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Perceptual difficulty in source memory encoding and retrieval: Prefrontal versus parietal electrical brain activity

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ABSTRACT

It is well established that source memory retrieval – remembering relationships between a core item and some additional attribute of an event – engages prefrontal cortex (PFC) more than simple item memory. In event-related potentials (ERPs), this is manifest in a late-onset difference over PFC between studied items which mandate retrieval of a second attribute, and unstudied items which can be immediately rejected. Although some sorts of attribute conjunctions are easier to remember than others, the role of source retrieval difficulty on prefrontal activity has received little attention. We examined memory for conjunctions of object shape and color when color was an integral part of the depicted object, and when monochrome objects were surrounded by colored frames. Source accuracy was reliably worse when shape and color were spatially separated, but prefrontal activity did not vary across the object-color and frame-color conditions. The insensitivity of prefrontal ERPs to this perceptual manipulation of difficulty stands in contrast to their sensitivity to encoding task: deliberate voluntary effort to integrate objects and colors during encoding reduced prefrontal activity during retrieval, but perceptual organization of stimuli did not. The amplitudes of ERPs over parietal cortex were larger for frame-color than object-color stimuli during both study and test phases of the memory task. Individual variability in parietal ERPs was strongly correlated with memory accuracy, which we suggest reflects a contribution of visual working memory to long-term memory. We discuss multiple bottlenecks for source memory performance.

Keywords: source memory, prefrontal cortex, object-based, difficulty, working memory

Episodic memory is defined as inherently relational, or as Schacter and Tulving (1994, p. 28) put it, consisting of “multifeature representations in which numerous different kinds of information – spatial, temporal, contextual, and so forth – are bound together”. However, different memory tests require retrieval of more or less information for successful performance. At one extreme are old/new recognition tests that require only an assessment of whether a stimulus was presented sometime in the laboratory experiment. In contrast, source memory tests are those that probe relational information more closely: what voice spoke a word, where was an object viewed, what color was a picture, was an action executed or only imagined, etc. (Johnson, Hashtroudi, & Lindsay, 1993). In these tests, memory for the core event – the word, object, or picture – is considered *item memory*, and *source accuracy* is defined by accurate retrieval of the additional information associated with that item. Introspection suggests that the strength of the binding between different bits of information varies both within and across memories for individual events: we might remember the location of an event, but not the time, or the exact date of a conversation, but not the clothing of the participants, etc. Empirical results confirm that retrieval of multidimensional memories does not happen in an all-or-none fashion, but that some aspects of a single event can be remembered while others are not (Dodson, Holland, & Shimamura, 1998; Light & Berger, 1976; Meiser & Bröder, 2002; Starns & Hicks, 2005; Vogt and Bröder, 2007)¹.

Demonstrations of the relative independence of different source attributes lead to a different question, namely, what determines which particular aspects of context will be bound to the core event during encoding and meet with retrieval success later? One clear answer to this question is provided by the principle of transfer-appropriate processing (Morris, Bransford, & Franks, 1977), that source accuracy will improve to the extent that the relevant relationships are processed during the study phase. Light and Berger (1976) found that when subjects were instructed that they would be tested for their memory of words and their fonts, word/font conjunctions were better remembered than word/color conjunctions, and vice versa when subjects were instructed that the word/color relationships were critical. In a previous experiment closely related to the current design, we have shown that the nature of the encoding task is important even under intentional encoding instructions (Kuo & Van Petten, 2006). In that experiment, participants were always aware that the memory test would require judgments about drawings and their colors. In one session, however, they performed an item-oriented study task of judging the real-life size of the objects depicted in the drawings, while in another session they performed an integrative encoding task of judging object/color relationships as good (red stop sign) or bad (blue apple). The integrative encoding task produced no benefit for recognition of the objects as studied or unstudied, but boosted source accuracy for object-color relationships by some 14%.

Categorizing source attributes: the *intra-item* versus *extra-item* distinction

Leaving aside the benefits of an appropriate encoding orientation, it has long been suspected that some sorts of source information might be easier to remember than others, and/or rely on different retrieval strategies, and/or rely on different brain circuits. Multiple schemes for categorizing varieties of source attributes have been proposed. For instance, Johnson and colleagues suggested that internally- versus externally-generated information might be a natural division, one that makes it more difficult to discriminate two classes of perceptual information (as might arise in a test of deciding which of two experimenters spoke a word) than to discriminate a perceptual source from a self-generated source (as might arise in test of deciding whether a word was spoken by an experimenter or one’s self; Hashtroudi, Johnson, & Chrosniak, 1989; Johnson et al., 1993). Moscovitch (1992) proposed a different fundamental division between “associative context” – aspects of an event that occur simultaneously and in the same location (e.g., perceptual source attributes) -- and “organizational context” derived from considering an event in relation to other events (e.g.,

temporal sequence). A variety of data (briefly reviewed below) indicate that PFC plays a larger role in source memory tests than in episodic memory tests that do not focus on relational information (item memory tests). Moscovitch initially suggested that memory encoded by the hippocampal system can offer the multidimensional details of an individual event, but that prefrontal cortex must be engaged when a task necessitates organizing multiple events retrieved from the hippocampal system. In later work, the associative/organizational dichotomy evolved to differentiate perceptual attributes from the spatial and temporal context of even a single stimulus. The multiple perceptual attributes that make up a stimulus (e.g., shape and color) were hypothesized to be more tightly bound to each other than to (for instance) the location in which the stimulus was presented (Troyer, Winocur, Craik, & Moscovitch, 1999). This latter division echoed earlier suggestions that different encoding mechanisms promote memory for “intra-item” versus “extra-item” attributes (Geiselman & Bjork, 1980; Smith, Glenberg, & Bjork, 1978). Bjork and colleagues found that rote rehearsal selectively enhanced recognition of intra-item relationships (such as a word and a voice) but not extra-item attributes (such as a word and the room where it was heard).

The present experiment was designed to compare brain activity during the encoding and retrieval of intra-item versus extra-item source attributes. A handful of studies have compared these two varieties of context, but their links to brain activity have been indirect. Troyer and colleagues compared memory for the temporal order of words (extra-item) to memory for ink color (intra-item), and in a second experiment compared voice to spatial location. In both studies, assigning a secondary task during the encoding and retrieval phases led to a greater accuracy impairment for the extra-item (spatiotemporal) source tests than for the intra-item source tests (Troyer et al., 1999; Troyer & Craik, 2000). Given the premise that attentional control critically involves prefrontal cortex (PFC), these results were taken as support for Moscovitch’s (1992) suggestion that extra-item source memory is more demanding of PFC than intra-item source memory.

A second sort of indirect link comes from comparisons between young and old adults. Even healthy older adults show a disproportionate deficit in source memory tests as compared to item tests, and it has been argued that this deficit reflects a special vulnerability of PFC to aging (West, 1996, 2000). In a meta-analysis of 46 studies, Spencer and Raz (1995) indeed observed a greater age-related deficit in spatiotemporal source memory compared to perceptual source memory. This result might then argue that spatiotemporal source tests are more taxing of PFC than perceptual source tests.

Experiments that include measures of brain activity have, to date, not addressed the intra-item versus extra-item distinction in source memory. Instead, results from a variety of methods have consistently indicated that PFC is both strongly engaged by, and necessary for good performance in source memory tests under most circumstances. The role of PFC in the temporal organization of memory was initially discovered through studies on patients with frontal lobe damage (Milner, Petrides, & Smith, 1988; Janowky, Shimamura, & Squire, 1989; see also Swick, Senkfor, & Van Petten, 2006 for a non-temporal source test in frontal patients). The relationship between PFC and spatiotemporal source memory was corroborated in healthy young adults via event-related potentials (ERPs) in list-discrimination and spatial source tests (Dywan, Segalowitz, & Arsenault, 2002; Trott, Friedman, & Ritter, 1997; Van Petten, Senkfor, & Newberg, 2000). On the other hand, a number of ERP studies have also demonstrated engagement of PFC during source tests that tap conjunctions of perceptual attributes that might be considered “intra-item”, such as word-voice and object-color pairings (Friedman, Cycowicz, & Bersick, 2005; Senkfor & Van Petten, 1998; Kuo & Van Petten, 2006; Wilding, Doyle, & Rugg, 1995). Finally, ERPs have also shown greater prefrontal engagement when judging what encoding task accompanied a studied object than during old/new discriminations (Senkfor, Van Petten, & Kutas, in press; see also Johansson, Stenberg, & Lindgren, 2002; Wilding, 1999 for related findings). This last variety of source memory test blurs the distinction between “intra-

item” and “extra-item” attributes given that properties of an object determine the specifics of how an encoding task is carried out. Functional magnetic resonance imaging (fMRI) results have similarly shown greater prefrontal activity in source tests than old/new recognition tests, when the source tests require spatial or temporal judgments (Rugg, Fletcher, Chua, & Dolan, 1999; Slotnick, Moo, Segal, & Hart, 2000; Suzuki et al., 2002), perceptual judgments (Fan, Snodgrass, & Bilder, 2003; Ranganath, Heller, & Wilding, 2007; Ranganath, Johnson, & D’Esposito, 2000; Raye, Johnson, Mitchell, & Nolde, 2000), and judgments about the encoding task that accompanied a stimulus (Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins & Han, 2006; Dobbins, Rice, Wagner, & Schacter, 2003). However, these observations of prefrontal activity across intra-item and extra-item source tests have little to say about the possibility that some varieties of source information place greater retrieval demands on PFC than others.

A single recent fMRI study includes a contrast between different source memory tests that might appear to bear on the intra-item versus extra-item distinction, although it was not designed for this purpose. Mitchell and colleagues included trials a source discrimination about the format of a studied item (object name studied as a picture versus a word), or about the location of a studied item (left or right side of the computer monitor). Contrary to the predictions of the intra/extra hypothesis, the location test elicited less activity than the format test in most of the prefrontal regions reported, as well as in occipital and inferior temporal cortex (Mitchell, Johnson, Raye, & Greene, 2004). Accuracy also tended to be lower in the location than format test, and the authors suggested that location information was less salient and tended to more rapidly forgotten.

The current experiment was designed to examine brain activity during the encoding and retrieval of intra-item versus extra-item conjunctions of visual attributes without the potential confounds that might arise from comparisons between fundamentally different attributes that might vary in their intrinsic memorability. Participants attempted to remember relationships between color and object identity (conveyed by shape) in two source tests: when color was an integral part of the object versus when it appeared outside the object, as illustrated in Figure 1. This manipulation has a long history in research performed by developmental psychologists and vision scientists, and has repeatedly led to the outcome of better immediate and long-term memory for color-shape relationships when the two are spatially unified (Ceraso, Kourtzi, & Ray, 1998; Hale & Piper, 1973; Spiker & Cantor, 1980; Walker & Cuthbert, 1998; Wilton, 1989). Multiple permutations of the basic paradigm have led to widespread support for the “unitization” proposal of Asch, Ceraso, and Heimer (1960), or what has come to be called “object-based” perception: that individual features are more readily bound and retained when they appear to form part of a single object (see Luck & Vogel, 1997 for confirmation in a working memory task). We thus predicted lower accuracy in the source memory task of remembering object-color relationships when the stimuli consist of monochrome objects surrounded by colored frames than when the objects are themselves colored. At issue is whether the more difficult extra-item version of the task will also produce greater prefrontal activity. In addition to the specific comparison between intra-item and extra-item memory associations, the current design and our prior manipulation of encoding task (Kuo & Van Petten, 2006) are the first direct comparisons of brain activity during two source discriminations that tap the same content but vary in difficulty.

Insert Figure 1 about here

Event-related potentials in source memory tests

ERP studies of source memory have used recognition tests in which (1) unstudied items are intermixed with (2) old items presented with the same source attribute as during the study phase (e.g., “dog” in Voice A, exactly as studied) and (3) old items paired with a source attribute that was also studied, but not in conjunction with that item (e.g., “dog” in Voice B, a

recombination of a studied word and studied voice). When participants are instructed to label the core items as only “old” or “new”, irrespective of the source attribute, recognized items elicit more positive ERPs than rejected new items beginning 200 to 400 ms after stimulus onset (earlier for pictures, later for auditory words, intermediate for visual words). This *early old/new effect* is spatially widespread, but maximal at centroparietal scalp sites, evident in incidental repetition paradigms as well as in explicit recognition tests, differentiates hits from false alarms and misses as well as correct rejections, and is substantially reduced or eliminated in amnesia due to medial temporal or diencephalic damage (Olichney et al., 2000; Van Petten & Senkfor, 1996). When participants are instead instructed to engage in a source recognition test that mandates judging the studied items as “old same” or “old different”, the early old/new effect is little changed, but is accompanied by a late-onset amplitude difference (~700 ms after stimulus onset) between studied and unstudied items that is maximal over prefrontal cortex (Ranganath & Paller, 2000; Senkfor & Van Petten, 1998; Van Petten et al., 2000). The late prefrontal old/new effect is also evident in cued-recall tests for which source attributes are not presented in the test-phase, as when participants attempt to remember what encoding task accompanied an item, judge which list an item occurred in, or make voice judgments on visual test words (Dywan et al., 2002; Johansson et al., 2002; Senkfor et al., in press; Trott et al., 1997; Wilding, 1999; Wilding & Rugg, 1996). The early old/new effect thus indexes successful item recognition while the later frontal component reflects PFC involvement in retrieval of source information in conjunction with the core item. The large amplitude and frontopolar maximum of the late prefrontal ERP effect securely localize it to the frontal lobe, although the spatial resolution of scalp recordings do not allow a more precise estimate of what Brodmann areas it may be generated by². Because the late prefrontal effect has been insensitive to the success or failure of source retrieval success in our lab, we have characterized it as reflecting the process of an extended search for source information after an item has been identified as old, or careful examination of retrieved item-source conjunctions before making a final decision (Van Petten, Luka, Rubin, & Ryan, 2002).

In a previous study, we showed that the prefrontal old/new effect was eliminated after an encoding task that was designed to encourage strong binding between two attributes, suggesting that PFC engagement was particularly associated with the attempt to retrieve weakly-bound conjunctions (Kuo & Van Petten, 2006). The current study provides a complementary perspective on the same issue regarding binding strength and the role of PFC in source memory retrieval. Instead of varying the assigned encoding task, the degree of feature integration is manipulated by varying the perceptual organization of the stimuli. For both the *object-color* and *frame-color* conditions illustrated in Figure 1, participants performed an encoding task that does not particularly promote binding of the object and color attributes – judging the real-life size of the objects. If PFC involvement in source memory retrieval is invariably modulated by the strength of attribute conjunctions during encoding, we should again observe a larger frontal old/new effect in the condition where objects and colors are more weakly connected, in the frame condition. Alternately, we may find that the perceptual organization offered by a stimulus does not act in the same manner as deliberate voluntary encoding operations.

In the current experiment, as in the previous one, participants are forewarned of the source memory test prior to the study phase, and receive a practice study-test cycle. Results of our prior manipulation of encoding task showed that the benefit of transfer-appropriate-processing was robust under intentional study instructions, in line with a general history of memory research suggesting that encoding operations enforced by an assigned task on every trial are more influential than the mere attempt to remember (Craik, 1977; Hyde and Jenkins, 1969, 1973). We expect the accuracy benefit from perceptual unitization to be similarly robust under intentional instructions.

A second issue of some interest is whether we will be able to detect the brain processes that act to integrate the objects and colors in the frame condition. *A priori*, this condition should be more demanding of visual attention and working memory, as the task-relevant elements are spatially separated and comprise two distinct “objects” (in the visual sense). Encoding-phase differences between the object-color and frame-color conditions that are tied to later memory performance are thus evaluated.

METHODS

Subjects. Twenty-four adults (11 men, 13 women, age range 18-37 years) were paid for their participation. All demonstrated normal color vision (assessed by the Ishihara plates) and reported no history of neurological or psychiatric disorder. The project was approved by the University of Arizona Institutional Review Board, and subjects offered informed consent.

Materials. Stimuli were 448 line drawings of natural and artifactual objects, each in a congruent and an incongruent color (e.g., yellow or blue banana). For the *object-color* condition, colored contours or blocks of color defined the object. The stimuli, encoding task, and recognition task for the object-color condition were identical to those of the item-oriented (non-integrative) encoding condition of our prior study; further description of the stimuli and counterbalancing of colors across objects are provided there (Kuo & Van Petten, 2006). For the *frame-color condition*, monochrome drawings were surrounded by colored frames, as shown in Figure 1. Four versions of each line drawing were made: congruent object color, incongruent object color, congruent frame color, and incongruent frame color.

Procedure. Each subject participated in two sessions conducted at least a day apart; the object-color condition was the first session for half the subjects and the frame-color condition was the first for the other half. Each session consisted of 7 study-test cycles with a single *stimulus type* (object-color or frame-color), after a practice block (study and test) of 16 drawings not used in the main experiment. In each study block, 16 drawings were presented individually for 500 ms, with a stimulus-onset-asynchrony of 4000 ms. Subjects performed a size judgment task of comparing the real-life size of the depicted object with the computer monitor in front of them. Button presses with the right and left index fingers were used to indicate the object as “larger than the monitor” or “smaller than the monitor” (assignment of hands counterbalanced across subjects). Three minutes after completion of a study block, 32 drawings were presented for test. Half of the test objects were unstudied and called for a response of “new”. One quarter of the test objects were presented in the same color as during the study phase (evenly divided between congruent and incongruent), and called for a response of “old same”. One quarter of the test objects were presented in a different color as during the study phase (evenly divided between congruent and incongruent), and called for a response of “old different”. Old-same and old-different responses were indicated by the two index fingers and new responses by either the right or left middle finger. Hand for old-same versus old-different was balanced across the two sessions for each participant; assignment of “new” to the old-same hand versus the old-different hand was rotated across participants (see Kuo & Van Petten, 2006 for a discussion on the effect of hand assignment on ERPs).

Electrophysiological recording. The electroencephalogram was recorded from 29 scalp sites, including 27 standard locations: seven spanning the midline of the scalp from prefrontal to occipital (Fpz, Fz, Fcz, Cz, Cpz, Pz, Oz), six lateral pairs closer to the midline (*dorsal sites*: Fp1, Fp2, F3, F4, Fc3, Fc4, C3, C4, P3, P4, O1, O2), and four lateral pairs farther from the midline (*ventral sites*: F7, F8, Ft7, Ft8, Tp7, Tp8, T5, T6). Two additional electrodes (far lateral prefrontal, Fp5, Fp6) were placed 10% of the head circumference lateral to Fpz. Electrodes below the right eye and at the external canthi of the two eyes were used to detect blinks and eye movements. Amplifier bandpass was .01 to 100 Hz; sampling rate was 250 Hz, and gain was 50,000. Trials contaminated by blink, eye movement, or amplifier saturation

artifacts were rejected prior to averaging the trials into ERPs for each condition. The ERPs were then referenced to an average of the right and left mastoids.

Measurement and analyses. Source accuracy was computed as correct “same” and correct “different” judgments (*hit-hits*), divided by the total number of trials with correct “old” responses (chance = 50%). Item recognition accuracy was computed as the number of recognized old objects (“old” responses, regardless of the accuracy of the “same” or “different” aspect of the judgment) plus rejected new objects (correct rejection, CR), divided by the total number of trials (chance = 50%). ERP measurements were based on trials with correct judgments only, and consisted of mean amplitudes with respect to a 200 ms pre-stimulus baseline. Session order was entered as a between-subject factor in all analyses. When discussing session order effects, the groups are referred to as *object-frame group* (object-color first) and *frame-object group* (frame-color first). Huynh-Feldt corrections for nonsphericity of variance were applied to all F-ratios with more than one degree of freedom in the numerator.

RESULTS

Behavior

Study Phase

For the size judgments performed during the study phase, ANOVAs used stimulus type (object- versus frame color) as a repeated measure and session order as a between-subject factor. The subjects’ size decisions matched those of the experimenters equally well in the object-color and the frame-color conditions, at 85.6% and 86.7%, respectively. Overall RT was marginally longer in the frame-color condition (1329 ms) than in the object-color condition (1283 ms), $F(1, 22) = 3.31, p = .08$. Size decisions were faster in the second session than the first session (stimulus type by session order interaction), $F(1, 22) = 5.67, p < .05$. Followup tests showed that the speed-up across sessions was significant for the subgroup who received the object-color session second, $t(11) = 2.64, p < .05$, but not in the subgroup who received the frame-color session second, $t(11) = 0.46$. This pattern of results reflects a practice effect for the second session, combined with generally faster RTs in the object- than frame-color condition.

Item memory

Table 1 summarizes memory performance for all subjects; Table 2 shows data from the two sub-groups with different session orders. Accuracy and reaction time in the test phase were analyzed with ANOVAs taking stimulus type (object- vs. frame-color) and same/different (whether or not study and test colors remained the same for a given item) as within-subject factors, and session order as between-subject factor. Overall item recognition accuracy (correctly recognizing studied items and rejecting unstudied items) did not differ between the object-color (96.6%) and frame-color (96.2%) conditions. Color change from study to test also had no impact on recognizing studied drawings. The high and invariant levels of accuracy in recognizing the identity of studied objects means that variations in source accuracy across conditions can be securely attributed to variation in remembering the associations between objects and colors, immune from confounds that might arise from differential accuracy in remembering colored versus monochrome line drawings *per se*.

Insert Tables 1 and 2 about here

Source memory

As predicted, conjunctions of objects and frame colors were remembered less accurately than conjunctions of objects and integral colors, 80.1% and 72.4%, respectively, yielding a main effect of stimulus type, $F(1, 22) = 19.8, p < .0001$. The stimulus-type effect interacted with session order, $F(1, 22) = 5.77, p < .05$. Followup tests showed that the difference in source

memory accuracy was significant in the group that had the frame-color condition first, $t(11) = 5.72$, $p < .0001$, but not in the other subgroup, $t(11) = 1.29$. This pattern of results indicates a general source memory advantage of object color over frame color, accompanied by a practice effect that boosted performance in the second session.

The practice effect could be further specified in relation to whether color was switched from study to test. Overall, same-color trials elicited higher source memory accuracy than different-color trials, $F(1, 22) = 10.4$, $p < .005$, as in many source memory studies using a recognition format (Dodson & Shimamura, 2000; Kuo & Van Petten, 2006; Palmeri, Goldinger, & Pisoni, 1993; Senkfor & Van Petten, 1998; Wilding, Doyle, & Rugg, 1995). However, accuracy was vulnerable to color switch at test only during the first session: the object-color session for the object-frame group, $t(11) = 3.06$, $p < .02$, and the frame-color session for the frame-object group, $t(11) = 2.27$, $p < .05$. Color changes from study to test did not affect source accuracy in the second session for either group. In other words, the practice effect consisted of better retrieval control during the second session in resisting the interference due to color switches³. The improvement across sessions in resisting interference due to color switches from study to test cannot be attributed to a change in response bias. Source memory errors for recognized old items consisted of a tendency to incorrectly label old-different items as “old-same”. However, analysis of false alarm rates showed that new items were more likely to be called “old different” than “old same” when in error (means of 5.3 versus 3.4 trials, respectively), $F(1,22) = 10.5$, $p < .005$. Fewer false alarms were made in the second session than the first (3.9 versus 5.5 trials, respectively), $F(1,22) = 5.0$, $p < .05$, but there was no change in the nature of the false alarms across sessions (first/second session by same/different, $F(1,22) = 0.01$), nor any significant interactions with the order of object-color and frame-color sessions.

Reaction times from hit-hits largely mirrored the accuracy data. Source memory decisions were faster in the object condition than in the frame condition, $F(1, 22) = 21.4$, $p < .0001$. Again, stimulus type interacted with session order, reflecting a speed-up across sessions, $F(1, 22) = 7.07$, $p < .05$. The response time advantage from object color was significant for the frame-object group, $t(11) = 4.25$, $p = .001$, but only marginally so for the object-frame group, $t(11) = 1.91$, $p = .08$. In contrast to accuracy, the same/different factor did not reach significance as a main effect or interaction. RTs to correct rejections were nearly identical in the object-color and frame-color conditions (1127 and 1126 ms, respectively), although second-session responses were marginally faster than first session responses (1055 and 1198 ms, respectively), $F(1,22) = 3.61$, $p = .07$. The practice effect was thus widespread, but the faster processing of object-color stimuli arose specifically from the process of retrieving studied stimuli rather than from generally faster processing of objects with integral color.

Semantic congruity between objects and their integral or frame colors was varied here in order to maintain continuity with our prior manipulation of encoding task (for which a color congruity judgment served as the integrative encoding task; Kuo & Van Petten, 2006). As in that prior study, source judgments were more accurate for items studied in a semantically congruent color over those studied in an incongruent color, 83% vs 70%. This phenomenon is of some interest, so that it is pursued in ongoing work. The impact of color congruity is, however, orthogonal to the core questions addressed here, and did not interact with the object-versus frame-color manipulation for either accuracy measures, or in ERP measures.

Event-related potentials

Object color versus frame color: Study and test phases

The manipulation of intra-item versus extra-item attribute in this study necessitated the use of physically distinct stimuli in the two conditions, as seen in Figure 1. We thus began by comparing the ERPs elicited by object- and frame-color stimuli. The ERPs were largely similar, with the exception of a more negative potential for the frame-color than object-color condition, evident from 200 to 500 ms after stimulus onset. Figure 2 shows that the effect of stimulus type

was evident in both the study and test phases of the experiment, and had a focal parietal scalp distribution.

Insert Figure 2 about here

The impact of stimulus type during the test phases was evaluated via ANOVAs taking session order, object vs. frame color, memory condition (hit-hits versus correct rejections), and a spatial factor reflecting anterior-to-posterior (AP) scalp location, separately for the midline, dorsal, and ventral chains of electrodes (the latter two analyses included a fourth factor of left vs. right scalp location). There were no significant effects of stimulus type in the first 200 ms after stimulus onset, nor in latency windows after 500 ms (500-800 ms, and 800-1200 ms). In the 200-500 ms latency window, the parietal distribution of the object/frame effect led to a stimulus-type by anterior-posterior interaction for the midline sites, $F(6,132) = 4.71$, $p = .01$, $\epsilon = .38$, and a trend toward such an interaction for the dorsal sites, $F(5,110) = 2.97$, $p = .06$, $\epsilon = .41$. Followup analyses examined the parietal sites (Pz, P3, P4) where the stimulus-type effect was largest; these showed a robust effect overall, $F(1,22) = 33.8$, $p < .0001$, but also that the enhanced negativity for frame-color was larger in the participants for whom frame-color occurred in the second session (stimulus type by session order, $F(1,22) = 5.73$, $p < .05$). Separate analyses showed that the stimulus-type effect was, however, significant in both sub-groups (object-color first, $F(1,11) = 25.4$, $p < .0005$; frame-color first, $F(1,11) = 8.65$, $p = .01$).

Analyses of the parietal ERPs during the study phases led to largely similar results: more negative ERPs overall for the frame-color stimuli as compared to the object-color stimuli, $F(1,22) = 16.8$, $p < .0005$, accompanied by an interaction with session order, $F(1,22) = 6.20$, $p < .02$. The stimulus-type effect during the study phase was significant only for those participants who had the frame-color stimuli in their second session, $F(1,11) = 18.3$, $p < .002$, and not for those who experienced frame-color first, $F = 1.60$. Other than these significant effects in the 200-500 ms latency window, no other influences of stimulus type during the study phase were observed.

The 200 ms onset of the stimulus-type effect is later than one might expect for an obligatory response to the physical difference between the object-color and frame-color stimuli, but consistent with an effortful process of attending to the spatially separated objects and colors in the frame-color condition. Although source accuracy was globally worse for the frame-color than object-color stimuli, attentional binding of objects and colors could be expected to improve memory in the difficult frame-color condition. We thus examined whether the parietal potentials were correlated with source accuracy across individuals. Within individuals, amplitudes across study trials, hit-hit trials, and correct-rejection trials, and across stimulus types were strongly correlated with one another (r s between .66 and .93, all p s $< .001$). Regardless of trial type, individuals with more negative potentials had better memory performance, as seen in Table 3. More critically, increased amplitudes in the frame-color session as compared to the object-color session were associated with smaller accuracy decrements in the frame-color session, $r = -.53$, $p < .01$ (study and test trials collapsed), as shown in Figure 3. Overall, the frame-color condition was more challenging for the task of remembering object-color conjunctions, but people who generated more negative parietal ERPs to frame-color stimuli were better able to tackle the challenge, resulting in a smaller accuracy drop for the frame-color condition as compared to the object-color condition.

Insert Table 3 and Figure 3 about here

For each subject, study phase trials were also divided into those that were associated with accurate responses during the subsequent test (*subsequent hit-hits*) versus those that led to inaccurate source judgments (*subsequent hit-misses*). Sixteen participants had sufficient

trials in the smaller categories associated with inaccurate responses to yield adequate ERPs (a minimum of 10 trials in every category, means of 70, 20, 63, and 28 trials in the object-color hit-hit, object-color hit-miss, frame-color hit-hit, and frame-color hit-miss categories, respectively). There were no detectable ERP differences between study phase trials that led to accurate versus inaccurate source judgments later. Instead, the enhanced parietal negativity for frame-color over object-color stimuli was present for stimuli that would later elicit accurate source judgments ($F(1,15) = 7.19, p < .02$) and for stimuli that would later elicit inaccurate judgments ($F(1,15) = 4.80, p < .05$). Large parietal negativities were thus associated with better source accuracy at the level of individual subjects, but not at the level of individual trials within a subject.

To summarize: 1) larger parietal negativities were elicited by the frame-color stimuli containing two visual objects than by the object-color stimuli containing a single visual object, 2) participants who generated larger parietal negativities had higher source accuracy overall, and were more resistant to a decrement in accuracy for the frame-color condition as compared to the object-color condition, but 3) the study-phase amplitude of this potential did not predict accurate memory judgments for particular trials (of a given stimulus type) within an individual. In the Discussion, we propose that the parietal negativity is likely to reflect visual working memory and individual differences in VWM capacity, and that short-term retention of the visual displays is necessary but not sufficient for successful encoding into longer-term memory.

Test phase: Overview of memory effects

Figure 4 shows ERPs elicited by the studied (hit-hit) and unstudied (CR) stimuli in the object-color and frame-color conditions. The right column displays the memory effects – difference waves for hit-hits minus correct rejections – and shows that these were broadly similar for the two stimulus-types. Starting at 200 ms, hit-hits elicited more positive ERPs than correct rejections. The initial phase of the old/new difference occupied a latency range of about 200 to 600 ms after stimulus onset; we refer to this initial effect as the *early old/new effect*, and measured it as mean amplitude in the 200-600 ms latency window as in our previous studies using line drawing stimuli (Kuo & Van Petten, 2006; Van Petten, Senkfor, & Newberg, 2000). As shown in Figure 5, the early old/new effect had a broad scalp distribution, but was maximal at central and parietal scalp. The difference waves in the right column of Figure 4 show that the difference between hit-hits and correct rejections was prolonged over prefrontal cortex, so that a later time window of 800-1200 ms was dominated by the prefrontal effect (Figure 5). Our previous studies show that the late prefrontal effect is most evident when subjects make source memory judgments, as opposed to simple old/new judgments (Senkfor & Van Petten, 1998; Senkfor, Van Petten, & Kutas, in press; Van Petten et al., 2000). The *late prefrontal old/new effect* was measured in an 800-1200 ms latency window, as in those previous studies. Finally, the right column of Figure 4 shows an effect that is specific to the current experimental design, namely that the object-color condition resulted in a larger old/new effect at occipital sites than the frame-color condition, but only late in the epoch. Analyses of these three effects are below.

Insert Figures 4 and 5 about here

Early old/new effect

ANOVAs included stimulus type (object vs. frame), old/new (hit-hit vs. CR), and scalp site as repeated measures, and session order as a between-subject factor. During the 200-600 ms latency window, hit-hits elicited more positive ERPs than correct rejections at midline, dorsal, and ventral scalp sites, $F_s(1,22) > 200, p_s < .0001$. The early old/new effect was insensitive to stimulus type and to session order. Generally recognized as reflecting item memory retrieval,

this early-onset old/new effect was robust in both conditions, concurrent with the excellent item memory performance in both conditions.

Late prefrontal old/new effect

Amplitudes in the 800-1200 ms latency window were analyzed by an ANOVA with the same factor structure as above. Hit-hits continued to elicit more positive ERPs than correct rejections (main effect of old/new: midline, $F(1, 22) = 12.4, p < .005$; dorsal, $F(1,22) = 21.5, p < .0001$; ventral, $F(1,22) = 28.9, p < .0001$). The prefrontal focus of the late effect also yielded interactions between old/new and anterior-to-posterior scalp location (midline, $F(6,132) = 19.1, p < .0001, \epsilon = .43$; dorsal, $F(5,110) = 12.3, p < .0001, \epsilon = .37$; ventral, $F(4,88) = 8.52, p < .01, \epsilon = .37$). These analyses yielded no suggestion that stimulus type modulated the late old/new effect (object/frame, old/new x object/frame, all $F_s < 1$). Figure 6 (top) shows the similarity of the prefrontal old/new effect across stimulus types. However, we proceeded to more sensitive analyses of the prefrontal ROI alone (Fp5, Fp1, Fpz, Fp2, Fp6).

Insert Figure 6 about here

The late old/new effect was significant at the prefrontal sites, $F(1, 22) = 28.3, p < .0001$, and unaffected by the object- versus frame-color manipulation (old/new x stimulus type, $F < 0.5$). However, there was a significant interaction between session order, old/new, and stimulus type, $F(1, 22) = 7.81, p = .01$. Examination of the data showed that the late prefrontal old/new effect increased from the first to the second session, regardless of whether object color or frame color occurred first, as seen in the lower half of Figure 6. Reanalyzing the data with the factors of first vs. second session, old/new, and session order (object-color or frame-color first) confirmed the observation that the prefrontal old/new effect was larger in the second session, $F(1,22) = 7.81, p < .01$, regardless of the stimulus type in that session (first/second x old/new x session order, $F < 0.5$). It thus appeared that all subjects benefited from the “training” through the first session to more effectively engage PFC during source memory retrieval in the second session. Followup tests showed that the increase in the late prefrontal positivity from the first to the second session was specific to the studied stimuli (hit-hits), $F(1,22) = 10.6, p < .005$, and did not include the unstudied stimuli (CRs), $F = 1.08$. The specificity of the session effect indicates that it did not reflect a global change of state, but was instead tied to the memory requirement of retrieving the color of studied objects.

As described above, source accuracy also showed an improvement from the first to second sessions, but only for trials in which there was a color change from study to test (*old-different* trials). The increased amplitude of the prefrontal old/new effect across sessions is consistent with the idea that subjects were able to exert greater strategic control during retrieval in the second session and were better able to resist the error of labeling recombinations of objects and colors as “old same”. However, such improved retrieval control appeared to have been sustained throughout the whole second session and not applied only to different-color trials. Adding the same/different factor to an ANOVA with prefrontal amplitudes yielded no interactions between same/different and any other factor, in particular no interaction between same/different and first/second session. More broadly, the factor of color switch between study and test had no impact on the ERPs on correct trials, as seen in Figure 7.

Insert Figure 7 about here

Perceptually-driven versus task-driven integration of attributes

As noted in the introduction, one motivation for the current experiment was to compare the impact of two distinct encoding manipulations that, *a priori*, could be expected to strengthen

or weaken the binding between the object and color attributes that need to be retrieved for accurate source judgments. In a previous experiment (Kuo & Van Petten, 2006), an encoding task that encouraged integration of the two attributes – judging the semantic congruity of an object-color combination -- both improved source accuracy and decreased the amplitude of the late prefrontal old/new effect during the retrieval phase, as compared to the same size-judgment task used in the current experiment. The current encoding manipulation also influenced source accuracy, but had no impact on late prefrontal ERPs during the retrieval phase, suggesting a fundamental difference in how the two encoding manipulations are implemented in the brain, despite their similar impact on memory accuracy. However, a potential concern is that the encoding-task manipulation in the previous experiment had a somewhat larger impact on accuracy than the current perceptual manipulation, resulting in a 14% accuracy difference between conditions as compared to the 8% difference between the object-color and frame-color conditions here. One might wonder if the two encoding manipulations were qualitatively similar in their impact on brain activity, but merely differed in strength.

We thus examined data from subsets of the participants in the two experiments who were matched on the strength of the encoding manipulation⁴. We focused on source accuracy for stimuli that remained in the same color from study to test, because retrieval-phase ERPs in the previous study were most sensitive to the encoding manipulation for these stimuli. Excluding two participants from the previous experiment who showed the largest accuracy benefit from the integrative encoding task, and four participants in the current experiment who showed the smallest accuracy change between the object- and frame-color conditions led to subsets of participants who were matched on their behavioral sensitivity to the two encoding manipulations. For the 22 participants from the previous experiment, the item-oriented (size-judgment) encoding task led to a source accuracy level of 82.8%, whereas the integrative encoding task led to accuracy of 93.7%, a 10.9% difference ($se = 1.7$). For the 20 participants from the current experiment, the frame-color condition led to a source accuracy level of 75.4%, whereas the object-color condition led to accuracy of 86.2%, a 10.7% difference ($se = 2.0$). An ANOVA with experiment and encoding manipulation as factors showed that, although accuracy was generally higher in the previous experiment, $F(1,40) = 7.63$, $p < .01$, and both encoding manipulations were very effective, $F(1,40) = 68.1$, $p < .0001$, there was no difference in the strength of the encoding manipulations across experiments in these matched subsets of participants, $F(1,40) = 0.01$.

Prefrontal amplitudes (800-1200 ms) elicited by old-same stimuli were subjected to an ANOVA taking experiment as a between-subject factor, and encoding condition and prefrontal scalp site (5 levels) as within-subject factors. This resulted in a marginal effect of encoding condition, $F(1,40) = 3.30$, $p = .08$, and critically, a significant interaction between experiment and encoding condition, $F(1,40) = 4.02$, $p = .05$. Followup analyses confirmed that the integrative encoding task in the previous experiment led to smaller prefrontal potentials than the item-oriented encoding task, $F(1,21) = 6.63$, $p < .01$, whereas the object- versus frame-color manipulation of the current experiment had no impact, $F(1,19) = 0.02$.

A different strategy for comparing the impact of encoding strategy and perceptual organization (suggested by a reviewer of the present paper) is to compare participants with equivalent source accuracy overall. The 14 least-accurate participants in the integrative encoding session of the prior experiment had a source accuracy rate of 87.6% ($se = 1.3$), whereas the 14 most-accurate participants in the object-color condition here had a source accuracy rate of 86.0% ($se = 1.4$), accuracy levels which are indistinguishable, $t(26) = 1.14$. Nonetheless, the matched participants in the current experiment showed a robust late prefrontal difference between studied and unstudied items (hit-hits versus correct rejections), $F(1,13) = 15.9$, $p < .002$, whereas those who achieved the same accuracy level via cognitive integration of object color and object identity in the prior experiment did not, $F(1,13) = 0.02$. These cross-experiment analyses thus confirm that although different sorts of encoding manipulations can

have identical impacts on source accuracy, or result in the same level of source accuracy, they need not have the same neural bases. This point is taken up in the Discussion.

Occipital old/new effect

In addition to the broadly distributed early old/new effect and the late onset prefrontal old/new effect that were shared by the object- and frame-color conditions, we observed an additional old/new effect that differentiated the two stimulus conditions. Starting around 650 ms, the object-color condition generated larger old/new differences at very posterior scalp sites, as shown in Figures 4 and 8. ERP amplitudes were measured in a 700-1100 ms latency window to capture this effect. The occipital focus of effect led to interactions between object/frame, old/new, and scalp site along the anterior-to-posterior axis for the midline ($F(6,132) = 4.35, p < .005, \eta^2 = .64$) and dorsal electrode chains ($F(5,110) = 5.81, p < .005, \eta^2 = .50$). Followup tests on the three occipital sites (Oz,O1,O2) confirmed the interaction between object/frame color and old/new, $F(1,22) = 8.87, p < .01$, and provided no suggestion that the order of the object-color and frame-color sessions mattered (object/border x old/new x order subgroup, $F = 1.07$).

Insert Figure 8 about here

DISCUSSION

The present experiment examined memory for conjunctions of object identity (shape) and color under two conditions: when the stimuli were single objects with integral colors and when the stimuli consisted of two spatially separated forms, a monochrome object surrounded by a colored frame. As in previous behavioral studies (Ceraso et al., 1998; Hale & Piper, 1973; Spiker & Cantor, 1980; Walker & Cuthbert, 1998; Wilton, 1989), memory for shape-color relationships was superior when color appeared as an integral attribute of an object than when it appeared to be part of a separate object. Two aspects of brain electrical activity -- with scalp foci over parietal and occipital cortex -- differentiated the object-color and frame-color conditions, suggesting that different perceptual processes support relational memory within versus across objects. However, contrary to proposals that retrieval of "extra-item" attributes should require greater prefrontal engagement than retrieval of "intra-item" conjunctions (Moscovitch, 1992; Troyer et al., 1999), we observed equivalent old/new effects over prefrontal cortex in the object-color and frame-color conditions. Below, we first take up the condition differences over posterior cortex, then the role of PFC in source retrieval.

Parietal ERPs, visual working memory and perceptual binding

In both the study and test phases, monochrome objects surrounded by colored frames elicited more negative potentials than colored objects, with a focal topography over parietal cortex. The stimulus-related difference showed substantial variability across individual subjects, and the individual variability was strongly correlated with accuracy in remembering color-object conjunctions. More specifically, participants with larger parietal negativities were more accurate overall (Table 3), and less prone to a decline in accuracy for the frame-color stimuli as compared to the object-color stimuli, whereas those with smaller parietal negativities were more likely to suffer an accuracy drop when encountering the frame-color stimuli (Figure 3). These results suggest that we should consider the role of the parietal negativity in the perceptual binding process that acts to unify spatially-separated attributes during both encoding and retrieval. An important point for this consideration is our observation that the parietal effect did not predict memory accuracy across trials within a single subject, but only across subjects. In other words, the parietal negativity indexed a stable individual ability or strategy that was useful for the memory task, but not a process that was sufficient to yield accurate long-term memory. We suggest that the best characterization of this process is visual working memory.

Current theories of visual cognition argue that attention to visual displays is distributed across unified visual objects rather than the separable dimensions (shape, color, motion) of objects (Duncan, 1996; Kahneman, Treisman, & Gibbs, 1992). Extracting identity (shape) and color information was thus expected to be more demanding for the frame-color stimuli than the object-color stimuli, in both the encoding and retrieval phases. Because the displays were brief (500 ms), it is likely that extraction of the relevant stimulus dimensions required maintenance of the displays in visual working memory for at least a short time. Like verbal working memory, visual working memory (WM) is described as having a relatively small capacity limit that varies across individuals, with estimates between 1.5 and 5 objects (Luck & Vogel, 1997; Vogel & Machizawa, 2004). The capacity limits of visual WM have largely been defined in experimental tasks that require only passive maintenance of information, whereas the current tasks required other processing at the same time: access to stored object representations to retrieve real-life size and comparison to the computer monitor's size during the study phase, and access to episodic memory during the retrieval phase. Maintenance of even two objects in the frame-color condition may thus have been fairly taxing of visual WM, as compared to a single object in the object-color condition.

ERP studies of visual WM in maintenance tasks have shown that a negative potential with a parieto-occipital scalp focus grows in amplitude as more objects must be maintained, but only up to the limit of an individual's capacity (McCollough, Machizawa, & Vogel, 2007; Vogel, McCollough, & Machizawa, 2005; Vogel & Machizawa, 2004). Similarly, hemodynamic activity in bilateral posterior parietal cortex increases in amplitude as the number of objects increases, but only up to a limit of three when individual capacity is not evaluated (Todd & Marois, 2004). The parietal negativity that differentiated the frame- and object-color stimuli here strongly resembles the visual WM potential of Vogel and colleagues in onset latency, topography and polarity, although it was shorter in duration. In the experiments of Vogel and colleagues, visual displays had to be maintained in WM until the appearance of a probe display about a second later. In the current study, the maintenance period would instead be self-limiting, lasting only as long as needed to extract identity and color information from the display. We suggest that the relationship between parietal negativities for the frame-color stimuli and better source memory stems from the ability of individuals with better WM to more efficiently extract the relevant shape and color information from a brief display, simply because they were better able to maintain the display until these operations were complete. This proposal is, of course, a hypothesis based on the current results, and could be strengthened by future observations that the amplitude of the parietal negativity observed here is larger in individuals with larger visual WM capacity as assessed by span tests of the sort used by Vogel and colleagues. It also remains to be determined whether the parietal effect is specific to tasks with spatial separation between the bits of task-relevant information, or if a similar result would emerge with temporally-separated information (i.e., a monochrome object followed by a color patch at the same location).

Early versus late memory retrieval: spatially widespread versus occipital old/new effects

During the source memory tests, studied objects elicited more positive potentials than unstudied drawings, as typical of ERPs in both simple recognition and source tests. The initial aspect of the old/new effect – from 200 to 600 ms after stimulus onset -- was broadly distributed across the scalp, and identical for object-color and frame-color stimuli. Somewhat later in time (700 ms), the retrieval effect became larger in the object-color condition, primarily at occipital scalp sites (Fig. 8). The initial similarity and then dissimilarity of the two retrieval effects serve as converging evidence that source memory retrieval involves sequential stages in which different aspects of an event are recollected, as first suggested by behavioral studies using response-deadline procedures (Doshier, 1984; Johnson, Kounios, & Reder, 1994; McElree, Dolan, & Jacoby, 1999). More specifically, the results suggest that general information related to item (object) identity was accessed early, followed by the availability of associated contextual

information that was qualitatively different for drawings with integral colors and those with colored borders. The ERP timecourse results here parallel those of an experiment examining memory for objects and the encoding task in which they were initially encountered: brain responses to old and new objects diverged ~300 ms after stimulus onset, but those studied via carrying out an action versus cost-estimation diverged ~700 ms (Senkfor, Van Petten, & Kutas, in press). The scalp topography of the action versus cost difference was maximal at central scalp over premotor regions, and quite different from the occipital focus of the frame- versus object-color difference observed here, consistent with the different content of the retrieved information (see Ueno et al., 2007 for hemodynamic evidence for occipital activity during the retrieval of colors previously associated with monochrome test stimuli).

Prefrontal cortex and difficulty of source retrieval

More extensive engagement of prefrontal cortex is typically observed during source memory retrieval than during non-relational memory tests. We have suggested that this may largely be true when attributes are weakly bound during encoding, and that prefrontal activity is less necessary when retrieving strongly-encoded conjunctions (Kuo & Van Petten, 2006). That suggestion was based on the elimination of the late prefrontal difference between studied and unstudied items after an encoding task that encouraged integration of object and color attributes as compared to an object-oriented encoding task. In the current experiment, conjunctive strength was manipulated by changing the perceptual organization of the stimuli. Although source accuracy was substantially lower in the frame-color condition, indicating that this manipulation was successful in altering the strength of the binding between attributes, prefrontal memory effects were unchanged between the frame-color and object-color conditions. The contrasting results of the two experiments indicate that prefrontal engagement during retrieval is not a simple response to task difficulty, and that perceptually-driven integration of stimulus attributes is much less effective in alleviating the need for prefrontal involvement than deliberate cognitive effort to link two attributes. The current results dispel the notion that PFC activity in source memory retrieval is due simply to task difficulty, independent of the underlying cause of that difficulty.

Regardless of the relative difficulty of the frame and object sessions and the order in which they occurred, subjects showed a larger prefrontal old/new effect in their second session (Fig. 6). It is particularly telling that this occurred even as the frame-object subgroup moved to their easier second session with more obvious object-color relationships in the stimuli. It is more likely that the late prefrontal old/new effect manifests control processes specific to a memory task rather than a more general accommodation to memory strength. The increased prefrontal effect in the second session was accompanied by a specific change in performance. In the first session, source accuracy was substantially lower for stimuli that had changed colors between study and test as compared to those that remained in the same color, an instance of the *same/different effect* frequently observed in source recognition tests (Dodson & Shimamura, 2000; Kuo & Van Petten, 2006; Palmeri et al., 1993; Senkfor & Van Petten, 1998; Wilding et al., 1995). In the second session, subjects were immune to this effect (Table 2). Dodson (2007; Dodson & Shimamura, 2000) proposed that the presence of a familiar but incorrect source attribute at test creates interference by activating multiple items previously associated with that attribute. Here, the “training” provided by the first session apparently led to a strategy change that prevented such interference. Resolution of interference is a function that has been attributed to PFC in neuropsychological studies (Baldo, Delis, Kramer, & Shimamura, 2002; Shimamura, Jurica, Mangels, Gershberg, & Knight, 1995) and to diverse regions of PFC in hemodynamic imaging experiments (Badre & Wagner, 2005; Henson, Shallice, Josephs, & Dolan, 2002; Sakai & Passingham, 2004). An association between greater prefrontal activity and higher accuracy in the face of interference has been demonstrated in the delay period of a working memory task (Sakai, Rowe, & Passingham, 2002), but not previously in long-term

memory tasks. Here, the association between better performance on old-different trials and enhanced prefrontal activity in the second session is likely to reflect a sort of strategic sharpening that made memory judgments more resistant to interference.

Multiple bottlenecks for source memory

A variety of results suggest that accurate performance in source memory tasks is subject to multiple bottlenecks, only some of which are likely to be directly related to prefrontal activity. The current results show that one such bottleneck occurs when the task requires integration of attributes across visually-separated objects. In the current paradigm, this process was associated with a parietal ERP whose amplitude was strongly related to individual accuracy, whereas later prefrontal potentials were not. We suggest above that the early parietal effect may be tied to visual working memory, a function long associated with a prefrontal-parietal circuit in primates (Chafee & Goldman-Rakic, 1998; Colby & Goldberg, 1999), but with recent suggestions from human studies that the capacity limit may be primarily parietal (McCoullough et al., 2007; Todd & Marois, 2004). A second bottleneck is, of course, in episodic memory *per se*, such that patients with damage to the medial temporal lobe who perform poorly on tests of memory for single items always perform at least as poorly on source and associative memory tests (Gold, Hopkins, & Squire, 2006; Gold et al., 2006; Kan, Giovanello, Schnyer, Makris, & Verfaellie, 2007; Stark, Bayley, & Squire, 2002). In contrast to these functions, the long latency of the prefrontal old/new effect during source retrieval – well after both the standard old/new effect and the parietal effect observed here – strongly suggests an executive role that will only serve as the performance bottleneck when other functions are adequate for task performance. This will be the case in patients with damage limited to prefrontal cortex (Janowsky et al., 1989), and in a subset of older adults whose frontal function has suffered greater decline than their basic episodic memory abilities (Glisky, Rubin, & Davidson, 2001).

The framework above suggests that there should be situations, even for healthy young adults, in which prefrontally-based executive processes are the final performance bottleneck. This outcome was observed in an associative memory task that required a “yes” response to studied pairs of words and “no” responses to pairs with new words as well as to recombined pairs, including recombined pairs with one word that had been studied many times. Participants showed dramatic variability in their ability to reject the recombined pairs with very familiar elements, with accuracy levels ranging from 14% to 80% (Van Petten et al., 2002). Accuracy in rejecting the recombined pairs was uncorrelated with accuracy for old pairs or completely new pairs. Early posterior ERPs (the standard old/new effect) showed a three-way differentiation between old, recombined and new pairs, and these posterior ERP differences were also unrelated to the ability to reject recombined pairs. The behavioral data and posterior ERPs both suggest that the difficulty in rejecting recombined pairs arose from later decisional factors rather than memory alone. Instead, individual ability to reject the recombined pairs was strongly predictable from the amplitude of the late prefrontal old/new effect ($R^2 = .58$). In the current paradigm, the primary performance bottleneck appears to occur at an earlier level, such that the more difficult frame-color stimuli did not elicit larger prefrontal ERPs than the easier object-color stimuli. However, there was a hint that prefrontal activity remained useful in overcoming the tendency to label recombinations of studied features as having been studied, in that errors of labeling “old different” stimuli as “old same” decreased across sessions, and were accompanied by an increase in the late prefrontal old/new effect.

NOTES

1. Some of the papers cited here (Meiser & Bröder, 2002; Starns & Hicks, 2005; Vogt & Bröder, 2007) are concerned with the degree of independence of multiple source attributes in memory, and whether any stochastic dependence arises from self-cuing effects during retrieval (remembering one attribute triggers retrieval of others) or from the binding of attributes during encoding. The different studies reached different conclusions as to whether attributes show complete independence versus some degree of dependence, and regarding the mechanism of that dependence. However, all three reject the “all-or-none” account that memory for one source attribute necessarily entails memory for all source attributes.

2. In our source memory studies, the maximum amplitudes of the late prefrontal difference between studied and unstudied items occur at the most anterior electrodes in a standard recording montage (Fpz, Fp1, Fp2, located ~3.6 cm above the bridge of the nose) as well at other scalp sites arrayed across the forehead just above the eyebrows (Kuo & Van Petten, 2006; Senkfor & Van Petten, 1998; Van Petten et al., 2000, 2002; see Figure 5 for typical spatial distribution). The effect is also relatively large in amplitude for a scalp-recorded ERP difference, about 4 μ V, and falls off rapidly in amplitude at locations posterior to the prefrontal sites, reaching less than half-maximal amplitude by scalp site Cz, located above the precentral sulcus and about 7.2 cm away from Fpz (Homan, Herman, & Purdy, 1987; Jasper, 1958). The memory effect appears to be a modulation of a potential that is even larger, about ~10 μ V at prefrontal sites and very much smaller at non-prefrontal sites (see current Figure 4). These amplitude and distributional properties, although insufficient to suggest what division of PFC gives rise to the effect, securely localize the effect to the frontal lobe. *A priori*, the amplitudes and spatial distributions of scalp potentials with respect to their cortical generators are determined by five factors: 1) voltages within the cortical tissue, 2) distance between each electrode and the active tissue (amplitude falls off with the square of the distance), 3) geometrical orientation of the active region of the cortical sheet with respect to the electrodes, and 4, 5) both amplitude attenuation and spatial “blurring” created by the poor electrical conductivity of the skull. When none of these factors are known, the relationship between intra- and extra-cranial location is mathematically unconstrained. However, knowledge about the physical properties of the head (size, electrical conductivity) places constraints on the degree of amplitude attenuation and spatial blurring to be expected (Nunez, 1995). When combined with physiological constraints (maximum voltages recorded by intracranial electrodes), realistic boundaries for the cortical origin of large-amplitude scalp potentials can be estimated. These boundaries are broad when neither the geometric orientation or depth (cortical layer) of a source are known, but do not exceed the size of entire brain lobes even for deep cortical layers (Birbaumer, Elbert, Canavan, & Rockstroh, 1990). Although broad, these constraints indicate that the frontopolar distribution of the memory effect discussed here is theoretically consistent only with a source in the frontal lobe. Empirical observations are generally consistent with Birbaumer and colleagues’ estimates. A well-studied ERP component – the Readiness Potential preceding a voluntary movement – is known to be generated in the motor regions of the frontal lobe (Shibasaki & Hallet, 2006). On the scalp, it is largest over the precentral sulcus, and shows an amplitude falloff from maximum to half-maximum amplitude in a span of 5-7 cm along the anterior-posterior axis of the scalp (Vaughan, Costa, & Ritter, 1968). The maximum amplitude and spatial frequency of the late prefrontal memory effect are similar to those of the Readiness Potential, although its topographic maximum is considerably anterior.

3. In a previous study, no change in accuracy patterns were observed across two source memory sessions with the same sort of auditory stimuli in the two sessions (Senkfor & Van Petten, 1998). However, a replication of the current paradigm with behavioral measures alone in 32 participants similarly yielded increased source accuracy across sessions, $F(1,30) = 7.54, p$

< .01, due to higher accuracy for old-different trials but not old-same trials (first/second session x same/different, $F(1,30) = 5.18$, $p < .05$; Kuo & Van Petten, unpublished). It is possible that stimulus variation across sessions (as in the current experiment and the replication) fosters strategic improvement in a way that repetition of the exact same task does not, but this is topic for further research.

4. Prior to these analyses, we first determined that the two groups of 24 participants produced equivalent behavioral and prefrontal ERP results in the experimental session that was the same in the two experiments: object-color stimuli after the non-integrative encoding task of size judgment. Source accuracy was analyzed via an ANOVA with old-same versus old-different as a within-subject factor and experiment as a between-subject factor; accuracy was higher for “sames”, $F(1,46) = 19.5$, $p < .001$, but there was no main effect of experiment, $F = 1.65$, and no interaction between same/different and experiment, $F < 1$. The late prefrontal memory effect was evaluated via amplitudes in the 800-1200 ms epoch for correct responses. Hit-hits and correct rejections were reliably different, $F(1,46) = 40.9$, $p < .0001$, but there was no interaction between this memory effect and experiment, $F = 1.09$, nor a main effect of experiment, $F < 1$. “Old same” and “old different” trials did not elicit different prefrontal ERPs in either experiment, $F_s < 1$ for main effect and for interaction with experiment (note that this is true after the non-integrative encoding task of size judgment in both experiments, but in Kuo & Van Petten, 2006, “old same” trials elicited smaller prefrontal potentials than “old different” after integrative encoding).

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Table 1: Old/new recognition and source memory accuracy, and reaction time.

	Old/new (%)	Source accuracy (%)	RT (ms)
	<u>Mean (se)</u>	<u>Mean (se)</u>	<u>Mean (se)</u>
<u>Object-color</u>			
Old-same	97.8 (0.5)	84.8 (2.1)	1440 (53)
Old-different	97.0 (0.5)	75.4 (2.5)	1499 (59)
New	95.8 (0.8)		1127 (48)
<u>Frame-color</u>			
Old-same	95.9 (0.6)	75.6 (2.5)	1590 (58)
Old-different	96.6 (0.8)	69.2 (2.6)	1628 (61)
New	95.7 (0.8)		1126 (47)

Table 2: Behavioral results from the subgroups with different condition orders

	Object-Frame group		Frame-Object group	
	Source acc. <u>Mean (se)</u>	RT <u>Mean (se)</u>	Source acc. <u>Mean (se)</u>	RT <u>Mean (se)</u>
<u>Object-color session</u>				
Old-same	83.5 (3.0)	1516 (84)	86.1 (3.0)	1363 (61)
Old-different	68.4 (3.4)	1635 (83)	82.4 (2.2)	1364 (66)
New		1218 (71)		1035 (55)
<u>Frame-color session</u>				
Old-same	73.7 (3.8)	1634 (83)	77.5 (3.4)	1546 (81)
Old-different	71.1 (3.7)	1636 (91)	67.2 (3.7)	1621 (84)
New		1177 (75)		1075 (58)

Table 3: Correlations between parietal ERP amplitudes and source accuracy

	Object-color session		Frame-color session	
	<u>r =</u>	<u>p <</u>	<u>r =</u>	<u>p <</u>
Study trials	-.43	.05	-.50	.01
Hit-hits	-.53	.01	-.54	.01
Correct rejections	-.61	.002	-.58	.005

Note: Pearson correlations between ERP mean amplitudes in the 200-500 ms latency range and source accuracy in the same session.

FIGURE CAPTIONS

1. Illustration of objects with integral colors (top panel) and frame colors (bottom panel). The assignment of objects to one or the other stimulus condition was rotated across participants, so that the two sets of drawings shown here would have been assigned to different participants.
2. **(A)** Grand-average ERPs from 24 subjects associated with study trials, hit-hits, and correct rejections at the midline parietal scalp site. **(B)** Spline-interpolated topographic map showing the spatial distribution of the difference between ERPs elicited by stimuli with colored frames versus colored objects, in the 200-500 ms latency window.
3. Relationship between the ERP effect of object vs. frame color (shown in Figure 2) and the source accuracy difference between conditions. Each dot represents one subject. Three parietal scalp sites (Pz, P3, P4) were averaged to obtain the ERP amplitude difference, calculated by subtracting the amplitudes in the object-color condition from those in the frame-color condition.
4. Grand-average ERPs from 24 subjects during the source memory tests. Left and middle columns show ERPs elicited by studied stimuli accompanied by correct source judgments (hit-hits) versus those elicited by unstudied stimuli with correct memory judgments (correct rejections). The right column shows the differences between hit-hit and correct rejection ERPs, contrasting the memory effects for stimuli with integral object colors to those for stimuli with colored frames.
5. Topographic maps showing the spatial distribution of the memory effects across time, from no effect in the first 200 ms after stimulus presentation, to a maximum at centroparietal sites in the 200-600 ms latency window, to a prefrontal maximum in the 800-1200 ms latency window. The 600-800 ms latency window represents a transition between the centroparietal and prefrontal effects, and was not statistically evaluated.
6. Grand-average ERPs from 24 subjects during the source memory tests for the objects with integral color versus those with colored frames (top row). Shown are the five frontopolar scalp sites, arrayed from left to right as they are on the forehead. The bottom row contrasts the first session of the experiment (object-color for half of the subjects, and frame-color for the other half) to the second session.
7. Grand average ERPs from 24 subjects, for trials with correct "old same" and "old different" decisions during the source memory tests. Shown are the prefrontal (Fpz) and parietal (Pz) midline scalp sites. The left two columns display responses according to stimulus type; right two columns instead display responses according to the order of sessions, independent of stimulus type (object-color or frame-color) in those sessions.
8. **(A)** Memory effects (amplitude difference between studied and unstudied stimuli with correct judgments) for objects with integral color versus those with colored frames, at the three occipital scalp sites (O1, Oz, O2). **(B)** Scalp distribution of the difference in memory effects between colored objects and colored frames: (Hit-hit minus correct rejection in the object-color condition) minus (Hit-hit minus correct rejection in the frame-color)

condition).

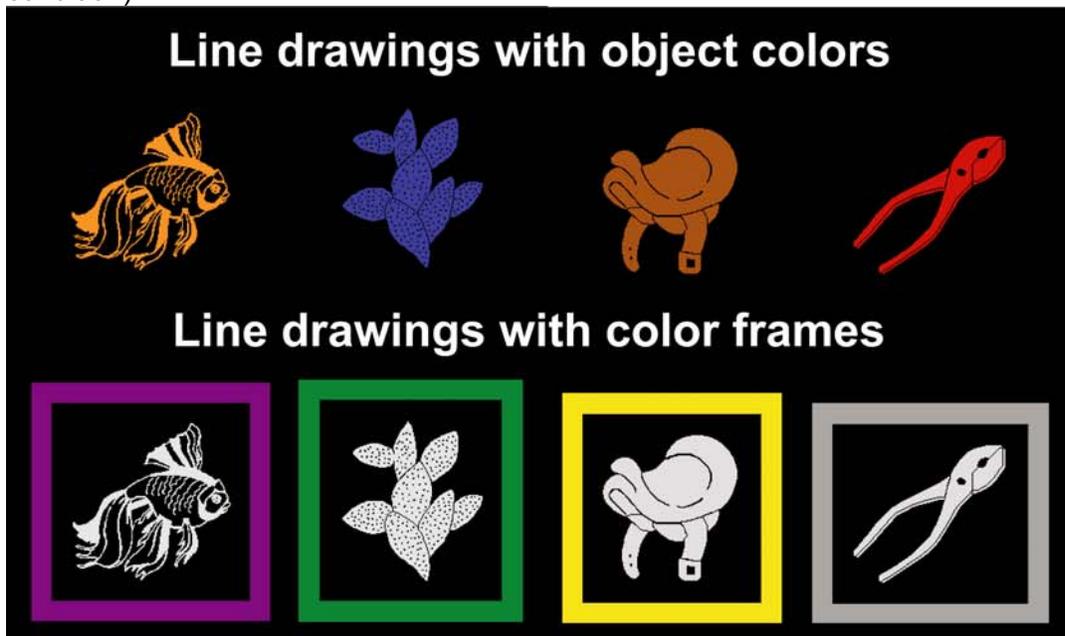
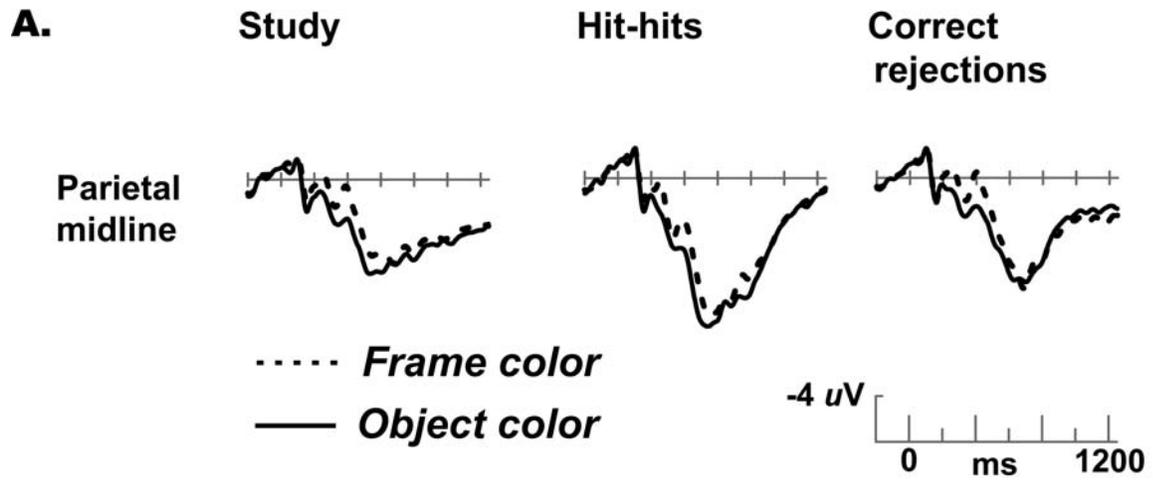


Figure 1



B. *Frame color minus object color*
200-500 ms

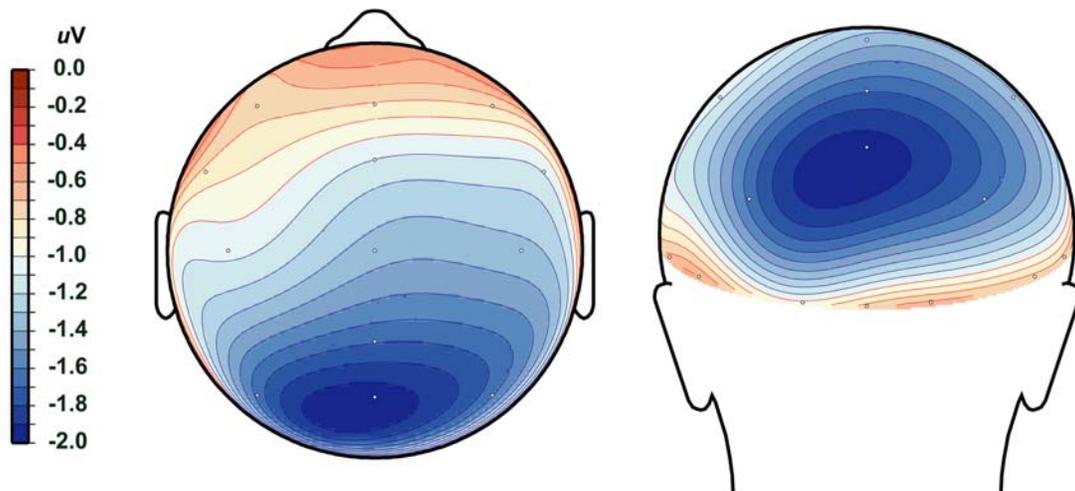


Figure 2

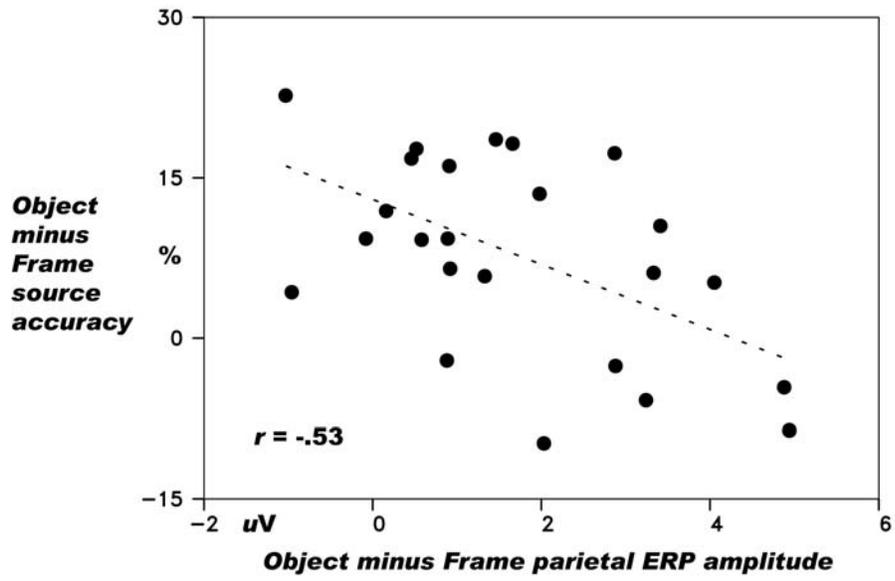


Figure 3

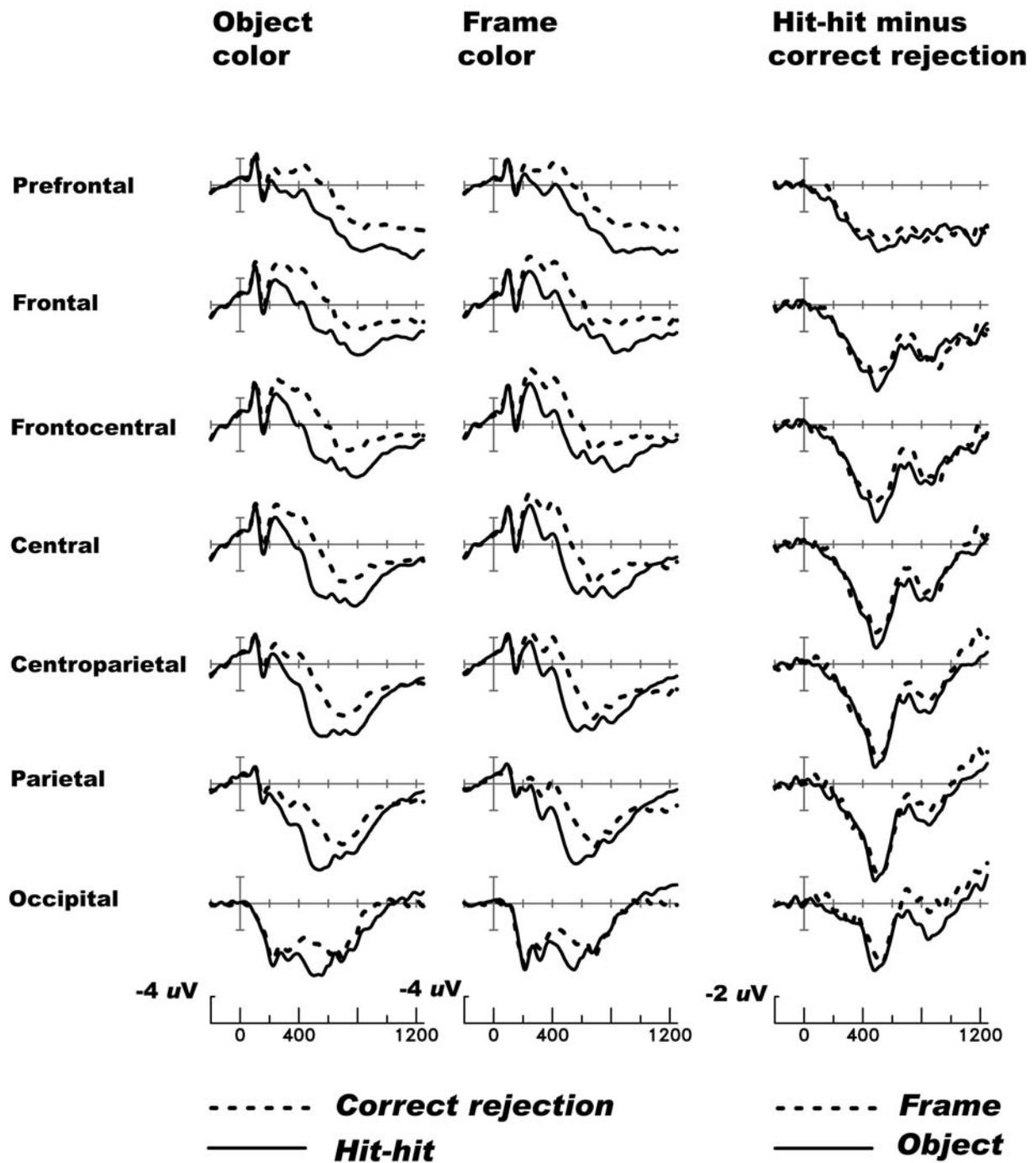


Figure 4

HIT-HIT MINUS CORRECT REJECTION
(collapsed across Object-color and Frame-color)

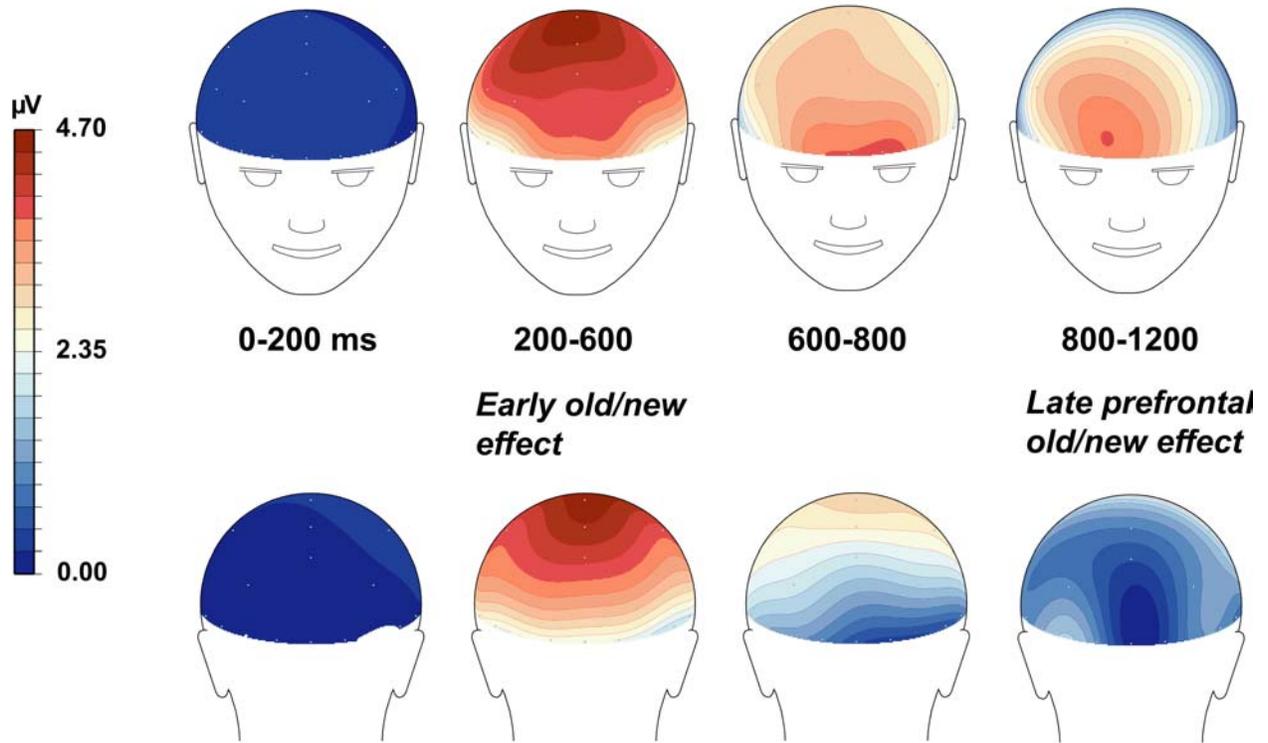


Figure 5

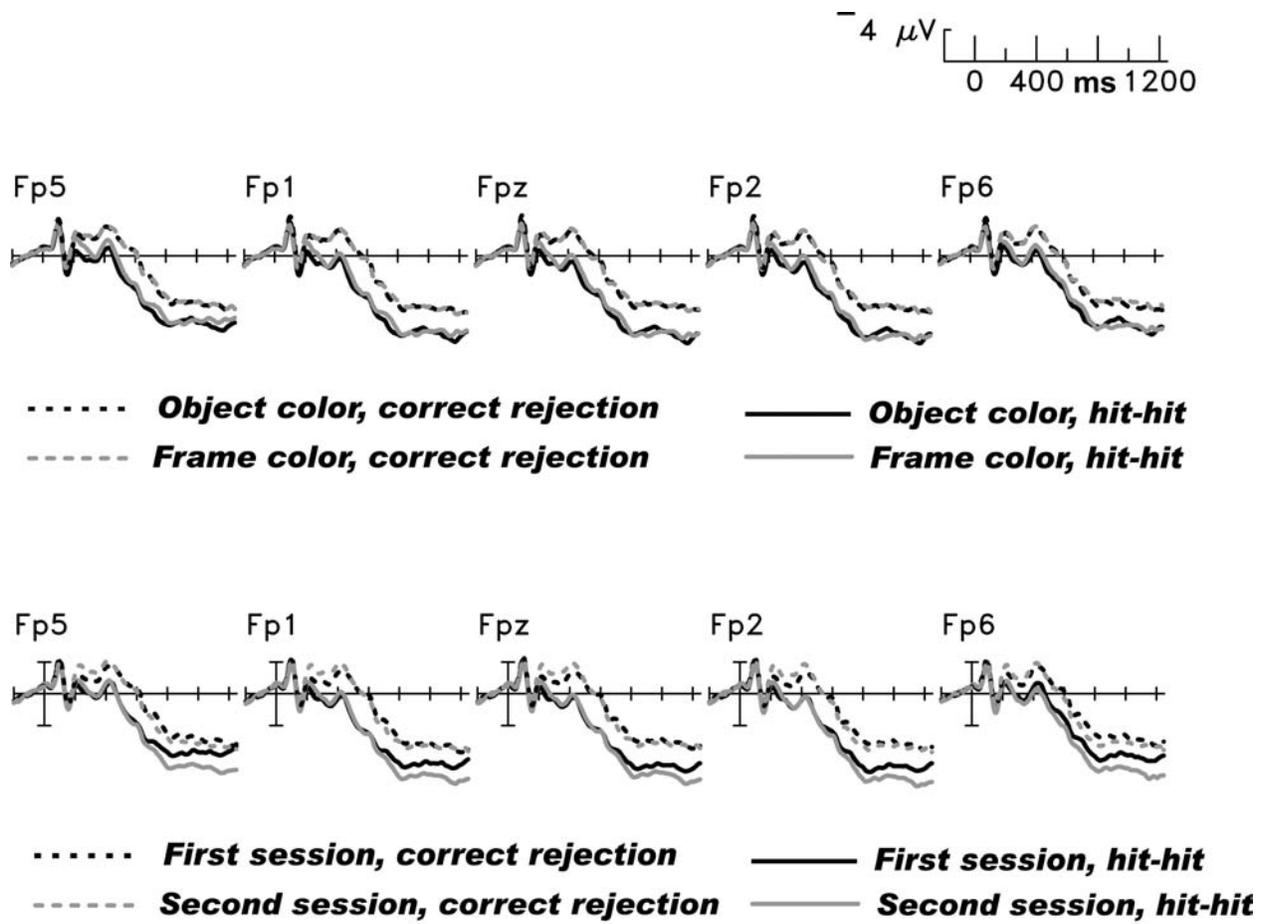


Figure 6

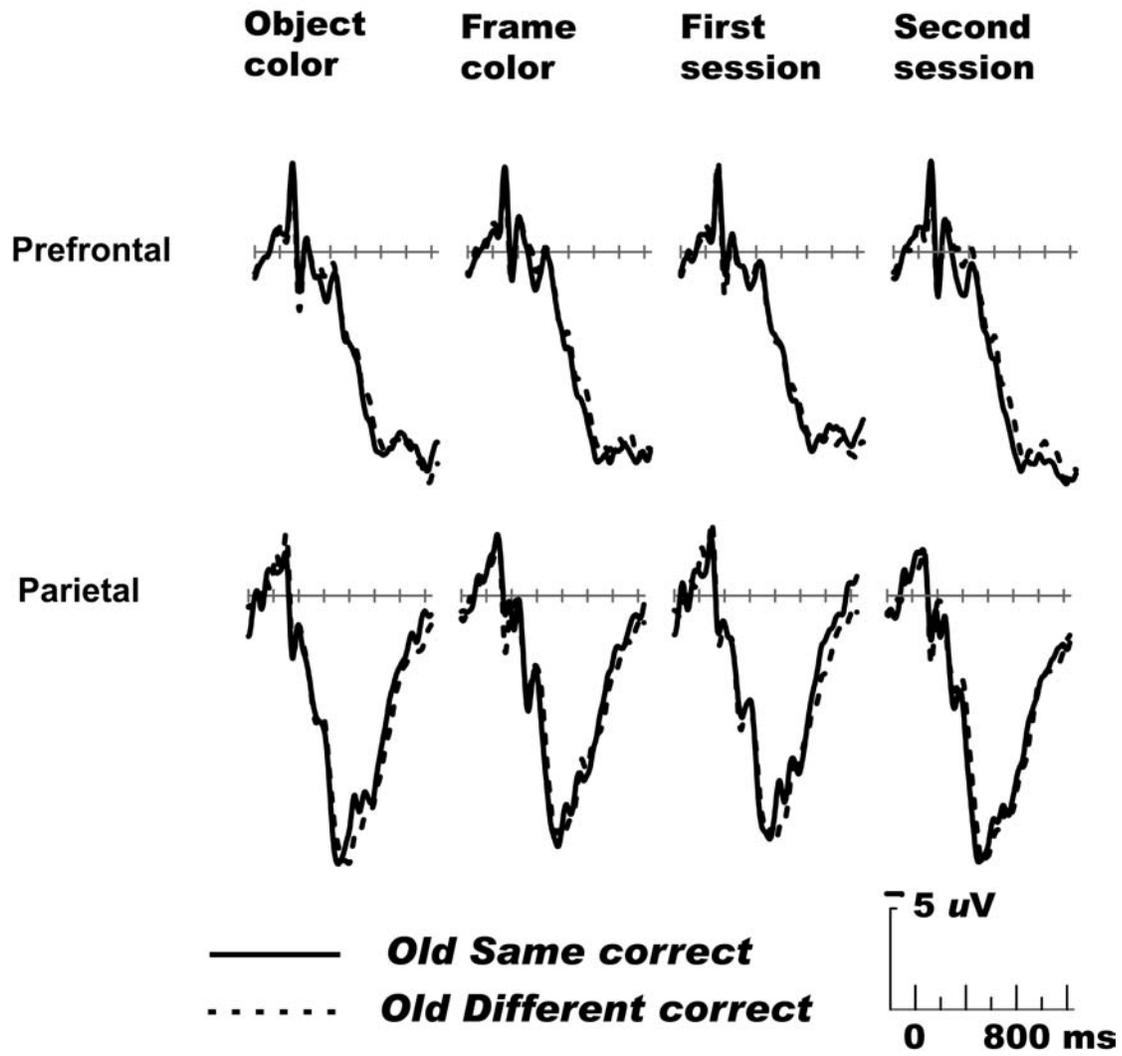
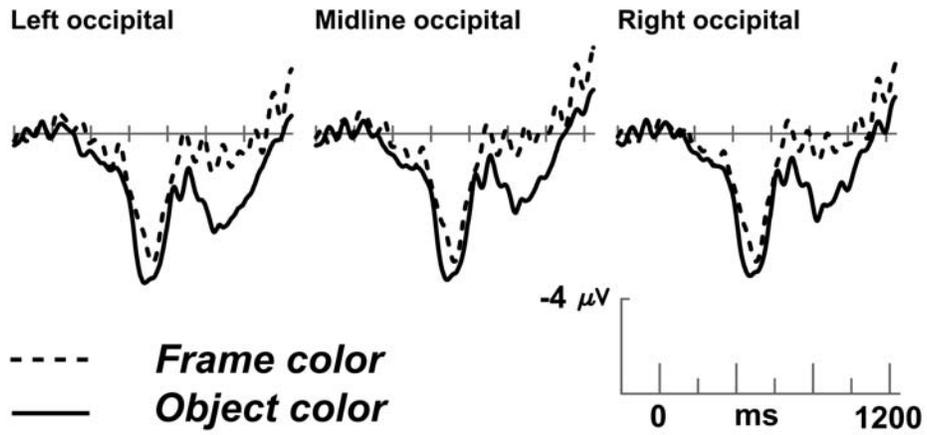


Figure 7

A. Hit-hit minus correct rejection



B. Object-color retrieval effect minus Frame-color retrieval effect

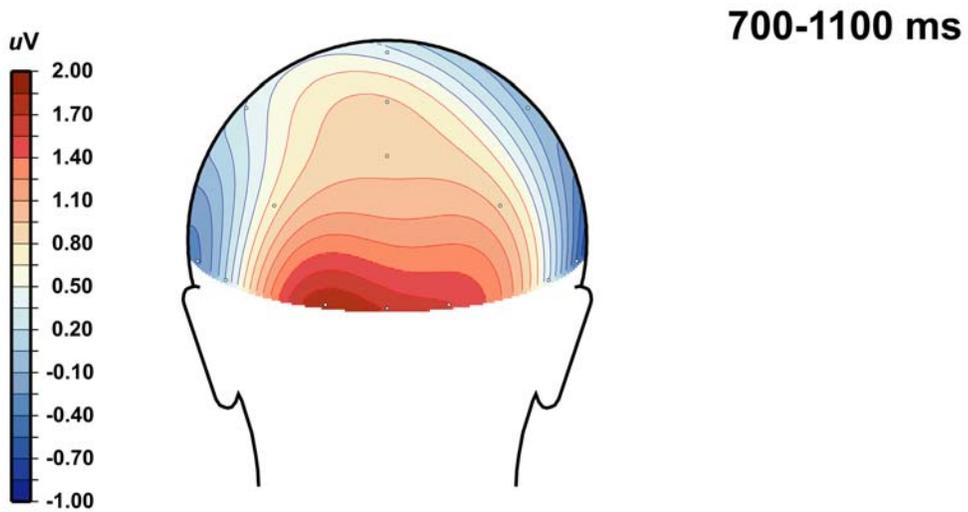


Figure 8