMN is reverse-workload dependent). In other words, because the primed conditions were less negative compared with the unprimed condition, the DMN was less deactivated during trials with repeated stimuli than trials with new stimuli.

Finally, a third interpretation of repetition effects in posterior-parietal cortex is supported by very recent fMRI findings. Neural repetition effects for shapes have been observed in posterior-parietal cortex, and just like repetition effects in the ventral visual stream, the repetition effects in the dorsal visual stream are viewpoint and size invariant (Konen & Kastner, 2008). The dorsal visual stream (the "where" stream) usually is understood as underlying visual spatial processing, and the ventral visual stream (the "what" stream) usually is understood as underlying visual shape processing (Ungerleider & Mishkin, 1982). However, Konen and Kastner suggest that their results may be evidence that the dorsal visual pathway performs object processing, but unlike ventral object processing, dorsal object processing is important for visually guided action, as opposed to shape perception (the dorsal visual stream has been labeled the "action" pathway; Goodale & Milner, 1992). This can be understood as priming in the action pathway, which facilitates potential future motor movements or action pathway processing.

To summarize, several brain regions exhibit neural correlates of repetition priming. Perhaps most intriguingly, repetition effects in posterior-parietal regions, including the precuneus, have been measured during visual object repetition priming experiments. Repetition effects measured in the precuneus during memorial tasks has been interpreted to reflect explicit memory retrieval; however, they could reflect a lesser degree of deactivation in the DMN for primed stimuli than for unprimed stimuli or a form of priming in the action pathway of vision. Evidence discussed thus far has all come from fMRI experiments. Could an ERP experiment be of use in distinguishing the underlying processes measured in posterior-parietal regions during a putatively implicit memory experiment?

Event-Related Potentials and Posterior-Parietal Repetition Effects

By collecting ERP data during the time course of processing primed and unprimed stimuli, one could test all three alternative explanations put forward to interpret fMRI findings of neural repetition effects in posterior-parietal cortex. Also, with the excellent temporal resolution of ERPs, one could assess when these implicated processes occur during the time course of object processing trials. By using a newly developed data analysis technique, time-frequency (TF) analysis (an advanced method to isolate frequency waves that make up the ERP waveform; see; Bernat, Williams, & Gehring, 2005), detailed tests of the cognitive processes that underlie the ERP waveform are possible.

This study was conducted to increase our understanding of fMRI repetition effects measured in posterior-parietal regions. These repetition effects have been interpreted as reflecting explicit memory contamination, changes in the DMN, or action pathway priming. Using the temporal and spatial information of ERPs and TF analysis in the proposed study, testing between these three potential interpretations is possible.

The three possible explanations for the measured repetition effects in posterior-parietal regions lead to different predictions for ERP results.

Explicit Memory Contamination. ERP markers of explicit memory processes have been established for both the time-domain (TD) and in specific frequency bands. Explicit memory processes have been distinguished in ERPs by a late positive deflection (e.g., > 500 ms) elicited by repeated stimuli relative to new stimuli, with an anterior electrode distribution (Rugg et al., 1998; Voss & Paller, 2008). In addition, explicit memory processes have also been associated with theta (4.5 - 7.5 Hz) and alpha (8 - 11.5 Hz) power with an anterior distribution (Düzel et al., 2003). In particular, enhanced anterior theta and alpha power should be observed when explicit memory processes occur (e.g., during involuntary explicit memory retrieval when primed stimuli are presented) relative to when explicit memory processes do not occur (e.g., when processing a new stimulus).

Changes in the Default Mode Network. The DMN has been used to describe a general network in the brain that is most active when the participant is not taxed with a cognitive task (i.e., during rest; Raichle et al., 2001; Raichle, & Snyder, 2007). Areas making up the DMN (including the precuneus and posterior-parietal regions; Fransson, 2006; Fransson, & Marrelec, 2008) exhibit increases in activation (or lesser deactivation) during resting state periods (e.g., with eyes closed) relative to non-resting state periods (e.g., when performing a cognitive task). In other words, the DMN is reverse-workload dependent (i.e., greater activation is measured in this region with lesser workload of a task). Primarily, DMN has been measured with fMRI but there have been a few published works linking ERP and specific TF measures to the DMN.

In particular, during resting state relative non-resting state, greater alpha power has been measured over posterior electrodes (Jaan et al., 2009; Laufs et al., 2003). Also, during resting state relative to non-resting state, lesser theta power has been measured over anterior electrodes (Chen, Feng, Zhao, Yin, Wang, 2008; Scheeringa et al., 2008). Therefore, if the DMN is engaged by primed stimuli to a greater degree than unprimed stimuli, an increase in posterior alpha or a decrease in anterior theta power should be observed for primed stimuli relative to unprimed stimuli.

Action Pathway Priming. The neural repetition effects in the aforementioned fMRI experiment (Deason et al., 2008) may be due to priming of visual object representations in the dorsal/action pathway. According to the action pathway priming hypothesis, important differences in object processing take place in the dorsal and ventral visual streams. Processing in the dorsal stream is important in planning future motor movements and therefore processing actionable objects should be different than processing non-actionable (or less actionable) objects in the dorsal stream. Indeed, manipulable objects like tools and non-manipulable objects such as windmills elicit different patterns of activity in the dorsal stream, because tools are more actionable (they can be acted upon with one's hands; Ghorashi, Enns, Klein, & Di Lollo, 2010; Kiefer, Sim, Helbig, & Graf, 2011; Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003; Konen, & Kastner, 2008; Mahon et al., 2007). Furthermore, highly actionable objects elicit a more positive early P1 (~75 ms to ~150 ms) ERP component in posterior electrodes (lateral occipital regions) than non-actionable objects (Handy et al., 2003; cf., Kiefer et al., 2011). Therefore, ERP repetition effects were compared between actionable and non-actionable objects. Actionability scores were assigned to each object using similar norming methods as used by Mahon et al. (2007). These scores were used to separate object stimuli into highly actionable and not highly actionable stimuli. If priming takes place in the action pathway of vision, greater positivity may be observed in the early P1 in lateral occipital leads for actionable objects than for non-actionable objects..

Summary of Hypotheses. ERP evidence may be useful to help explain fMRI repetition effects in posterior-parietal areas during a putative implicit memory experiment (Deason et al., 2008). The effects may be due to explicit memory contamination, changes in the DMN, or priming in the action pathway of vision. The new experiment reported here tested these hypotheses.

To arbitrate between the three potential cognitive processes that could account for the measured posterior-parietal repetition effects, an ERP study used the same procedure as used in the previous fMRI repetition priming experiment (Deason et al., 2008; see Figure 1). The experiment had two phases, an encoding phase and a test phase. During the encoding phase, objects and concrete nouns (words) were presented individually (for 1750 ms each) to participants who performed a likeability rating for each stimulus. During the test phase, four types of grayscale objects were presented (for 16 ms each). They were same-exemplar primed (objects repeated from encoding), different-exemplar primed (objects that were different exemplars within the same categories as objects presented at encoding), word primed (objects for which a corresponding object name was presented at encoding), and unprimed objects (new objects unrelated in any way to stimuli presented at encoding). Participants performed a perceptual identification task (i.e., press one button if they can identify the briefly presented stimulus and another button if they are not). ERPs from the test phase were examined in the TD, and TF analyses were carried out to investigate alpha and theta frequency bands.

With this experimental and analytical procedure, the three potential interpretations of posterior-parietal fMRI repetition effects will be directly tested. The explicit memory contamination hypothesis will be supported if: both 1) primed stimuli do not differ from unprimed stimuli in the TD until 500 ms or later, but there is a positive deflection (primarily anterior in topography) for repeated stimuli compared to unprimed stimuli and 2) anterior alpha or theta power is greater for primed stimuli than for unprimed stimuli. The change in DMN hypothesis will be supported if: 1) posterior alpha power is greater for primed stimuli than for unprimed stimuli or 2) anterior theta power is lesser for primed stimuli than for unprimed stimuli. The priming in the action pathway hypothesis will be supported if a difference in activity between primed and unprimed conditions in the early P1 component in occipital temporal leads is greater for highly actionable objects than for non-actionable objects.

Method

Participants

A total of 35 participants (20 female) were recruited from the University of Minnesota to participate in this experiment. These participants received course credit or monetary compensation in exchange for their participation. Twenty-four participants (half female) were selected for full analysis (mean age = 21, range = 18 – 28). This was the same number of participants as tested in the parallel fMRI experiment (Deason et al., 2008). They were the first 24 participants for which stimuli assignments to experimental conditions were fully counterbalanced across participants, for which no programming errors occurred, and who followed instructions correctly. Each participant had normal or corrected to normal vision, was right handed (laterality quotient mean = 0.87, range 0.3 - 1.0 on the Edinburgh Handedness Inventory; Oldfield, 1971), a native English speaker, and had no history of neurological disorder or damage (these inclusion criteria are in line with previous fMRI and ERP experiments).

Stimuli

The same set of visual objects and words that was used in the preceding fMRI experiment (Deason et al., 2008) was used here. These were grayscale images of familiar objects and words corresponding to these familiar objects. A total of 200 categories of objects were selected with 2 exemplars for each object category (i.e., two different exemplars of piano). In a separate behavioral norming session, several stimulus dimensions were assessed, including: 1) the level of agreement of the best name for each object, 2) the typicality of that particular exemplar with respect to all others in its category, 3) the frequency with which participants judged they saw instances of that category in everyday life, and 4) the visual similarity of the two exemplars in each category (see Figure 1 for examples). Four stimulus lists of 50 categories each were created for counterbalancing purposes; these lists were balanced on the four stimulus dimensions assessed in the separate behavioral norming session.

In an additional two-step norming process, one set of participants (N = 6) was asked to rate whether each stimulus was living or non-living. Though only 6 participants were recruited to rate the stimuli as living or non-living, the raters highly agreed (97% or greater) on which of these stimuli were living or non-living. In the second step, additional participants (N = 13) answered three questions for each of the non-living stimuli (see Appendix A). Following Mahon et al. (2007), to assess the actionability of each exemplar, participants were asked to rate: 1) how difficult would it be, while playing charades, to act out the item? 2) how central is the pattern of movement(s) associated with the use of the object/thing in determining its function? 3) how frequently do you interact with the object/thing with your hands? These ratings were designed as measures of actionability (e.g., an item rated as easily acted out in charades and/or the pattern of movements associated with the object are central to determining its function and/or the item is frequently interacted with would be considered highly actionable; see Table 1 for stimulus set by actionability question information for all stimuli classified as non-living).

Table 1. Number of stimuli in each stimulus set classified as non-living, means, and standard deviations of actionability ratings within each stimulus set by each actionability question. Actionability ratings for question 1 were reversed scored for easy comparison across questions (high numbers reflect highly actionable stimuli and low numbers reflect not highly actionable stimuli).

	Set 1 (N = 35)	Set 2 (N = 40)	Set 3 (N = 41)	Set 4 (N = 38)
Question	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
1	4.83 (1.32)	4.57(1.37)	4.84 (1.23)	4.40 (1.45)
2	3.89 (1.16)	4.15 (1.47)	4.18 (1.40)	4.05 (1.37)
3	4.26 (1.52)	3.78 (1.82)	3.91 (1.42)	3.99 (1.76)

The actionability ratings were used to identify stimuli that were highly actionable and compare those stimuli to stimuli judged to be not highly actionable. Actionability ratings for question 1 were reversed scored for easy comparison across questions (i.e., for each question, high numbers reflect highly actionable stimuli and low numbers reflect not highly actionable stimuli). The actionability score for question 1 (Q1) was correlated with questions 2 (Q2) and 3 (Q3; $r(154) = 0.709$, $p < .001$; $r(154) = 0.412$, $p < .001$, respectively) but Q2 and Q3 were not significantly correlated with each other ($r(154) = 0.119$, $p = .142$). Therefore, it can be safely assumed that the three norming questions overlapped somewhat in measuring actionability, though Q2 and Q3 did not similarly measure actionability. Correlations of the three norming questions within stimulus sets was similar to the overall actionability correlations presented above (see Table 2). For three of the four stimulus sets, Q1 was highly correlated with Q2 and

Q3 (see Table 3). In stimulus set 3, Q1 and Q2 were correlated but Q3 was not correlated with either Q1 or Q2. Across all four stimulus sets, Q2 and Q3 were not correlated. Therefore, the four stimulus sets had similar though not perfectly counterbalanced distributions of actionable and not actionable stimuli. Within each stimulus set and each norming question, terciles were calculated and each stimulus was assigned to one of three terciles. To identify the greatest actionability differences, only the first and third tercile within each stimulus set were selected for analysis in the actionability tests (see Table 4).

Table 2. Correlations (N = 154) between actionability questions, collapsed across stimulus sets.

	Question 1	Question 2	Question 3
Question 1	X	.709***	.412***
Question 2		X	.119
Question 3			X

Note. *** = p< .001

Table 3. Correlations between actionability questions, separated out by stimulus sets; A) stimulus set 1, B) stimulus set 2, C) stimulus set 3, D) stimulus set 4.

A – Stimulus Set 1 (N = 35)

	Question 1	Question 2	Question 3
Question 1	X	.546*	.407*
Question 2		X	.007
Question 3			X

B – Stimulus Set 2 (N = 40)

	Question 1	Question 2	Question 3
Question 1	X	.760**	.471**
Question 2		X	.210
Question 3			X

C – Stimulus Set 3 (N = 41)

	Question 1	Question 2	Question 3
Question 1	X	.795***	.104
Question 2		X	-.032
Question 3			X

D – Stimulus Set 4 (N = 38)

	Question 1	Question 2	Question 3
Question 1	X	.739***	.589***
Question 2		X	.258
Question 3			X

Note. * = p< .05, ** = p< .005, *** = p< .001

Table 4. Actionability scores for the first and third tercile split by stimulus set (1-4) separated out by actionability norming question (1-3). Actionability ratings for question 1 were reversed scored for easy comparison across questions (high numbers reflect highly actionable stimuli and low numbers reflect not highly actionable stimuli).

		Set 1	Set 2	Set 3	Set 4
Question	Tercile	Score (N)	Score (N)	Score (N)	Score (N)
1	1st	3.29 (11)	3.00 (13)	3.42 (14)	2.75 (13)
	3rd	6.42 (11)	6.06 (13)	6.16 (13)	6.02 (12)
2	1st	2.71 (12)	2.62 (14)	2.58 (13)	2.50 (12)
	3rd	5.18 (12)	5.93 (13)	5.78 (14)	5.53 (13)
3	1st	2.48 (11)	2.01 (13)	2.33 (13)	1.97 (13)
	3rd	5.98 (11)	6.08 (13)	5.57 (14)	6.01 (12)

Procedure

Participants were seated in a dimly lit room and viewed stimuli on a computer screen from a distance of approximately 60 cm. Stimuli were presented one at a time using E-Prime software (Psychology Software Tools, Inc. www.pstnet.com) and a serial response box. The same procedure used in the preceding fMRI repetition priming experiment (Deason et al., 2008) was used here (see Figure 1). The experiment included two phases, an encoding phase and a test phase. The encoding phase included 300 trials and the test phase included 400 trials. Half of the trials (150 in the encoding phase and 200 in the test phase) included the experimental stimuli of interest and the other half (in which only a fixation point was presented) were not analyzed. Before each phase, a brief practice session was presented to each participant. Each practice session included 20 trials (10 fixation), using an additional set of stimuli that were not used in the main experimental trials. Practice was designed to acquaint participants with the timing of the experimental trials in each phase.

During the encoding phase, objects and concrete nouns (words) were individually presented (for 1750 ms each) to participants who performed a likeability rating for each stimulus (see Appendix B). At test, four types of grayscale objects were individually presented (for 16 ms each), including same-exemplar primed (objects repeated from encoding), different-exemplar primed (objects that were different exemplars within the same categories as objects presented at encoding), word primed (objects for which a corresponding object name was presented at encoding), and unprimed objects (new objects unrelated in any way to stimuli presented at encoding). During the test phase, participants performed a perceptual identification task (i.e., press one button if they could identify the briefly presented stimulus and another button if they could not). Participants were instructed to decide if they were absolutely certain what the object was before making their button press. If they were absolutely certain what the object was, they were to press the button indicated they can identify the stimulus. Otherwise, the participant was to press the button indicating they could not identify the stimulus (see Appendix C). Throughout both phases of the experiment, a fixation point appeared whenever an object did not appear. Trial order was optimized using optseq2 (MGH NMR Center, Charlestown MA) which allowed for optimal trial timing for fMRI analysis (i.e., the same trial orders were used here as the aforementioned fMRI experiment; Deason et al., 2008). Only trials that were identified by participants were use in subsequent analyses.

Electrophysiological Recording

Electrophysiological data were collected using a two-computer setup. The first computer used E-Prime version 2.0 software (Psychology Software Tools, Inc.) to deliver the stimuli, accept responses, and send digital triggers to the other computer indicating when stimulus events occurred. The second computer acquired physiological data using NetStation version 4.2 software in conjunction with the 128-channel NetStation amplifier. A 128 Ag/AgCl electrode array HydroCel Geodesic Sensor Net (see Figure 3), placed in accordance with the 10-20 International System (Jasper, 1958), was used to collect EEG activity. Data were collected at a 1000 Hz sampling rate and a 0.01-Hz high-pass hardware filter was applied. EEG activity was recorded using Cz as the reference, and then re-referenced offline to an average mastoid reference. All impedances were kept below 50 kΩ during data collection.

After data collection, a two-stage data processing stream was carried out. The data from the test phase of the experiment were initially processed with NetStation software then exported in a format easily imported to matlab (http://www.mathworks.com/). In matlab, the data were further processed using EEGLab software (Delorme & Makeig, 2004). Description of each processing step is explained below.

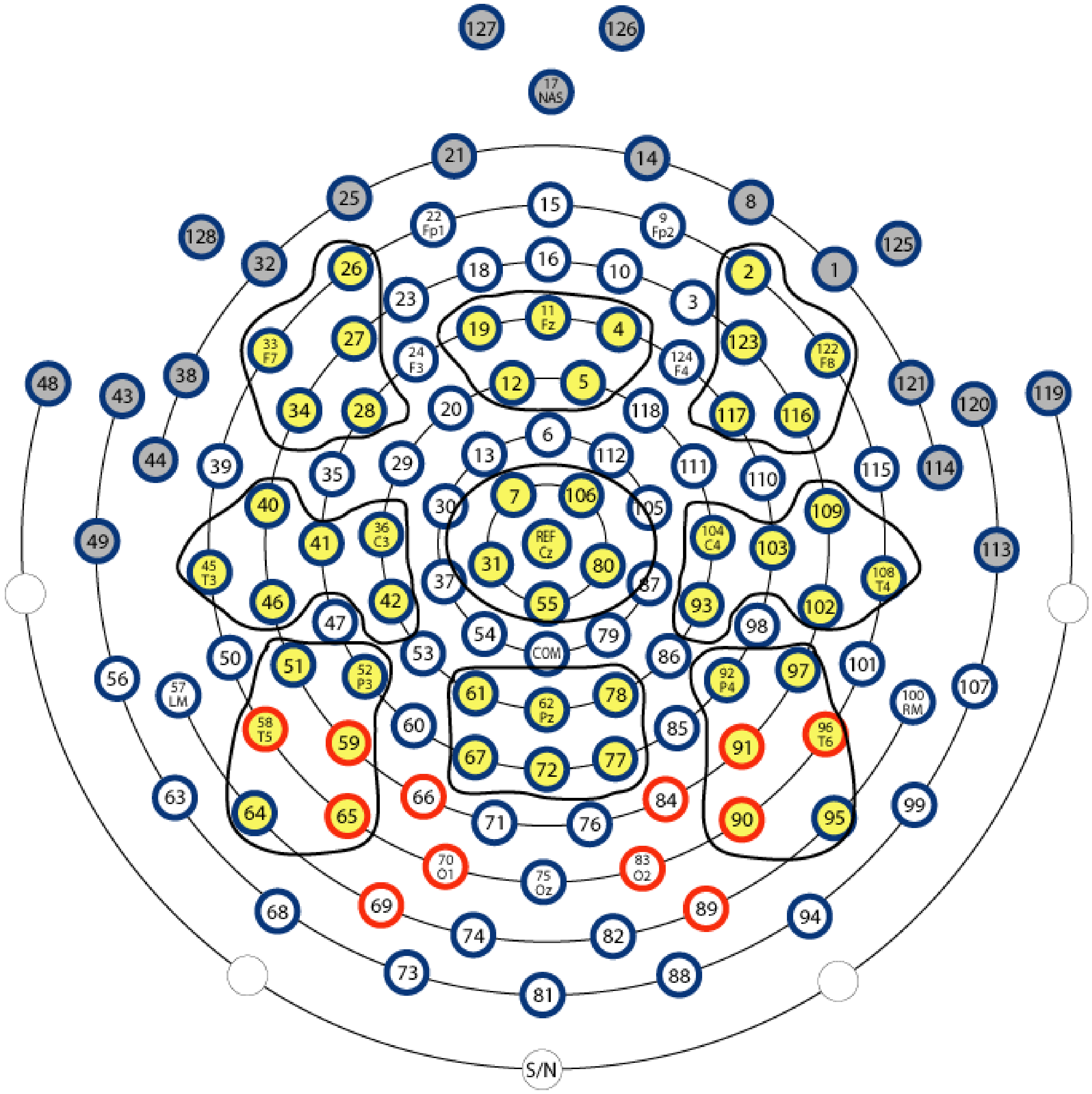

Figure 3. Electrode locations for the 129 electrodes in the NetStation geodesic sensor net. Electrodes with gray background were deleted in preprocessing due to excessive noise during recording. Electrodes with yellow background were used in the ANOVAs. A lateral and coronal term was used in the ANOVA and the electrodes were split into nine lateral by coronal locations. These nine locations were defined as: Anterior – Left (26, 27, 28, 33, 34); Anterior – Center (4, 5, 11, 12, 19); Anterior – Right (2, 116, 117, 122, 123); Central – Left (36, 40, 41, 42, 45, 46); Central – Center (Cz, 7, 31, 55, 80, 108); Central – Right (93, 102, 103, 104, 108, 109); Posterior – Left (51, 52, 58, 59, 64, 65); Posterior – Center (61, 62, 67, 72, 77, 78); Posterior – Right (90, 91, 92, 95, 96, 97; each lateral by coronal electrode subset is circled)). Electrodes outlined in red were selected to test the action pathway hypothesis. For this analysis, Left (58, 59, 65, 66, 69, 70) and Right (83, 84, 89, 90, 91, 96) lateral locations were used in the ANOVAs.

NetStation Preprocessing

Initial preprocessing steps were carried out using NetStation version 4.4 software. Each subject's data were filtered, run through an artifact detection script, run through a channel replacement script, then re-referenced before exporting to a matlab readable format. A bandpass filter of 0.3 – 30 Hz FIR filter was applied to these data. The artifact detection was liberal in order to tag the very noisy trials and bad data before exporting to matlab and EEGLab, where more thorough artifact detection was implemented. With the NetStation artifact detection, trials were marked as bad but not deleted; these trials were excluded when the data were re-referenced. Once trials were marked as bad with the artifact detection tool, a bad channel replacement tool was run on these data**.** Because of the liberal nature artifact detection tool, no channels were marked as bad and none were replaced. This step was implemented to assure that no bad channels were present during re-referencing. After these steps, an average mastoid reference was used to re-reference the data offline (channels and trials marked as bad were not used when calculating this reference). After these steps, data files for each subject were exported to simple binary with floating point precision to be imported into matlab and processed with EEGLab.

EEGLab Preprocessing

Data were imported into EEGLab for further pre-processing. After importing and down sampled to 256 samples per 1000 ms, an independent components analysis (ICA) was computed for each participant. The components derived from these data were used when identifying and correcting for eye-blinks. Data from four participants were randomly selected (2 males and 2 females) to create an eye-blink template. In each case, components that represented eye-blinks were selected from each of these four participant's data and averaged together into a single template. This template was designed to easily identify eye-blinks in all data collected for this experiment. To identify eye-blinks in each participant, the template was compared to the independent components derived from each participant's data. Components that correlated with the template (a correlation of > = 0.6) were identified as eye-blinks and deleted from each participant's data (M = 1.4 components deleted per participant). Several electrode (N = 21) locations were then deleted from analysis due to large artifacts throughout the experiment (see Figure 3). Data were then epoched -1000 ms pre-stimulus and 2000 ms post-stimulus. Within each trial, individual electrode sites at which activity exceeded ± 75 μV in either the pre (-500 to 0) or post stimulus (0 to 1700) time regions (relative to one another) were omitted from analysis. Applying these criteria, 5.37 % of trials were excluded. Only trials used in the behavioral analysis were used in the ERP analysis. For each participant, all trials for each condition were averaged together. These averages served as the starting point for all analyses of the electrophysiological data detailed below.

Data Reduction

Time-Domain Components. Time-domain (TD) components were fitted to the average waveforms to best characterize the negative and positive deflections in the ERP waveform. These components carried significant or marginal condition effects (N2, P3, Late Positivity). The N2 time window was defined as the negative deflection between

250.00 ms and 449.22 ms post-stimulus. The P3 time window was defined as the positive deflection between 347.65 ms and 750.00 ms post-stimulus. The Late Positivity (LP) time window was defined as the positive deflection between 500.00 ms and 800.78 ms post-stimulus. An additional component window as selected to directly test the action-pathway priming hypothesis: the P1 window was defined as the positive deflection between 74.22 ms and 152.34 ms post-stimulus. These time windows were baseline corrected using the -150 to -10 ms pre- stimulus window and only trials that participants were able to identify the stimulus were analyzed. In addition to these TD components, two frequency bands were explored with TF analysis (alpha and theta).

All but the deleted 21 electrodes were used when plotting the distribution of activation for all subsequent decompositions; however, for simplicity, 51 electrodes from the overall montage were selected for the main statistical analyses (Cz, 2, 4, 5, 7, 11, 12, 19, 26, 27, 28, 31, 33, 34, 36, 40, 41, 42, 45, 46, 51, 52, 55, 58, 59, 61, 62, 64, 65, 67, 72, 77, 78, 80, 90, 91, 92, 93, 95, 96, 97, 102, 103, 104, 106, 109, 116, 117, 122, 123). In the TD and TF analyses, a subset of electrode sites representing three coronal levels of location crossed with three lateral levels of location was examined (see Figure 3). To directly test the action pathway hypothesis (electrodes and time-windows selected to be similar to Kiefer et al., 2011 & Handy et al., 2003), 12 specific electrodes (58, 59, 65, 66, 69, 70, 83, 84, 89, 90, 91, 96) were selected for analysis (see Figure 3).

Time-Frequency Components: Alpha and Theta. Time-frequency principal-component analysis (TF-PCA; Bernat et al., 2005), was performed to test for condition differences within alpha and theta frequency bands measured during the test phase of this experiment. In this approach, TF activity in specific ranges was delineated by using principal component analysis. Alpha (8-12 Hz) and theta (2.5 - 8 Hz) frequency bands were of primary interest here. Isolating these frequency bands with bandpass filtering allowed for direct comparisons between condition differences within the alpha and theta frequency ranges. All Cohen's class (Cohen, 1995) TF transforms and TF-PCA were conducted following the methods detailed by Bernat et al. (2005).

Results

Repeated-measures ANOVAs were conducted to analyze behavioral performance, ERP time-domain (TD) effects, and ERP time-frequency (TF) decompositions. Simple effects as well as orthogonal linear and quadratic contrasts were calculated to clarify significant main effects and interactions. Correlations between behavioral, TD, and TF measures were also carried out. Unless directly testing a priori predictions, effects that did not reach statistical trend ($p > .10$) are not reported.

Behavioral Results

Separate repeated-measures ANOVAs were conducted using response times for identified trials and proportion of unidentified trials as the dependent variables, with participants as the random variable. In each analysis, experimental condition (same-exemplar primed, different-exemplar primed, word primed, and unprimed) was the (within-participants) independent variable, and the random variable was participant. Additional repeated measures ANOVAs of response times and proportion unidentified were carried out on restricted sets of trials to examine effects of high versus low actionability. In these analyses, actionability split (high or low actionability based on the tercile split discussed above) was an additional (within participants) independent variable. Three sets of such analyses were performed, one for each actionability rating (Q1, Q2, and Q3).

Response Times. In the analysis of response times, the main effect of experimental condition was significant, $F(3,69) = 9.49$, $MSe = 586.14$, $p < .001$ (see Figure 4). In line with a priori predictions that repeated stimuli would elicit faster identification, response times were significantly faster in the same-exemplar condition (488 ms) than in the different-exemplar primed condition (516 ms), $F(1,69) = 16.47$, $MSe = 586.14$, $p < .001$, word primed condition (517 ms), $F(1,69) = 17.43$, $MSe = 586.14$, $p < .001$, and unprimed condition (521 ms), $F(1,69) = 22.29$, $MSe = 586.14$, $p < .001$.

Proportion Unidentified. In the proportion unidentified analysis, the main effect of experimental condition was significant, $F(3,69) = 5.95$, $MSe = 0.003$, $p = .001$ (see Figure 4). In line with a priori predictions that repeated stimuli would have lower unidentified rates than other conditions, proportion unidentified in the same-exemplar condition (0.09) was significantly lower than in the word primed condition (0.12), $F(1,69) = 4.48$, $MSe = 0.003$, $p = .038$, and unprimed condition (0.16), $F(1,69) = 17.51$, $MSe = 0.003$, $p < .001$. Unidentified rates for the different-exemplar primed (0.12) and word primed (0.12) conditions were significantly lower than the unprimed condition (0.16), $F(1,69) = 6.55$, $MSe = 0.003$, $p = .013$, $F(1,69) = 4.27$, $MSe = 0.003$, $p = .043$, respectively.

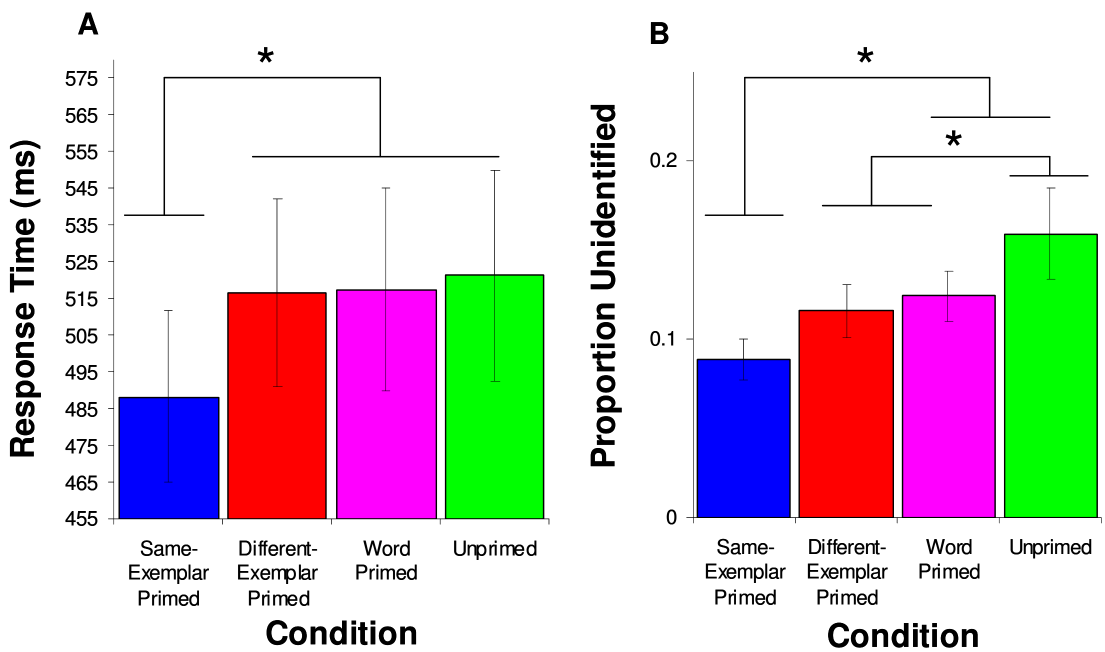

Figure 4. Mean response times (A) in ms and proportion of unidentified trials (B; *±SEM*) overall are depicted for the four experimental conditions (same-exemplar primed, different-exemplar primed, word primed, and unprimed). Response time for same-exemplar primed was faster than for unprimed and the proportion unidentified for same-exemplar primed was less than for unprimed. Also, proportion unidentified for different-exemplar primed and word primed was less than for unprimed.
Note. * = p < .05

Actionability Rating Q1 (Charade Playing). In the analysis of response times, the main effect of experimental condition was significant, $F(3,69) = 5.42$, $MSe = 2166.88$, $p = .002$ (see Figure 5). The same-exemplar primed condition (490 ms) elicited faster response times than the different-exemplar primed condition (520 ms), $F(1,69) = 4.78$, $MSe = 2166.88$, $p = .032$, word primed condition (520 ms), $F(1,69) = 4.83$, $MSe = 2166.88$, $p = .032$, and unprimed condition (524 ms), $F(1,69) = 6.41$, $MSe = 2166.88$, $p = .014$. The main effect for actionability split was significant, $F(1,23) = 17.76$, $MSe = 1573.19$, $p < .001$. The stimuli rated as highly actionable (501 ms) elicited faster response times than the stimuli that were rated as not highly actionable

(525 ms). The experimental condition by actionability split interaction was marginally significant, $F(3,69) = 2.48$, $MSe = 1120.67$, $p = .068$. Specifically, not highly actionable objects elicited a greater priming effect (response time for the unprimed condition minus response time for the same-exemplar primed condition; 50.71 ms) than did highly actionable objects (17.34 ms), $t(1,23) = 2.65$, $p = .014$. However, this result should be interpreted with caution. Because the highly actionable objects were faster to identify overall, the smaller priming effect for highly actionable objects could have been due to uninteresting statistical pressures from the floor.

In the proportion unidentified analysis, the main effect of experimental condition was significant, $F(3,69) = 5.07$, $MSe = 0.010$, $p = .003$ (see Figure 5). The proportion unidentified in the same-exemplar primed (0.09) condition was significantly lower than in the different-exemplar primed (0.13) condition, $F(1,69) = 5.20$, $MSe = 0.005$, $p = .026$, the word primed (0.14) condition, $F(1,69) = 6.64$, $MSe = 0.005$, $p = .012$, and the unprimed (0.17) condition, $F(1,69) = 14.59$, $MSe = 0.005$, $p < .001$. The main effect for actionability split was significant, $F(1,23) = 8.61$, $MSe = 0.007$, $p = .007$. The stimuli rated as highly actionable (0.12) were unidentified at a lower rate than the stimuli that were rated as not highly actionable (0.15).

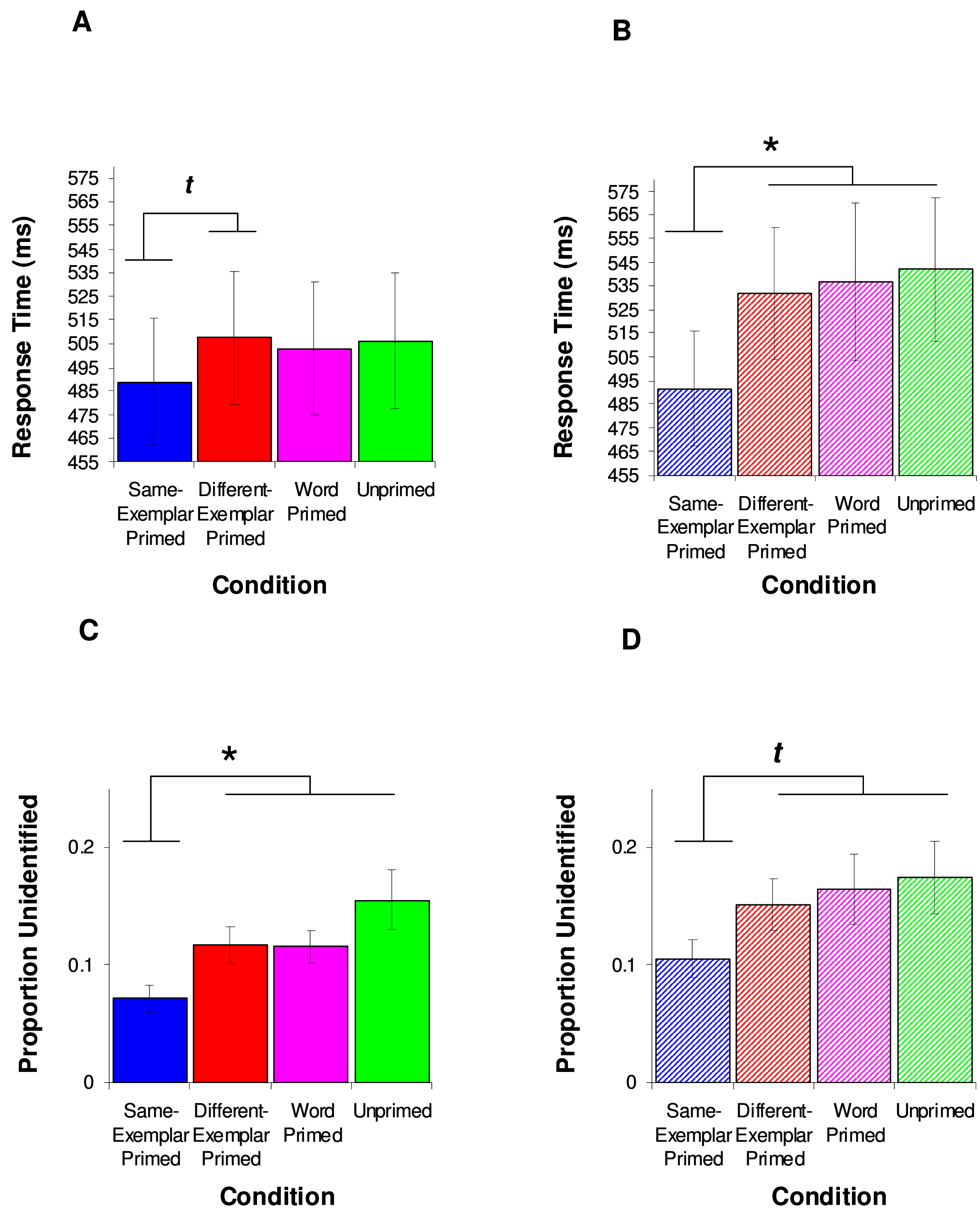

Figure 5. Mean response times (A–B) in ms and proportion of unidentified trials (C–D; *±SEM*) for highly actionable items (A and C; solid bars) and not highly actionable items (B and D; hashed bars) according to actionability question 1 (charade playing). These data are depicted as a function of the four experimental conditions (same-exemplar primed, different-exemplar primed, word primed, and unprimed). *Note.* * = $p < .05$, ***t*** = $p < .10$

Actionability Rating Q2 (Movement/Function). In the analysis of response times, the main effect of experimental condition was significant, $F(3,69) = 6.81$, $MSe = 1951.44$, $p < .001$ (see Figure 6). The same-exemplar primed (491 ms) condition elicited marginally faster response times than the different-exemplar primed condition (515 ms), $F(1,69) = 3.65$, $MSe = 1951.44$, $p = .060$, and significantly faster response times than word primed condition (519 ms), $F(1,69) = 5.02$, $MSe = 1951.44$, $p = .028$, and unprimed condition (530 ms), $F(1,69) = 9.53$, $MSe = 1951.44$, $p = .003$. The main effect for actionability split was significant, $F(1,23) = 10.84$, $MSe = 1951.44$, $p = .003$. The stimuli rated as highly actionable (504 ms) elicited faster response times than the stimuli that were rated as not highly actionable (524 ms).

In the analysis of proportion unidentified, the main effect of experimental condition was significant, $F(3,69) = 3.93$, $MSe = 0.04$, $p = .012$ (see Figure 6). The proportion unidentified in the same-exemplar primed (0.06) condition was significantly lower than in the word primed (0.11) condition, $F(1,69) = 5.90$, $MSe = 0.005$, $p = .018$, and the unprimed (0.13) condition, $F(1,69) = 10.85$, $MSe = 0.005$, $p = .002$.

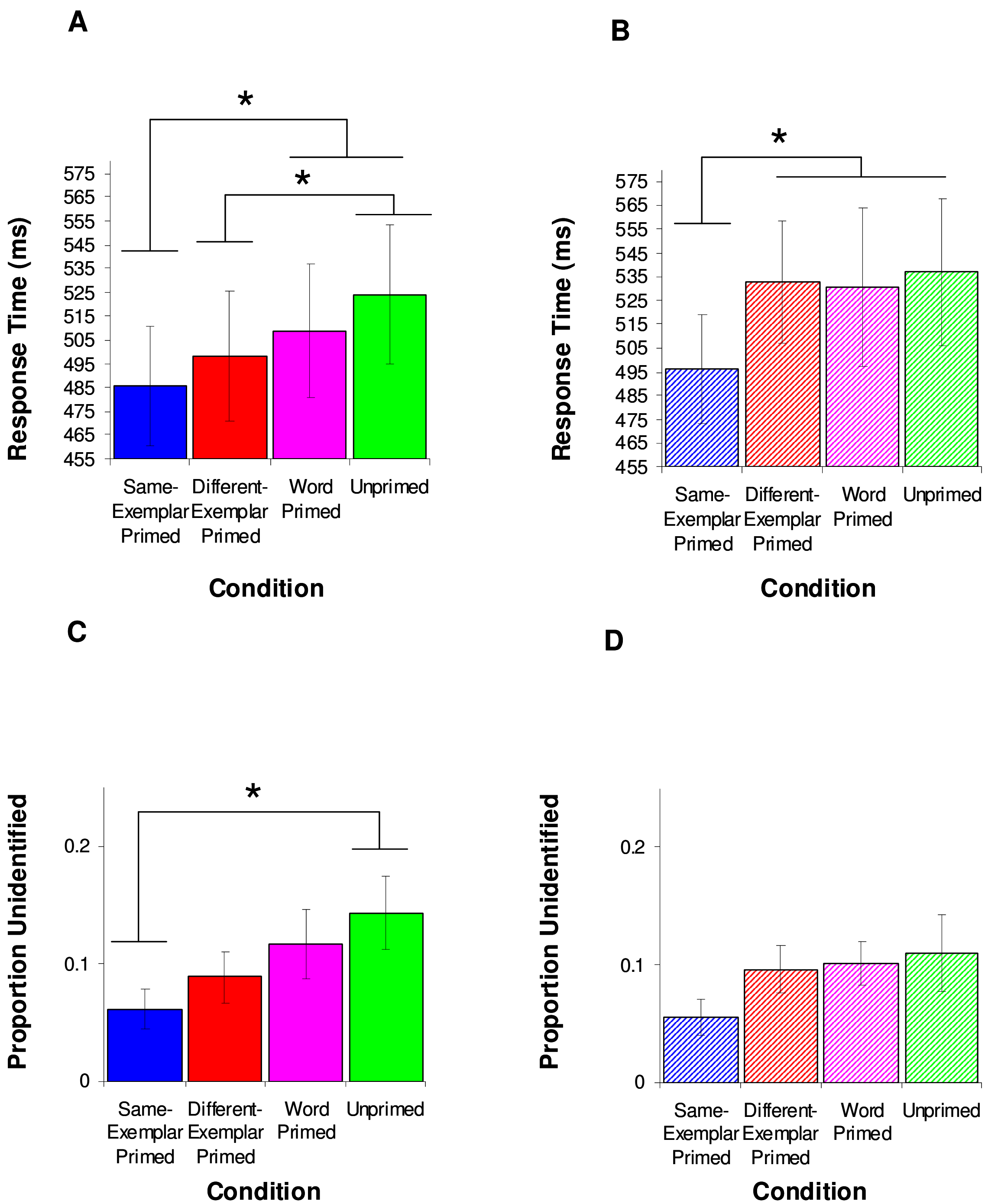

Figure 6. Mean response times (A–B) in ms and proportion of unidentified trials (C–D; ±*SEM*) for highly actionable items (A and C; solid bars) and not highly actionable items (B and D; hashed bars) according to actionability question 2 (movement/function). These data are depicted as a function of the four experimental conditions (same-exemplar primed, different-exemplar primed, word primed, and unprimed). *Note.* * = $p < .05$

Actionability Rating Q3 (Hand Interaction). In the analysis of response times, the main effect of experimental condition was significant, $F(3,69) = 7.62$, $MSe = 1887.37$, $p < .001$ (see Figure 7). The same-exemplar primed (492 ms) condition elicited faster response times than the different-exemplar primed condition (522 ms), $F(1,69) = 5.70$, $MSe = 1887.37$, $p = .020$, word primed condition (524 ms), $F(1,69) = 6.82$, $MSe = 1887.37$, $p = .011$, and unprimed condition (531 ms), $F(1,69) = 9.57$, $MSe = 1887.37$, $p = .003$. The experimental condition by actionability split interaction was significant, $F(3,69) = 2.92$, $MSe = 1257.70$, $p = .040$. Specifically, not highly actionable stimuli elicited a marginally greater priming effect (response time for the unprimed condition minus response time for the same-exemplar primed condition; 50.77 ms) than did highly actionable stimuli (26.82 ms), $t(1,23) = 1.93$, $p = .066$. However, as with actionability question 1, this effect should be interpreted with caution. The highly actionable objects were faster to identify overall, thus the smaller priming effect for highly actionable objects could have been due to uninteresting statistical pressures from the floor.

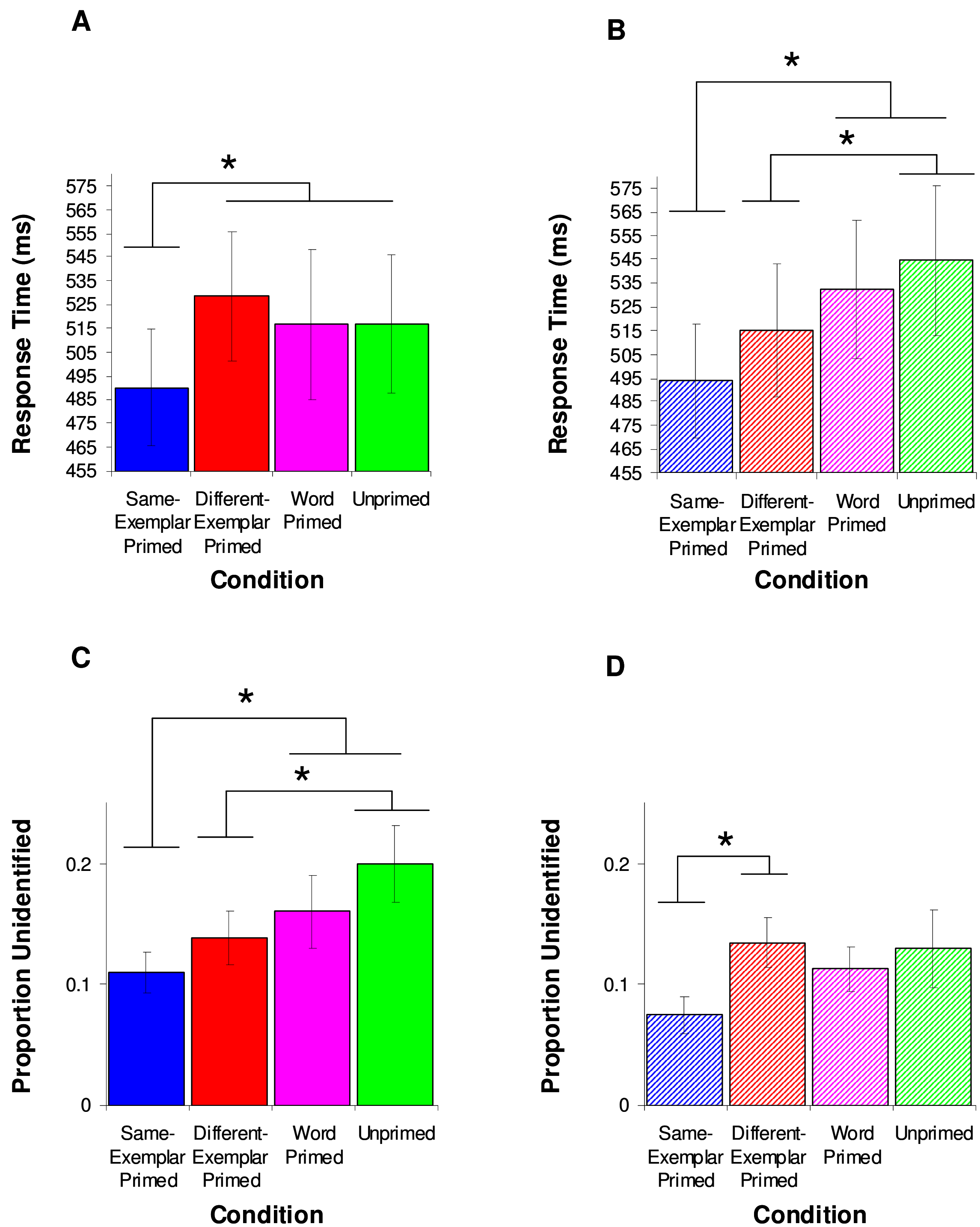

Figure 7. Mean response times (A-B) in ms and proportion of unidentified trials (C-D; *±SEM*) for highly actionable items (A and C; solid bars) and not highly actionable items (B and D; hashed bars) according to actionability question 3 (hand interaction). These data are depicted as a function of the four experimental conditions (same-exemplar primed, different-exemplar primed, word primed, and unprimed). *Note.* * = $p < .05$

In the analysis of proportion unidentified, the main effect of experimental condition was significant, $F(3,69) = 3.82$, $MSe = 0.01$, $p = .014$ (see Figure 7). The proportion unidentified in the same-exemplar primed (0.09) condition was significantly lower than in the different-exemplar primed (0.14) condition, $F(1,69) = 4.190$, $MSe = 0.005$, $p = .045$, the word primed (0.14) condition, $F(1,69) = 4.11$, $MSe = 0.005$, $p = .046$, and the unprimed (0.17) condition, $F(1,69) = 11.87$, $MSe = 0.005$, $p = .001$. The main effect for actionability split was significant, $F(1,23) = 16.75$, $MSe = 0.004$, $p < .001$. The stimuli rated as highly actionable (0.11) were unidentified at a lower rate than the stimuli that were rated as not highly actionable (0.15).

Time-Domain ERP Results

In the analyses of TD components, a two-part analysis strategy was applied. First, preliminary repeated-measures ANOVAs were conducted with mean amplitude of the TD component as the dependent variable and participant as the random variable. One of the (within-participants) independent variables was experimental condition with two levels (same-exemplar primed and unprimed). A subset of electrode sites representing three coronal levels of location crossed with three lateral levels of location were examined (see Figure 3). Thus, two additional (within-participants) independent variables were coronal level of electrode location (anterior, central, posterior) and lateral level of electrode location (left, center, right; see Figure 8). The preliminary repeated-measures ANOVAs were conducted to identify TD windows of interest. TD windows with a significant or marginally significant main effect of experimental condition (with two levels) were identified for further analysis. When a TD window was identified for further analysis, a follow-up repeated measures ANOVA was conducted with the experimental condition variable having all four levels (same-exemplar primed, different-exemplar primed, word primed, and unprimed). This two-step analysis strategy mirrored the analyses applied in the preceding fMRI experiment for identifying posterior-parietal regions of interest (Deason et al., 2008). Additionally, to test a priori predictions regarding coronal distribution of effects, if a condition by coronal interaction was found in the preliminary ANOVA, then that TD component was identified for further analysis.

The analysis of the P1 component differed from the analyses of the other components, in order to test predictions from the actionability hypothesis. Previous research indicates that highly actionable objects (e.g., tools) elicit a more positive early P1 (~75 ms to ~150 ms) in posterior electrodes (lateral occipital regions) than non-actionable objects (Handy et al., 2003; cf. Kiefer et al., 2011). Thus, to examine an ERP component known to be affected by actionability, the analysis of the P1 involved 12 lateral occipital electrodes and the time window implicated in the Handy et al. study (see Figure 3). In this analysis, the independent variables were experimental condition, lateral level of electrode location (left and right), and actionability (high and low). Three sets of such analyses were performed, one for each actionability rating (Q1, Q2, and Q3).

Effects of lateral electrode location and interactions involving this lateral factor, which had a quadratic distribution with an uninteresting increase in activation over midline electrodes, were not of theoretical interest and are not reported here. When significant violations of sphericity were detected, Greenhouse-Geisser corrected effects and epsilon (ε) are reported, as recommended by Jennings and Wood (1976; see also Picton et al., 2000).

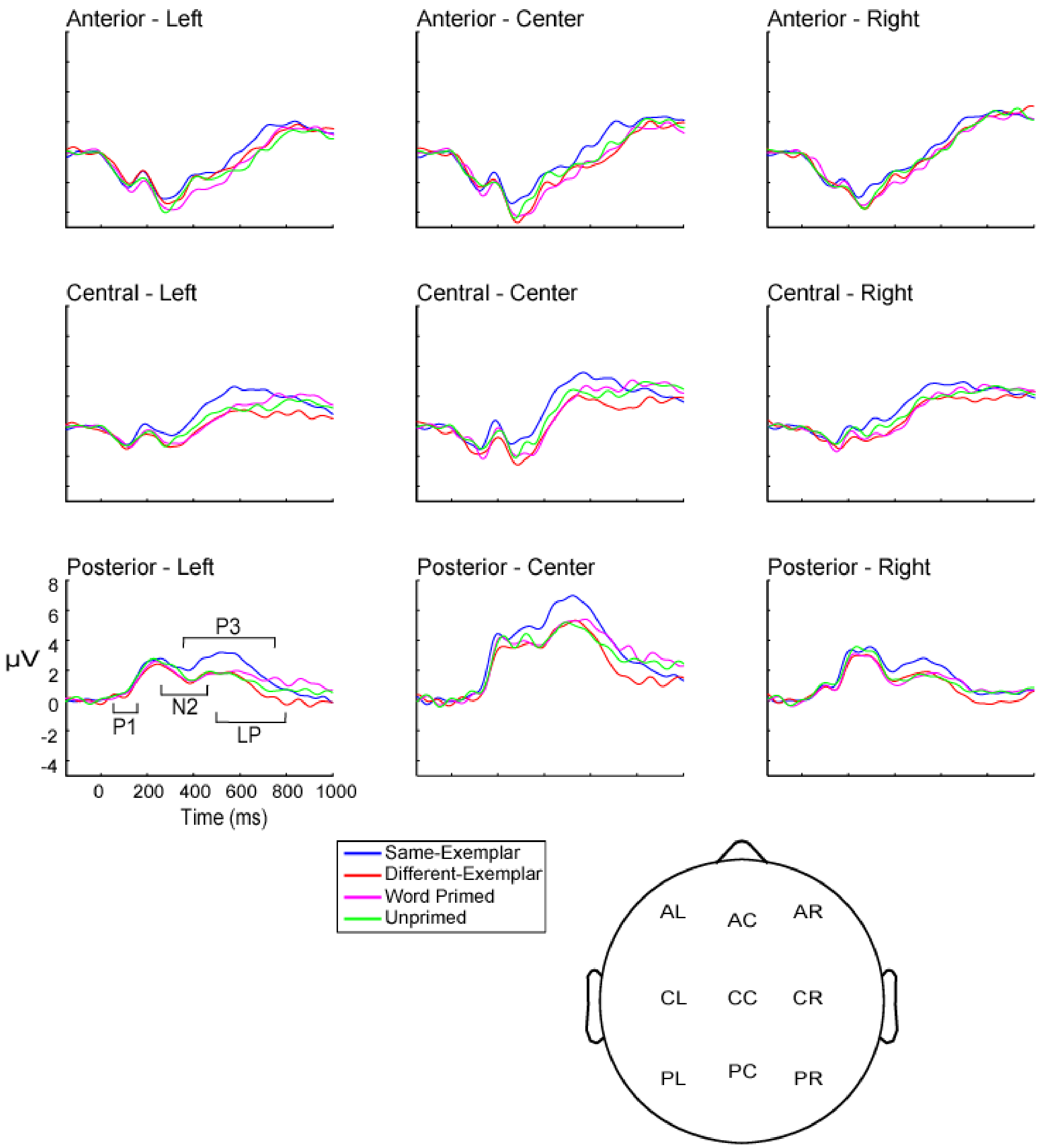

Figure 8. ERP waveforms (amplitude in μV, and time in ms) for the four experimental conditions of interest (same-exemplar primed, different-exemplar primed, word primed, and unprimed) across nine lateral by coronal locations used in the ANOVAs. The four time-windows analyzed (P1, N2, P3, LP) are indicated in the lower left ERP waveform plot.

P1. In the preliminary analysis of the P1 TD component, the main effect of experimental condition did not approach significance (Q1, $F < 1$, Q2, $F < 1$, Q3, $F < 1$). Also, the condition by lateral interaction did not approach significance (Q1, $F < 1$, Q2, $F < 1$, Q3, $F < 1.3$, $p > .265$). Therefore, no repetition priming effect was apparent in the P1. It is noteworthy that there was no significant main effect of actionability in all three analyses based on different actionability ratings (Q1, $F < 1$, Q2, $F < 1$, Q3, $F < 1.73$, $p > .210$), unlike previous reports (Handy et al., 2003, cf., Keifer et al., 2011).

N2. In the preliminary analysis of the N2 TD component, the main effect of experimental condition was marginally significant, $F(1,23) = 3.54$, $MSe = 10.73$, $p = .073$. In this time-window, the same-exemplar primed (0.48 µV) condition elicited a more positive N2 than the unprimed condition (-0.11 µV). There was a main effect for coronal electrode location, $F(2,46) = 28.90$, $MSe = 62.85$, $p < .001$, $\varepsilon = 0.56$. Linear contrasts indicated that the N2 was reduced towards posterior electrode locations relative to anterior locations, $F(1,23) = 30.49$, $MSe = 22.08$, $p < .001$ (i.e, less of a negative deflection from the anterior electrode sites [-2.34 µV] to the posterior electrode sites [2.95 µV], with the central electrode sites falling numerically between the two [0.05 µV]).

When all four experimental conditions were included in the follow-up analysis of the N2 TD component, the main effect of experimental condition was significant, $F(3,69) = 4.70$, $MSe = 9.82$, $p = .005$. The same-exemplar primed (0.48 µV) condition elicited a more positive N2 than the different-exemplar primed (-0.43 µV) and the word primed conditions (-0.55 µV), $F(1,69) = 9.11$, $MSe = 1.09$, $p = .004$, $F(1,69) = 11.70$, *MSe* = 1.09, $p = .001$, respectively. There was a main effect for coronal electrode location, $F(2,46) = 31.40$, $MSe = 119.38$, $p < .001$, $\varepsilon = 0.56$. Linear contrasts indicated that the N2 was reduced towards posterior electrode locations relative to anterior locations, $F(1,23) = 32.93$, $MSe = 41.83$, $p < .001$ (i.e, less of a negative deflection from the anterior electrode sites [-2.68 µV] to the posterior electrode sites [2.68 µV], with the central electrode sites falling numerically between the two [-0.45 µV]).

P3. In the preliminary analysis of the P3 TD component, the main effect of experimental condition was significant, $F(1,23) = 4.50$, $MSe = 16.78$, $p = .045$. In this time-window, the same-exemplar primed (1.81 µV) condition elicited a more positive P3 than the unprimed condition (0.98 µV). There was a main effect for coronal electrode location, $F(2,46) = 20.51$, $MSe = 27.70$, $p < .001$, $\varepsilon = 0.61$. Linear contrasts indicated that the P3 was reduced towards anterior electrode locations relative to posterior locations, $F(1,23) = 22.09$, $MSe = 10.16$, $p < .001$ (i.e, less of a positive deflection from the posterior electrode sites [2.74 µV] to the anterior electrode sites [-0.33 µV], with the central sites falling between the two [1.77 µV]).

When all four experimental conditions were included in the follow-up analysis of the P3 TD component, the main effect of experimental condition was significant, $F(3,69) = 4.13$, $MSe = 12.28$, $p = .009$. The same-exemplar primed (1.81 µV) condition elicited a more positive P3 than the different-exemplar primed (0.76 µV) and the word primed conditions (0.85 µV), $F(1,69) = 9.77$, $MSe = 1.36$, $p = .003$, $F(1,69) = 8.21$, $MSe = 1.36$, $p = .006$, respectively. There was a main effect for coronal electrode location, $F(2,46) = 23.31$, $MSe = 49.62$, $p < .001$, $\varepsilon = 0.62$. Linear contrasts indicated that the P3 was reduced towards anterior electrode locations relative to posterior locations, $F(1,23) = 25.47$, $MSe = 18.19$, $p < .001$ (i.e, less of a positive deflection from the posterior electrode sites [2.49 μV] to the anterior electrode sites [-0.61 μV], with the central sites falling between the two [1.41 μV]).

LP. In the preliminary analysis of the LP TD component, the main effect of experimental condition was marginally significant, $F(1,23) = 3.44$, $MSe = 20.31$, $p = .076$. The same-exemplar primed (2.18 μV) condition elicited a more positive LP than the unprimed condition (1.37 μV). There was a main effect for coronal electrode location, $F(2,46) = 9.92$, $MSe = 22.80$, $p < .001$, $\varepsilon = 0.64$. Linear contrasts indicated that the LP was reduced towards anterior electrode locations relative to posterior locations, $F(1,23) = 9.09$, $MSe = 20.26$, $p = .006$ (i.e, less of a positive deflection from the posterior electrode sites [2.40 μV] to the anterior electrode sites [0.61 μV], with the central sites falling between the two [2.31 μV]).

When all four experimental conditions were included in the follow-up analysis of the LP TD component, the main effect of experimental condition was significant, $F(3,69) = 3.01$, $MSe = 14.46$, $p = .036$. The same-exemplar primed (2.18 μV) condition elicited a more positive LP than the different-exemplar primed (1.13 μV), $F(1,69) = 8.22$, $MSe = 1.61$, $p = .006$, and a marginally more positive LP than the word primed condition (1.52 μV), $F(1,69) = 3.21$, $MSe = 1.61$, $p = .078$. There was a main effect for coronal electrode location, $F(2,46) = 11.25$, $MSe = 40.80$, $p < .001$, $\varepsilon = 0.63$. Linear contrasts indicated that the LP was reduced towards anterior electrode locations relative to posterior locations, $F(1,23) = 10.73$, $MSe = 14.90$, $p = .003$ (i.e, less of a positive deflection from the posterior electrode sites [2.22 μV] to the anterior electrode sites [0.40 μV], with the central electrode sites falling numerically between the two [2.03 μV]).

Time-Frequency ERP Decompositions

All electrodes were subjected to the initial TF surface analyses (Cz, 2, 4, 5, 7, 11, 12, 19, 26, 27, 28, 31, 33, 34, 36, 40, 41, 42, 45, 46, 51, 52, 55, 58, 59, 61, 62, 64, 65, 67, 72, 77, 78, 80, 90, 91, 92, 93, 95, 96, 97, 102, 103, 104, 106, 109, 116, 117, 122, 123). In the TF analyses, the same subset of electrode sites as used in the TD analyses, representing three coronal levels of location crossed with three lateral levels of location, was examined (see Figure 3). Separate repeated measures ANOVAs were conducted for different components and different frequencies, with activity measured on the TF surface as the dependent variables and participant as the random variable. As in the TD analysis, a two-part analysis strategy was applied, with the (within-participants) independent variable of experimental condition having two levels (same-exemplar primed and unprimed) in the preliminary analysis. When a TF component was identified for further analysis by exhibiting a significant or marginally significant main effect of experimental condition in the preliminary analysis, a follow-up analysis of that component was conducted with the experimental condition variable having four levels (same-exemplar primed, different-exemplar primed, word primed, and unprimed). In both levels of analysis, coronal level of electrode location (anterior, central, posterior) and lateral level of electrode location (left, center, right were the other (within-participants) independent variables. The two-step analysis strategy mirrored the analyses carried out in the preceding fMRI study (Deason et al., 2008). Additionally, to test a priori predictions regarding coronal distribution of effects, if a condition by coronal interaction was found in the preliminary ANOVA, then that TF component was identified for further analysis. Significant main effects and interactions were clarified using simple effects tests as well as orthogonal linear and quadratic contrasts. For reasons similar to those applied in the TD analysis, uninteresting interactions involving the lateral electrode location variable are not reported here. When significant violations of sphericity were detected in the ANOVAs, as discussed above, Greenhouse-Geisser corrected effects and epsilon (ε) are reported.

A four-component alpha decomposition and a four-component theta decomposition best fit the data (see scree plots of singular values in Figure 9 and Figure 10); thus alpha and theta decompositions were analyzed in separate ANOVAs. Each decomposition accounted for a substantial amount of variance (alpha, 47.35 %; theta, 62.67 %).

Alpha Activity Decomposition. In the preliminary analysis of the alpha TF components, the main effect of experimental condition was not significant for any of the four alpha principal components, *F's* < 1. Also, no condition by coronal interaction was significant for any of the four principal components, *F's* < 2.09, *p's* > .137. To directly test a priori experimental condition effects at anterior and posterior electrode locations, *t*-tests were calculated for each alpha principal component. Specifically, mean frequency power at anterior electrode locations was calculated for the same-exemplar primed and the unprimed condition. Then a paired-samples *t*-test was calculated to assess specific condition differences at that location. This same calculation, using posterior electrode locations, was performed to test for posterior condition differences. None of these *t*-tests for any of the four alpha principal components proved significant, *t's* < 1.06. Therefore, no interesting priming effects were observed in the alpha TF component.

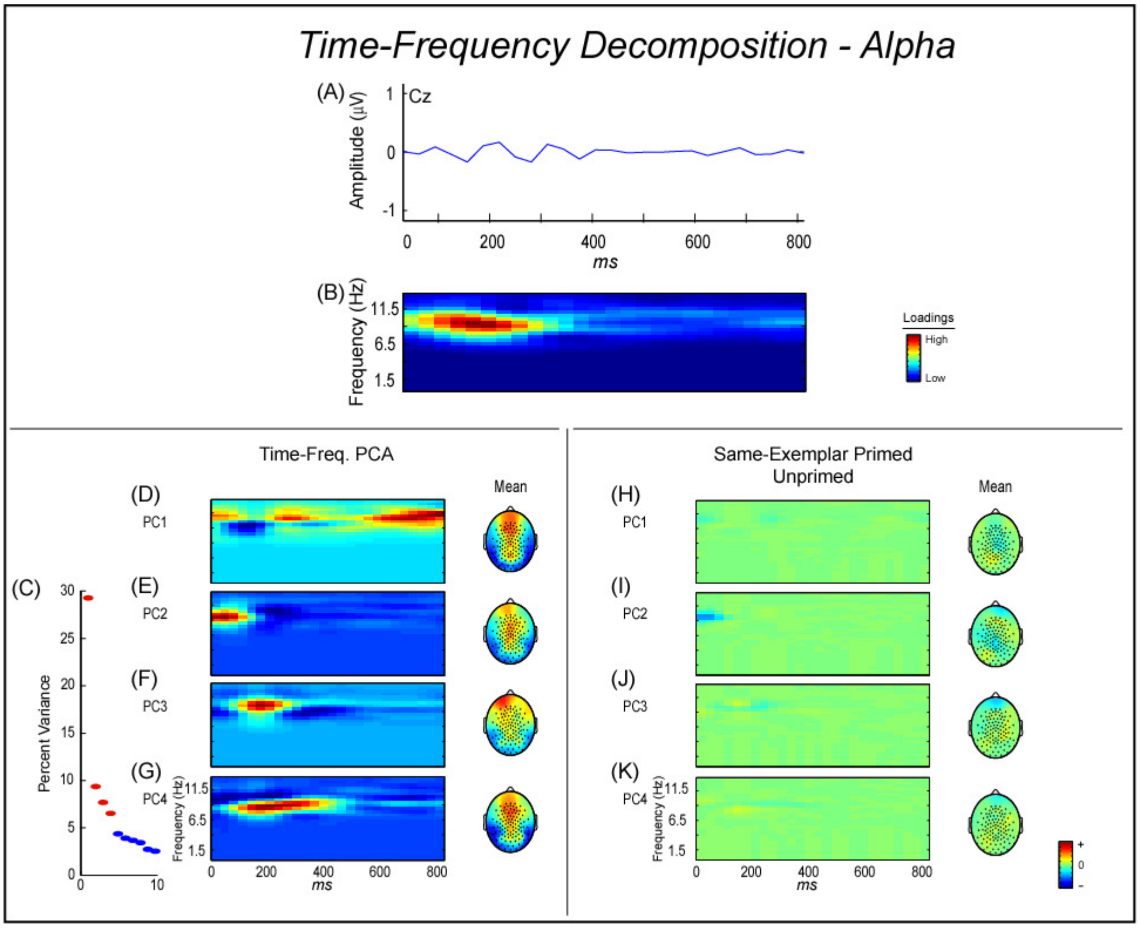

Figure 9. Time-frequency (TF) decomposition plotted at Cz: Alpha. (A-G) TF-PCA decomposition of alpha band pass filtered (8 - 12 Hz) data. (H-K) Alpha TF condition differences: TF surfaces and headmaps are plotted with a midpoint of 0, red reflecting a positive difference, and blue reflecting a negative difference. (A) Alpha filtered (8 - 12 Hz) grand average ERP time-domain waveform. (B) TF grand average of the alpha filtered data. (C) Scree plot of singular values which was used to determine a four factor alpha solution (red circles depict extracted components that account for 47.35% of the variance). (D-G) TF alpha principal components 1-4 TF surfaces and topographical (mean) representation. (H-K) TF surfaces and topomaps depicting the difference scores between same-exemplar primed and unprimed for each extracted principal component. None of the initial ANOVAs with same-exemplar primed and unprimed conditions were significant and none were selected for further analysis.

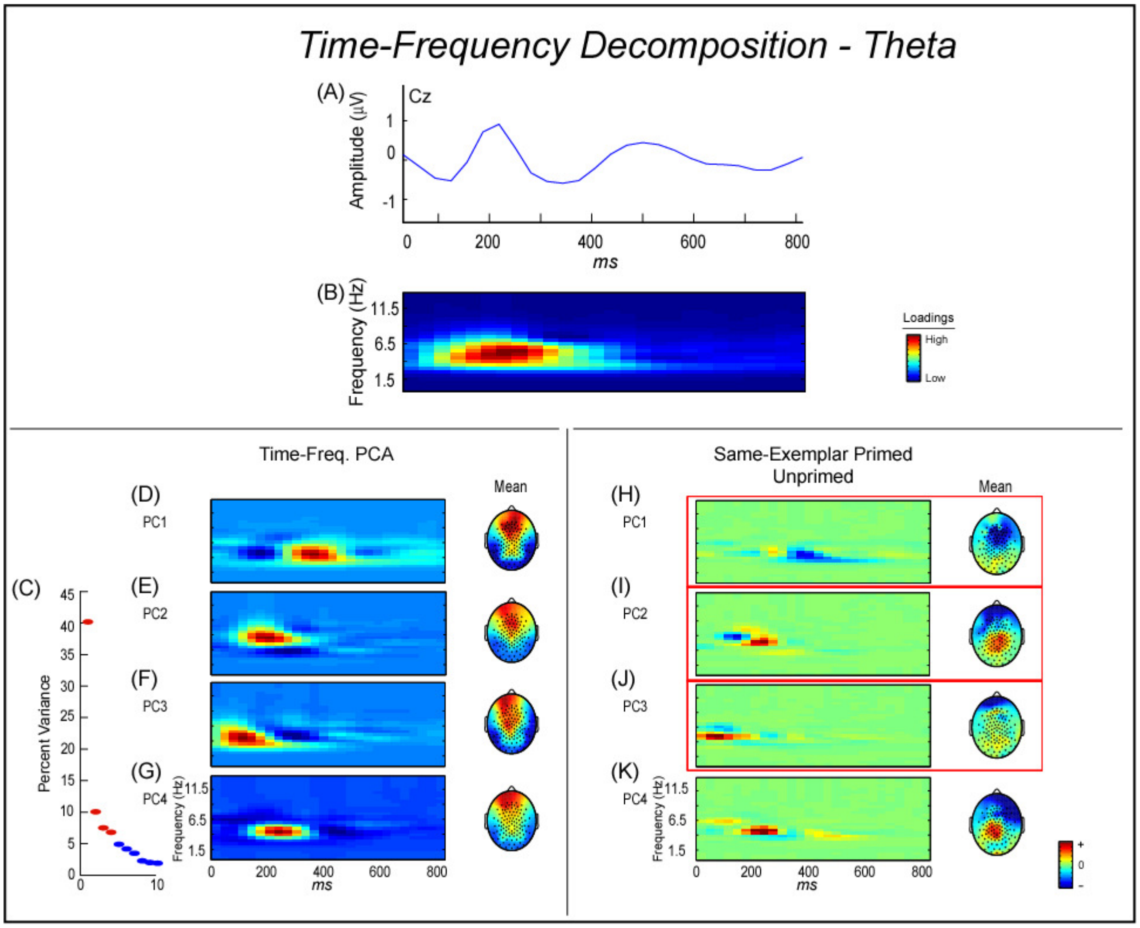

Figure 10. Time-frequency (TF) decomposition plotted at Cz: Theta. (A-G) TF-PCA decomposition of theta band pass filtered (2.5 - 8 Hz) data. (H-K) Theta TF condition differences: TF surfaces and headmaps are plotted with a midpoint of 0, red reflecting a positive difference, and blue reflecting a negative difference. (A) Theta filtered (2.5 - 8 Hz) grand average ERP time-domain waveform. (B) TF grand average of the theta filtered data. (C) Scree plot of singular values which was used to determine a four factor theta solution (red circles depict extracted components that account for 62.67% of the variance). (D-G) TF theta principal components 1-4 TF surfaces and topographical (mean) representation. (H-K) TF surfaces and topomaps depicting the difference scores between same-exemplar primed and unprimed for each extracted principal component. Three of the four principal components proved significant in an initial ANOVA of same-exemplar primed and unprimed conditions. Theta principal components 1, 2, and 3, (outlined in red) were selected for further analysis.

Theta Component 1. In the preliminary analysis of theta component 1, the interaction of experimental condition by coronal electrode location was significant, $F(2,46) = 8.33$, $MSe = 30.80$, $p = .004$, $\varepsilon = 0.67$. In particular, theta activity was greater in the unprimed condition than in the same-exemplar primed condition in the frontal electrode sites but not in the posterior electrode sites, $t(23) = 2.93$, $p = .008$.

When all four experimental conditions were included in the follow-up analysis of theta component 1, the main effect of coronal electrode location was marginally significant, $F(2,46) = 2.69$, $MSe = 0.003$, $p = .096$, $\varepsilon = 0.74$. Linear contrasts indicated that greater theta activity was measured at anterior electrode locations relative to posterior locations, $F(1,23) = 3.37$, $MSe = 0.001$, $p = .079$ (i.e, more theta activity was measured in the anterior electrode sites than in the posterior electrode sites). The interaction of experimental condition by coronal electrode location was marginally significant, $F(6,138) = 2.32$, $MSe = 0.0002$, $p = .069$, $\varepsilon = 0.61$. The previous finding of greater unprimed theta than same-exemplar primed theta in frontal electrodes sites but not in posterior electrode sites, $t(23) = 2.93$, $p = .008$, was not observed (when comparing unprimed against the different-exemplar primed or word primed conditions, t's < 1.75, p's $> .09$).

Theta Component 2. In the preliminary analysis of theta component 2, the main effect of coronal electrode location was significant, $F(2,46) = 10.33$, $MSe = 0.001$, $p = .002$, $\varepsilon = 0.65$. Linear contrasts indicated that greater theta activity was measured at anterior electrode locations relative to posterior locations, $F(1,23) = 15.62$, $MSe = 0.0003$, $p = .001$. Also, the interaction of experimental condition by coronal electrode location was significant, $F(2,46) = 3.32$, $MSe = 0.0001$, $p = .045$. In particular, theta activity was greater in the unprimed condition than in the same-exemplar primed condition in the frontal electrode sites but the opposite was true in the posterior electrode sites in a marginally significant effect, $t(23) = -2.05$, $p = .052$.

When all four experimental conditions were included in the follow-up analysis of theta component 2, the main effect of coronal electrode location was significant, $F(2,46) = 10.91$, $MSe = 0.002$, $p = .001$, $\varepsilon = 0.67$. Linear contrasts indicated that greater theta activity was measured at anterior electrode locations relative to posterior locations, $F(1,23) = 16.93$, $MSe = 0.0005$, $p < .001$. Also, the interaction of experimental condition by coronal electrode location was marginally significant, $F(6,138) = 2.58$, $MSe = 0.0002$, $p = .051$, $\varepsilon = 0.58$. In particular, previous finding of greater unprimed theta than same-exemplar primed theta in frontal electrodes sites but not in posterior electrode sites, $t(23) = 2.05$, $p = .05$, also was observed when comparing unprimed and different-exemplar primed conditions, $t(23) = 2.391$, $p = .025$, STATS, but not when comparing unprimed and word primed conditions, $t < 1$.

Theta Component 3. In the preliminary analysis of theta component 3, the main effect of coronal electrode location was significant, $F(2,46) = 7.71$, $MSe = 0.0007$, $p = .001$, $\varepsilon = 0.74$. Linear contrasts indicated that greater theta activity was measured at anterior electrode locations relative to posterior locations, $F(1,23) = 10.40$, $MSe = 0.0002$, $p = .004$. Also, the interaction of experimental condition by coronal electrode location only approached significance, $F(2,46) = 2.62$, $MSe = 0.0002$, $p = .084$, $\varepsilon = 0.73$.

When all four experimental conditions were included in the follow-up analysis of theta component 3, only the main effect of coronal electrode location was significant, $F(2,46) = 9.55$, $MSe = 0.001$, $p < .001$, $\varepsilon = 0.70$. Linear contrasts indicated that greater theta activity was measured at anterior electrode locations relative to posterior locations, $F(1,23) = 12.04$, $MSe = 0.0004$, $p = .002$ (i.e, more theta activity was measured in the anterior electrode sites than in the posterior electrode sites).

Correlations between Measures

To better understand associations between behavioral measures (response time and identification rates), TD components, and TF components, Pearson correlations were calculated. Only the TF components that carried condition effects were used in these analyses (i.e., theta components 1, 2, and 3). A difference score between the same-exemplar primed condition and the unprimed condition was calculated (unprimed – same-exemplar primed) for each measure. For example, the difference between the same-exemplar primed condition and the unprimed condition in a behavioral measure (e.g., response time) was correlated with the same difference in a TD component measure (e.g., N2).

As expected, the behavioral response time and proportion unidentified priming scores were positively correlated (a fast response time coincided with higher unidentification rates), $r(24) = .508$, $p = .011$ (see Table 5). The only neural measure to correlate with a behavioral measure was the negative correlation between response time priming and the theta component 2 priming effect, $r(24) = -.420$, $p = .041$. Specifically, a greater response time difference between the same-exemplar primed and unprimed conditions (unprimed producing longer response times than same-exemplar primed) was correlated with a greater theta power difference between these two conditions (unprimed producing more theta power, especially greater fronto-central theta power, than same-exemplar primed). Finally, the N2 TD component was positively correlated with the P3, $r(24) = .904$, $p < .001$, and the LP, $r(24) = .837$, $p < .001$. The TD component P3 was positively correlated with the LP, $r(24) = .980$, $p = .001$. The TF theta component 1 was positively correlated with theta component 2, $r(24) = .515$, $p = .010$, and marginally positively correlated with theta component 3, $r(24) = .347$, $p = .097$.

Table 5. Pearson r correlations (N = 24) between behavioral, time-domain, and time-frequency measures.

	Response Time	Proportion Unidentified	N2	P3	LP	Theta PC 1	Theta PC 2	Theta PC 3
Response Time	X	.508*	.002	-.025	.008	-.317	-.420*	.024
Proportion Unidentified		X	.315	.109	.059	.014	.094	.096
N2			X	.904***	.837***	.208	.219	.315
P3				X	.980***	.167	.047	.160
LP					X	.091	-.019	.12
Theta PC 1						X	.515*	.347
Theta PC 2							X	.183
Theta PC 3								X

Note. * = p < .05 , *** = p< .001

Discussion

This study was proposed to follow up a repetition priming fMRI experiment in which repetition effects were observed, unexpectedly, in posterior-parietal regions. These repetition effects could be attributed to explicit memory contamination, changes in the DMN, or action pathway priming. Using the temporal and spatial information of ERPs and TF analysis, these three potential interpretations were tested, allowing for a more thorough understanding of processes that occur in implicit memory experiments.

Primed stimuli elicited faster identification responses and fewer unidentified responses than did unprimed stimuli. Primed stimuli also elicited a more positive deflection (beginning between 300 and 400 ms) in the TD ERP measures relative to unprimed stimuli, replicating many previous ERP studies (Bentin et al., 1992; Doyle et al., 1996; Paller & Gross 1998; Rugg, 1995; Rugg et al., 1998). In the TF analyses, the theta frequency band differentiated between primed and unprimed stimuli. More anterior theta power was measured for the unprimed stimuli relative to the primed stimuli at frontal electrode sites.

The three potential interpretations of posterior-parietal repetition effects were tested in the following ways. The explicit memory contamination hypothesis was not supported because: 1) primed stimuli differed from unprimed stimuli before 500 ms; however, the TD marker of explicit memory is that old stimuli do not differ from new stimuli until 500 ms or later; 2) no alpha power differences were measured between primed and unprimed stimuli and the theta power differences that were measured were in the opposite direction than that predicted by the explicit memory hypothesis. In particular, there was greater anterior theta for unprimed stimuli than primed stimuli. These findings do not match previous TD (Rugg et al., 1998; Voss & Paller, 2008) and TF (Düzel et al., 2003) markers for explicit memory; therefore, the explicit memory contamination hypothesis was not supported.

The action pathway priming hypothesis likewise was not supported. Behavioral measures but no neural measures of action pathway priming were observed. Previous research indicates that highly actionable objects elicit a greater early P1 in occipital temporal leads than not highly actionable objects (Handy et al., 2003; cf., Kiefer et al., 2011). However, there was no difference in activity between primed and unprimed conditions in that P1 component in the present study, both for highly actionable objects and for not highly actionable objects. Thus, no evidence of priming was observed in a neural measure that is sensitive to actionability. The null effect of actionability in the P1 in the present study suggests that the significant effect of actionability in the P1 in the previous studies (Handy et al.; cf., Kiefer et al.) may require a task that more overtly requires engaging action pathway processes (e.g., presenting sequential, highly actionable stimuli that afford similar actions to elicit motor priming or presenting actionable stimuli to the right or upper visual fields).

By contrast, the change in DMN hypothesis was partially supported in this study. As predicted by that hypothesis, lesser anterior theta power was measured for primed stimuli than for unprimed stimuli, in line with the hypothesis that the DMN was more engaged by primed stimuli than by unprimed stimuli. Lesser theta power has been measured over anterior electrodes when the DMN is engaged during resting states than when the DMN is less engaged during non-resting states (Chen et al., 2008; Scheeringa et al., 2008). However, another prediction from the DMN hypothesis was not supported. No difference in posterior alpha power was observed between primed and unprimed conditions. This fails to support the hypothesis that the DMN was more engaged by primed stimuli than by unprimed stimuli. Greater alpha power has been measured over posterior electrodes when the DMN was engaged during resting states than when the DMN was less engaged during non-resting states (Jaan et al., 2009; Laufs et al., 2003).

General Findings/Interpretations

In this experiment, I used ERPs in an attempt to attribute effects measured in posterior-parietal regions with fMRI to one of three potential interpretations. In the fMRI experiment (Deason et al., 2008), no predicted ventral visual stream effects were apparent in a standard univariate BOLD signal analysis. The predicted effects were found when a more intensive multi-variate pattern analysis was used (McMenamin et al., 2009; 2011). Interestingly, fMRI effects were unexpectedly measured in the dorsal stream (e.g., posterior-parietal region). These effects were interesting because little evidence exists that this region specifically contributes to repetition priming (see Korsnes et al., 2008). In using ERPs, I set out to test what process(es) could be attributed to these posterior-parietal activations measured in fMRI.

Two main ERP results were measured during this task. The first was a priming effect measured in the TD (i.e., a positive deflection for repeated stimuli relative to unprimed stimuli beginning between 300 and 400 ms). This effect is in line with previous findings of positive deflections beginning around 250 ms for repeated relative to new stimuli (Bentin et al., 1992; Doyle et al., 1996; Paller & Gross 1998; Rugg, 1995; Rugg et al., 1998). One interesting aspect of the current results is that of the three primed stimuli (same -exemplar primed, different-exemplar primed, and word primed) only the same-exemplar primed stimuli elicited this positive deflection relative to unprimed stimuli. This is an example of specific-exemplar priming which is distinguishable from abstract-category priming (discussed in more detail below; Marsolek, 1999). Differentiating these two types of repetition priming with ERPs would be an interesting and informative future research direction.

The second main result indicates that changes in DMN processing can occur in a repetition priming experiment. By using TF analyses, lesser anterior theta power was measured for primed stimuli than for unprimed stimuli, which is in line with evidence that such an effect indicates a change in the DMN (Chen et al., 2008; Scheeringa et al., 2008). These two findings taken together can help explain unexpected effects measured with ERP and fMRI. In other words, unexpected effects measured in the posterior-parietal regions measured with fMRI during a putatively implicit memory experiment may be attributed to DMN processing. There are, however, limitations of the current experiment and findings that could be addressed in future experiments.

Limitations

Of the three hypotheses tested here, the test of the action pathway priming hypothesis may have been the weakest, largely because little has been established about action pathway priming in previous work. A stronger test would be to use stimuli more suited for differentiation of actionability processes (e.g., tools vs. non-tools, cf., Kiefer et al., 2011; Handy et al., 2003). With the current stimulus set, one can only tentatively rule out the action pathway priming hypothesis as a contributing factor to the posterior-parietal activation measured in the initial fMRI experiment. Additional follow-up implicit memory fMRI and ERP experiments with a stimulus set specifically designed to directly test this hypothesis would be necessary to sufficiently support or refute action pathway priming as a contributor to repetition effects measured in posterior-parietal regions.

With a stronger stimulus set and a different experimental method, the action pathway hypothesis could be more directly tested. For example, Kiefer et al., (2011), presented subjects with two manipulable objects in sequence (e.g., tools) and each was to be named. The second stimulus afforded a similar (congruent) or dissimilar (incongruent) action as the first stimulus. Congruent trials were 'action primed' relative to incongruent trials. Several methodological differences are apparent between the current experiment and Kiefer et al.'s experiment. First, the long duration between presentation of the prime and the target in the current experiment (the time between the encoding phase and the test phase) could have reduced the likelihood of measuring a small action priming effect. In the Kiefer et al., experiment, the prime and target were separated by a mere 70 ms and thus could lead to a maximal measurement of a priming effect (i.e., little time or few intervening stimuli between prime and target that could reduce the priming effect). Second, unlike Kiefer et al. in which stimuli were named, participants in the present experiment responded as to whether they could identify the object or not. This task was selected, initially, to reduce movement artifacts due to naming objects while measuring BOLD signal in the fMRI scanner. In the ERP experiment, a similar rational was implemented as naming tasks can add unwanted muscle artifacts to EEG recordings. These steps were taken in the current experiment of object repetition priming, but if the action pathway priming hypothesis were to be more directly tested, a stimulus set and experimental methodology better suited would be necessary.

Another limitation of the current study could also be interpreted as a positive attribute. The same exact experimental design was used in both the fMRI experiment and the ERP experiment. Although much time and effort was put into piloting the experiment before collecting fMRI data, the experimental paradigm was optimized for an fMRI experiment and not necessarily an ERP experiment. For example, it is common to include several fixation trials, sometimes an equal number of fixation trials as stimuli of interest trials (as was done here), in an fMRI experiment but this is much less common in ERP experiments. One could argue that having many more fixation trials than normal in the ERP experiment has, in some way, affected the ERP results in such a way that does not allow for direct comparisons between the fMRI and ERP results. Though this confound is possible, it is very unlikely to have actually affected these results or interpretations.

One final limitation of this ERP experiment could be the number of participants in the experiment. In both the fMRI and ERP experiments, 24 subjects were used in the analyses. Unlike the fMRI analysis, the ERP analysis proved weaker in magnitude between conditions and few differences between the three types of repeated stimuli were found. In the original set-up of this experimental paradigm, small but predictable differences between the three types of repeated stimuli were expected. It is possible that with a larger number of participants in an ERP analysis these small but predictable differences could be measured.

Next Steps

Though these findings are intriguing and potentially useful for helping to explain unexpected results (i.e., posterior-parietal findings) in previous studies, additional analyses could be carried out to more fully understand these effects. For example, source localization of the ERP effects could be helpful in identifying, and potentially matching, neural generators of ERP effects with the fMRI findings. It would be quite helpful if the anterior theta effects found in this ERP experiment could be linked to posterior-parietal activations allowing for direct comparison between the ERP and fMRI findings. If the source localization does not connect the anterior theta effects with posterior-parietal regions (i.e., the precuneus), there were additional regions of interest identified by Deason et al. (2008) to examine, including left and right lateral inferior parietal cortex and left angular gyrus. Exploration of these regions and the potential link to ERP and TF effects presented here could help explain both the fMRI and ERP findings in more detail.

Another line of inquiry circles back to the beginning of the fMRI experiment. Initially, three repetition priming conditions were included in this experiment to measure and identify subsystems of specific-exemplar and abstract-category repetition priming. That is, repetition priming effects are elicited by repeated individual exemplar and repeated categories of stimuli (e.g., different exemplars of the same category of object; Bartram, 1974). For example, after prior encoding of an upright piano, priming can be shown when either the same (upright piano) or different piano (grand piano) is presented at test. The magnitude of facilitation for same exemplar priming is greater than that found for different exemplar priming (Bartram, 1974). When same-exemplar primed items are processed faster and more accurately than different-exemplar primed items, this reflects visually 'specific' exemplar priming. Also, priming can be measured to an image of a piano at test after prior encoding of the word piano. When different-exemplar primed items are processed faster and more accurately than word primed exemplars, this reflects 'abstract' category visual priming (Marsolek, 1999). By using divided visual field experiments, hemispheric asymmetries associated with specific-exemplar and abstract-category visual priming have been identified (Burgund & Marsolek, 2000; Marsolek, 1995, 1999; Marsolek & Burgund, 1997, 2003, 2008). Neuroimaging methods such as fMRI were necessary to measure specific, within hemisphere neural processes of priming (e.g., Koutstaal et al., 2001).

Because visual object repetition priming effects were predicted in the ventral visual stream, the initial BOLD signal analyses in Deason et al. (2008) were focused on that region. As discussed above, little differentiation between experimental conditions were found in the ventral stream using a typical univariate fMRI analysis. A multivariate technique was necessary to observe differentiation between experimental conditions (McMenamin et al., 2009; 2011). This is evidence of a neural marker for a specific-exemplar and an abstract-category subsystem at work during this task implemented in both fMRI and ERP. Are there accompanying neural markers for these subsystems in the ERP findings? In the TD (e.g., P3), there is a clear marker for the specific-exemplar subsystem (the same-exemplar primed [1.81 μV] condition elicited a more positive P3 than the different-exemplar primed [0.76 μV], $F(1,69) = 9.77$, $MSe = 1.36$, $p = .003$). However, no TD or TF measure captured a neural marker for the abstract category (the different-exemplar primed [0.76 μV] and the word primed [0.85 μV] conditions did not differ in the P3 window, $F < 1$). Further data analysis of this data set should be targeted at finding the ERP neural marker of abstract-category priming which is apparent in the aforementioned fMRI experiment using the same method (Deason et al.).

Conclusions

In conclusion, the current ERP experiment offers insight into posterior-parietal activation measured with fMRI during putatively implicit memory experiments. Unexpectedly, dorsal stream repetition effects were found in a putatively implicit memory experiment. Because the posterior-parietal activations could be attributed to three different cognitive processes, an ERP experiment was undertaken to arbitrate between potential interpretations. In using the superior temporal resolution of ERPs to inform the superior spatial resolution of fMRI, a more complete picture of the underlying cognitive processes was accomplished. In the ERP TD and TF analyses, one hypothesized cognitive process was supported: the default mode network. With this finding, it is interpreted that the posterior-parietal activation initially measured with fMRI may be attributed to DMN processing. Future steps to further link the fMRI measurement and the ERP measurement of this phenomenon would be an exciting and important avenue to explore. These explorations should focus on better delineating the contribution of the DMN and the cognitive process(es) of interest during cognitive tasks, such as this implicit memory task. Also, understanding the interconnection of the DMN and the cognitive process(es) of interest would be vital for an overall understanding of brain networks and that specific cognitive process. Finally, future analytical steps should be carried out to identify the neural marker, measured with ERPs, of abstract-category priming measured in fMRI.

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Appendix A

Judgment Instructions

In this experiment, you will be presented pictures of individual objects/things that will be shown, one at a time, on the computer screen. Your task is simply to rate each of the pictures as it is shown. You will be asked to make 3 ratings per picture.

First, suppose you were playing charades, such that one person had to identify an object/thing based on how another person mimed various actions that might be associated with the object/thing. For each picture, we would like you to give a rating (1 – 7) for how difficult it would be to play that game with these items (1= very easy; 7 = very difficult/impossible). For example:

> For many people, it would be easy to play charades with a ring but it would be difficult to play charades with a bridge.

Second, how central is the pattern of movement(s) associated with the use of this object/thing in determining its function (1 = not central at all; 7 = very central)? Please note that the instructions are "how central is the pattern of movement(s) associated with the use of this object/thing in determining its function?" The movements to consider are movements that involve using the thing. For example:

> For many people, the pattern of movements associated with the use of a wrench is central in determining its function (e.g., the typical pattern of movements made with a wrench is central for enabling its function of tightening a nut). In contrast, the pattern of movements associated with the use of a chimney is not central in determining its function (e.g., any pattern of movements you may have associated with a chimney is not central for its function of venting heat/ash).

Third, rate each object based on how frequently you interact with the object/thing with your hands (1 = no experience interacting with the object/thing; 7 = frequently interact with the object/thing).

> For many people, interactions with a glass (for drinking) using one's hands is frequent, but interactions with a rake using one's hands is not frequent.

The way the presentation works is like this: A picture appears on the screen and stays there for a short time before a prompt appears. When this prompt appears, please make the first rating (how difficult it would be to play charades with the object/thing). After you make this response, another prompt will appear. When this prompt appears, please make the second rating (how central is the pattern of movement(s) associated with the use of the object/thing). After you make this response, the third prompt will appear. When this prompt appears, please make the third rating (how frequently you interact with the object/thing with your hands). The program will not continue until you make each rating. After you make the 3 ratings for a given picture, the next picture will appear, and so on. Note that you cannot change your responses; if you feel you have made a mistake, please just continue to focus, responding to each picture.

Please feel free to ask any questions that you have now.

Before we begin, please briefly paraphrase these instructions for me.

Appendix B

Liking Instructions

Step 1

You will be presented with a series of pictures of objects intermixed with printed words that name other objects, one at a time.

After a stimulus is presented, please decide how much you like that thing. Please use a 4-point scale and make responses by pressing one of the four keys under the four fingers of your right hand.

- Press the button under your index finger if you like it very much.
- Press the button under your middle finger if you like but not very much.
- Press the button under your ring finger if you dislike it but not very much.
- Press the button under your pinkie or little finger if you dislike it very much.

When making your decision, please consider the meanings associated with the object, as opposed to how they sound, or what they look like, etc. It is very important that you judge your true feelings about the stimulus; it is important that you choose a number that truly shows how much you like or dislike it. Also, please distribute your judgments across the whole 4-point scale over the course of the many judgments you will be making.

The sequence of events is as follows: First, a crosshair or fixation point will appear in the center of the display. Whenever the fixation point appears, please focus your eyes on it, because objects and words will appear at that location. When an object or word appears, your task is to decide how much you like or dislike it. As soon as possible after a stimulus is presented, please press a key that corresponds to your rating for that stimulus.

Before you begin, let's recap the procedure. Please keep your eyes on the fixation point whenever it appears. Immediately after making your decision about each object or word, please press a key that indicates how much you like or dislike that stimulus.

If you have any questions at all, please ask the researcher.

We will now go through a short practice to get you more acquainted with the procedures. This practice is identical to the actual task with the exception of being shorter in overall length.

Appendix C

Identification Instructions

Step 2

Next, you will participate in a study of how people identify familiar objects. We are investigating how well people can identify common objects that appear very briefly on the display.

After a picture of an object appears, please decide whether you are absolutely certain about what the object was. As soon as you've made your decision, please indicate your response by pressing one of two buttons.

- Press the button under your index finger if you are certain about what the object was.
- Press the button under your middle finger if you are not certain about the object was.

The clock measuring your response time starts when the object appears on the screen, therefore you should try to respond just as soon as you have made your decision. Each object will appear very briefly—these exposures may seem too brief to see them accurately, but we've found that, with practice, people can identify some objects that go by that quickly.

The sequence of events is as follows: First, a crosshair or fixation point will appear in the center of the display. Whenever the fixation point appears, please focus your eyes on it, because objects will appear very briefly at that location. When an object appears, your tasks is to decide whether you can identify the object, and then press the button under your index finger if you are absolutely certain what the object was or the button under your middle finger if you are not absolutely certain what the object was. Please press a button as soon as you have made your decision.

Note that you cannot change your responses; if you feel you have made a mistake, please just continue to focus, responding as accurately and quickly as possible on all the trials.

Before you begin, let's recap the procedure. Please keep your eyes on the fixation point whenever it appears. As soon as you can after an object is presented, please press the button under your index finger if you are absolutely certain what the object was or press the button under your middle finger if you are not absolutely certain what the object was.

If you have any questions at all, please ask the researcher.

We will now go through a short practice to get you more acquainted with the procedures. This practice is identical to the actual task with the exception of being shorter in overall length.