Material-specific Neural Correlates of Recollection: Objects, Words, and Faces

Giulia Galli and Leun J. Otten

Abstract

■ It is unclear how neural correlates of episodic memory retrieval differ depending on the type of material that is retrieved. Here, we used a source memory task to compare electrical brain activity for the recollection of three types of stimulus material. At study, healthy adults judged how well visually presented objects, words, and faces fitted with paired auditorily presented names of locations. At test, only visual stimuli were presented. The task was to decide whether an item had been presented earlier and, if so, what location had been paired with the item. Stimulus types were intermixed across trials in Experiment 1 and presented in separate study–test lists in Experiment 2. A graded pattern of memory performance was observed across objects, words, and faces in both experiments. Between 300 and 500 msec, event-related potentials for recollected objects and faces showed a more frontal scalp distribution compared to words in both experiments. Later in the recording epoch, all three stimulus materials elicited recollection effects over left posterior scalp sites. However, these effects extended more anteriorly for objects and faces when stimulus categories were blocked. These findings demonstrate that the neural correlates of recollection are material specific, the crucial difference being between pictorial and verbal material. Faces do not appear to have a special status. The sensitivity of recollection effects to the kind of experimental design suggests that, in addition to type of stimulus material, higher-level control processes affect the cognitive and neural mechanisms underlying episodic retrieval. ■

INTRODUCTION

Decades of research in the field of cognitive neuroscience have shown that the processing of different stimulus materials involves specific brain regions and cognitive operations. It is well known, for example, that the perception of different types of visual stimuli activates separate areas in occipito-temporal cortex and elicits specific electrophysiological responses (Allison, Puce, Spencer, & McCarthy, 1999; Kanwisher, McDermott, & Chun, 1997; Malach et al., 1995). In contrast to an extensive body of research on the early processing of stimuli belonging to different categories, however, relatively little is known about the material-specific nature of neural correlates of episodic memory.

Episodic memory concerns the long-term retention of specific events that happen in daily life. Several models of episodic memory incorporate the notion that the processes involved in the retrieval of episodic information ("recollection") differ depending on the content of the retrieved episode. For example, the Source Memory Framework (Mitchell & Johnson, 2009; Johnson, Hashtroudi, & Lindsay, 1993) suggests that the quality of an episodic memory is dependent on the degree of differentiation between features that define an episode, including perceptual, spatio-temporal, semantic, and affective attributes. Different stimulus categories may involve distinct features with variable levels of separation. The recollection of objects, for instance, may involve more differentiated perceptual information compared to words, and this may lead to material-sensitive neural activity.

The idea that retrieval is content specific is also embodied in neural models of memory. It has been proposed that activity engaged when a new event is encountered differs qualitatively depending on the characteristics of the event, and that recollection depends on a reinstatement of some of that activity (e.g., Norman & O'Reilly, 2003; Rolls, 2000). Consistent with this general idea, recent neuroimaging studies have demonstrated that activity in separate brain regions is linked with the retrieval of different types of stimuli, or identical stimuli that were processed differently during encoding (e.g., Woodruff, Johnson, Uncapher, & Rugg, 2005; Vaidya, Zhao, Desmond, & Gabrieli, 2002; Simons, Graham, Owen, Patterson, & Hodges, 2001; Kim et al., 1999). For example, studies using fMRI or PET have shown that accurate recognition of words primarily activates frontal and temporal areas of the left hemisphere, whereas recognition of objects and faces activates posterior parts of the right hemisphere (Guerin & Miller, 2009; Simons et al., 2001; Kim et al., 1999; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999). Material-specific correlates of recollection have also been observed in patients (Moscovitch & McAndrews, 2002; Jones-Gotman et al., 1997).

University College London

The above studies suggest that neural correlates of recollection are sensitive to the type of material that is retrieved. However, an inherent limitation of hemodynamic neuroimaging techniques is that it is difficult to establish the temporal dynamics of neural activity. Thus, it cannot be established on the basis of fMRI data alone whether brain regions demonstrating recollection-related activity reflect processes that lead up to the recovery of information from memory, or processes contingent on it (for a similar argument, see Johnson, Minton, & Rugg, 2008; Yick & Wilding, 2008). Memory retrieval can be fractionated into a number of cognitive operations, including the evaluation of the cue available to probe memory, the initial orienting to relevant kinds of encoded information, searching for and making contact with stored information, recovery of that information, and postretrieval processes (see Wilding & Herron, 2006; Rugg & Wilding, 2000 for review). The slow time course of hemodynamic activity means that any, or all, of these operations can underlie retrieval-related fMRI activity. Understanding which processes are sensitive to the type of material that is retrieved is fundamental to shed light on the functional organization of episodic memory and, ultimately, the nature of memory representations.

Because of the high temporal resolution of electrical brain activity, studies using ERPs have made important contributions to our understanding of the time course of episodic memory retrieval (for reviews, see Wilding & Herron, 2006; Friedman & Johnson, 2000; Rugg & Wilding, 2000). A typical finding is that items correctly identified as old elicit more positive-going ERPs than items correctly endorsed as new ("old/new effect"). This effect can be decomposed into distinct neural and cognitive processes. The "parietal old/new effect" is elicited over posterior scalp regions, with a focus over the left, between around 400 and 800 msec. It varies in a manner consistent with recollection. For example, the effect is larger for items given remember than know judgments (Düzel, Yonelinas, Mangun, Heinze, & Tulving, 1997), larger for items encoded in deep processing tasks (Rugg et al., 1998), and larger for items whose retrieval is accompanied by contextual information (Donaldson & Rugg, 1999; Wilding & Rugg, 1996; see Friedman & Johnson, 2000; Mecklinger, 2000 for review). The parietal effect can be dissociated from an earlier-onsetting (200–500 msec), frontally focused effect (the "mid-frontal old/new effect" or "FN400"), which has been linked to familiarity (Woodruff, Hayama, & Rugg, 2006; Curran, 2000) or conceptual priming (Yovel & Paller, 2004). The parietal effect can, in addition, be dissociated from earlier retrieval orientation and later postretrieval ERP effects (Wilding & Herron, 2006; Rugg & Wilding, 2000).

Most ERP retrieval studies employed words as stimuli. Interestingly, studies utilizing other stimulus materials have found different onsets or scalp distributions of recollection-related old/new effects. Compared to words, old/new effects for recollected objects tend to be more widely distributed, encompassing anterior areas in addition to the typical posterior ones. For example, Duarte, Ranganath, Winward, Hayward, and Knight (2004) used a remember/know paradigm and found a frontally distributed old/new effect for objects given remember judgments. Similarly, studies using source memory paradigms have found widespread (Kuo & Van Petten, 2006; Johansson, Stenberg, Lindgren, & Rosén, 2002) or early, frontally focused (Ranganath & Paller, 2000) distributions of recollection responses with objects. A notable exception is Curran and Cleary (2003), who found a posteriorly distributed recollection effect when using line drawings instead of photographs.

ERP studies on the recollection of faces also provide findings that do not match previous work with words. In particular, three recent studies used a similar approach to investigate the ERP correlates of recognition memory for unfamiliar faces (Curran & Hancock, 2007; MacKenzie & Donaldson, 2007; Yovel & Paller, 2004). Faces of unknown individuals were paired with occupations (Curran & Hancock, 2007; Yovel & Paller, 2004) or names (MacKenzie & Donaldson, 2007) at study. At test, old and new faces were intermixed. Faces were considered to be recollected if participants not only recognized the face but were also able to retrieve the occupation or name that was paired with the face at study (Johnson, 2005; Tulving, 1983; Mandler, 1980). Recollected faces engaged more anterior locations in addition to parietal sites in the studies of MacKenzie and Donaldson (2007) and Yovel and Paller (2004). Curran and Hancock (2007) reported a traditional parietal old/new effect for recollected faces. However, their data showed an additional frontal effect (see Figure 4B, p. 469), which was, unfortunately, not discussed as the analyses were restricted to posterior electrodes.

The results from studies with a single type of stimulus material thus point to the possibility that the recollection of objects and faces is associated with more anteriorly distributed, and earlier, old/new effects than the recollection of words. This view is further substantiated by the few ERP studies that directly compared stimulus materials. Ally and Budson (2007) and Schloerscheidt and Rugg (1997) found parietal old/new effects for pictures and words, but the former category elicited an additional frontal effect that was absent for words. Yick and Wilding (2008) found the same results when comparing words and faces: Parietal old/new effects occurred for both materials with an added frontal effect for faces. Unfortunately, all these studies required a simple old/new judgment, preventing a clear separation of processes related to familiarity and recollection. This limitation was recently overcome by MacKenzie and Donaldson (2009), who used the remember/know procedure to demonstrate that remembered faces and names elicit anterior and posterior old/new effects, respectively. Together, these findings lend support to the view of a direct role of material-sensitive neural activity in episodic recollection.

To the best of our knowledge, no ERP study has directly compared the retrieval of more than two types of stimulus material. This comparison is essential to determine the sort(s) of stimulus feature that gives rise to distinct neural correlates of recollection. One scenario is that recollecting any kind of pictorial information (objects or faces) involves the recruitment of neural activity that is qualitatively distinct from activity recruited by words. Alternatively, each type of stimulus may have distinct features that are incorporated into its representation in memory and used during retrieval. It would, for example, be of interest to establish whether faces have a privileged status relative to other stimulus categories (MacKenzie & Donaldson, 2007). Considering the limited number of existing within-subject comparisons, a direct comparison between multiple stimulus categories is also important to ensure that the different old/new ERP effects observed with words, objects, and faces can be attributed to the type of stimulus material rather than other variables that differed across experiments.

Accordingly, the first aim of the present study was to contrast recollection-related ERP effects across three types of stimulus material: objects, words, and faces. We employed a modified version of the source memory paradigm used by Curran and Hancock (2007), MacKenzie and Donaldson (2007), and Yovel and Paller (2004). In the study phase, visually presented objects, words, and faces were paired with auditorily presented names of locations. In the test phase, all visual items were presented again, along with new objects, words, and faces. Subjects chose between three response options. A *location* response was given if a subject recognized that an item had been presented earlier and could retrieve the location that was paired with the item at study. A *no specifics* response was given if a subject endorsed the item as old, but could not retrieve the location information. Finally, a *new* response was given if a subject judged the item as being new to the experiment. Items given a correct *location* response were considered to be recollected, as the retrieval of such items was accompanied by the recovery of specific, contextual details concerning the study phase (Johnson, 2005; Tulving, 1983; Mandler, 1980).

A variable that may exert a critical role in recognition memory for different stimulus categories is the study–test list composition. Stimuli belonging to different categories can be intermixed across trials within the same study–test list (intermixed design) or presented in separate study–test lists (blocked design). This feature is of potential significance because different designs involve different cognitive mechanisms and have been found to yield different results. Blocked designs increase list homogeneity, whereas intermixed designs promote heterogeneity, and this may, in turn, affect recognition memory differentially. For example, Kahana and Sekuler (2002) found a higher proportion of *old* responses when study–test lists are highly heterogeneous. Recognition judgments may also vary as a function of the degree of heterogeneity within a stimulus set (Curran & Hancock, 2007), raising the possibility that study–test list composition affects stimulus categories differentially. Faces, which share highly similar physical features and have a lower degree of interitem discriminability per se, may be more affected by study–test list composition than other stimulus categories. Study–test list composition may also affect the strategies or cognitive operations set in train during encoding and retrieval. In intermixed designs, materials vary unpredictably across trials. The set of processes needed for the decision about a specific stimulus category cannot be maintained across trials in such circumstances, and this requires subjects to reset these processes for the impending stimulus on a trial-by-trial basis. In blocked designs, subjects may adopt the same cognitive operations or retrieval orientation throughout successive trials. The degree to which material-specific retrieval processes are engaged may therefore differ between intermixed and blocked designs (cf. Wilding & Nobre, 2001).

In the light of this, the second aim of the present study was to determine how study–list composition affects recognition memory for different stimulus materials. This question is important as it determines whether stimulus material interacts with higher-level cognitive processes in exerting an influence on neural correlates of recollection. The recognition of different stimulus categories may inherently be associated with distinct types of cognitive and neural processes, or this may interact with the particular circumstances under which stimuli are encoded and retrieved. Any differences observed between intermixed and blocked designs would also dictate caution when comparing results across studies that vary in study–test list composition. Here, we varied study–test list composition of words, objects, and faces across two experiments. The first one employed an intermixed design, the second a blocked design. Stimuli, task, and procedure were held constant to allow a direct comparison across experiments.

METHODS

Experiment 1

Participants

Twenty-four healthy adults (mean age = 21.7 years, range = 19–26, 9 men) were paid to participate in the experiment. Each volunteer gave written informed consent and reported to be right-handed, native English speaking, and to be without neurological and psychiatric history. Data from one additional participant were excluded from the analyses because of an insufficient number (<15) of accurate source judgments for faces. The experiment was approved by the joint University College London and University College London Hospital ethics committee.

Stimulus Materials

Stimuli consisted of 189 objects, 189 words, 189 faces, and 354 locations. Five stimuli from each category were used for a practice session, and the remaining for the experiment proper. Objects were black and white pictures of animals, tools, accessories, furniture, food, and clothes, selected from a standardized set (Viggiano, Vannucci, & Righi, 2004). Each object was presented in its canonical orientation (Viggiano & Vannucci, 2002). Faces were black and white, frontal view pictures (94 women, 95 men) from the PAL face database (Minear & Park, 2004). Faces depicted adults of all ages and were shown with hair, neck, and part of the shoulders. Half of the women had long hairstyles; all men had short hair, and half had moustaches and/or beards. Faces had no further distinctive features such as jewellery or glasses, and had neutral emotional expressions. Words were concrete nouns with a length of 5–10 letters and a written frequency of 0–500 occurrences per million (Kučera & Francis, 1967). Words were presented in a black uppercase Helvetica script. Objects and faces subtended visual angles of about 2.6° horizontally and 2.6° vertically. Words subtended horizontal visual angles of 1°–2.2° and vertical visual angles of 0.6°. Locations names were common and possessive nouns (locations are listed in Appendix) and no proper names were included. Each location was used only once for each participant. Auditory renditions of the locations were generated through AT&T Natural Voices (AT&T Labs, Inc, Florham Park, NJ). Half of the locations were spoken by a female voice, and half by a male voice (mean duration = 670 msec, range = 282–998 msec).

Design

The experiment incorporated 23 study–test blocks. In each block, participants first studied unique associations between visual and auditory stimuli, and then immediately performed a source memory test for the visual items. Study lists consisted of 15 items and contained equal proportions of randomly intermixed objects, words, and faces, each paired with an auditory name of a location. At test, all 15 visual items were presented again, along with nine new items (three items for each material). Stimuli within a category were randomly assigned as old and new items and old stimuli were randomly paired with locations. New stimulus lists were generated for each participant.

Procedure

After electrode application (see EEG Acquisition and Analysis section), participants received instructions about the study and test tasks and completed a short practice session. Figure 1 depicts a sample study and test trial. All stimuli were presented on a computer monitor on a gray background. A fixation point (a black plus sign) was continuously present in the center of the screen except when stimuli were presented. Study trials began with a 500-msec neutral warning stimulus (an exclamation mark), followed by the simultaneous presentation of a visual item (an object, word, or face) and auditory name of a location. The visual item was on the screen for 1000 msec and its onset coincided with the onset of the location name. The location was delivered at comfortable hearing level through speakers. For each pair, participants were asked to judge whether or not the item fitted with the accompanying location by pressing one of two buttons. They were told that the judgment was arbitrary and that the task was designed to help them encode the item–location association for the

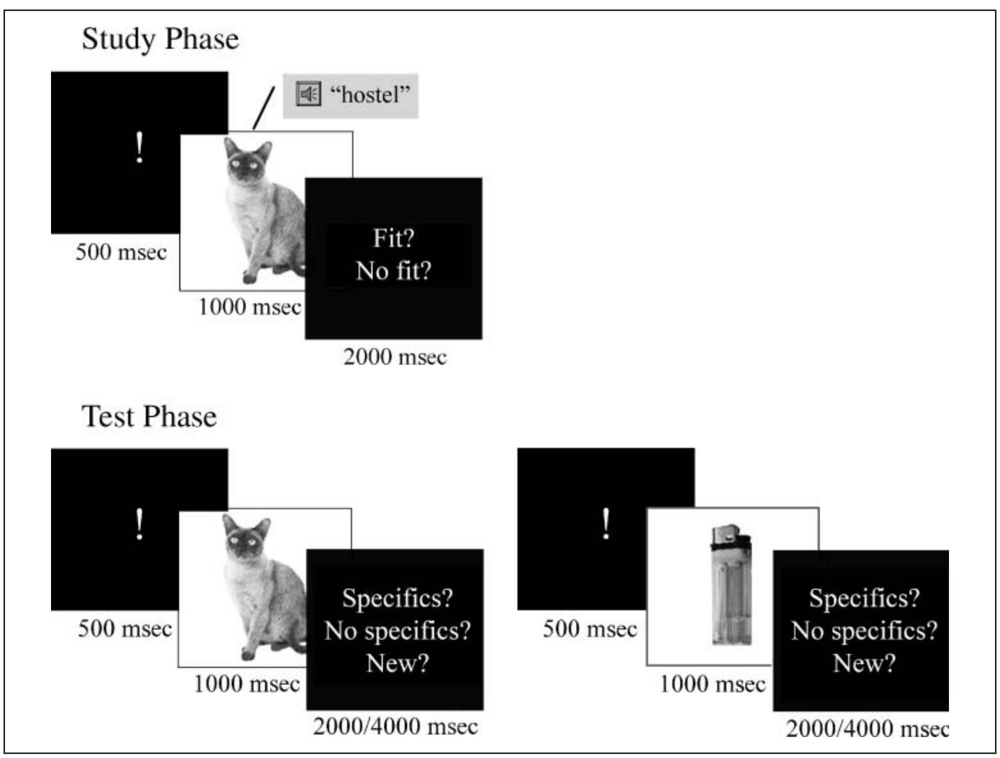


Figure 1. Example study and test trial for objects. The trial structure is identical in Experiments 1 and 2. Note that the questions at the end of the trial are displayed for clarification purposes only, and were not physically present on the screen during the experiments.

following memory task. The time in between successive study trials varied randomly between 2.5 and 4 sec.

At the end of the study list, memory for the associations in that list was tested without delay. Old items were presented without the associated location, along with new items. Each trial began with a fixation point presented for 500 msec, followed by the appearance of the visual item for 1000 msec. After stimulus offset, the fixation point was displayed again while participants indicated their response. A *location* response had to be given if participants recognized that the item had been presented in the study list and could recall the location associated with that item. If participants chose this response option, they were given 4 sec to verbally report the location, after which the next trial started automatically. Pilot work determined that this time was sufficient to make a verbal response and prepare for the following trial. Participants were asked to give a *no specifics* response if they recognized the item as being old, but could not retrieve the location paired with the item in the study list. Finally, participants gave a *new* response when they thought the item had not been presented earlier. When a *no specifics* or *new* response was given, 2 sec elapsed before the next trial started. No verbal response was required in these cases. Responses were assigned to one of three buttons on a keypad. Response assignment was counterbalanced across participants. Participants rested briefly in between study–test blocks.

As mentioned in the Introduction, old items given *location* responses and correct verbal reports were considered to involve recollection, as contextual details from the study episode were retrieved on those trials (Johnson, 2005; Tulving, 1983; Mandler, 1980). The memory processes underlying *no specifics* responses are less clear. At first glance, these trials primarily rely on familiarity. However, recollection-related processes may also be involved as contextual details other than an item's location may have been retrieved. In our pilot work, we incorporated an additional *other specifics* response, which allowed participants to indicate the recall of such details (cf. MacKenzie & Donaldson, 2007; Curran & Hancock, 2007; Yovel & Paller, 2004). However, participants rarely used this response category (~5 times during the whole experiment) and, even when they did, they failed to provide the identity of other details when requested. This category was therefore removed from the design. Because of the primary interest in recollection, and the difficulties surrounding the interpretation of *no specifics* trials, we restricted the ERP analyses to trials given correct *location* responses.

EEG Acquisition and Analysis

EEG was recorded from 32 scalp sites using silver/silver–chloride electrodes embedded in an elastic cap according to an equidistant electrode montage (see montage 10 at www.easycap.de/easycap/e/electrodes/13_M10.htm). Vertical and horizontal eye movements were recorded bipolarly from electrodes attached to the supra- and infraorbital ridges of the right eye and the outer canthus of each eye. A mid-frontal site (corresponding with Fz in the 10–20 system) was used as on-line reference, and an electrode placed just anterior served as ground. Signals were amplified and band-pass filtered between 0.01 and 35 Hz (3 dB roll-off) and digitized at a rate of 250 Hz (12-bit resolution).

Off-line, the data were digitally filtered between 0.05 and 20 Hz (96 dB roll-off, zero phase shift filter) and algebraically re-referenced to linked mastoids (reinstating the mid-frontal on-line reference site). Epochs of 1024 msec were extracted from the continuous EEG record, including a 100-msec prestimulus baseline. ERP waveforms were computed for each electrode site by averaging epochs corresponding with source hits (test trials containing old items given *location* judgments and correct verbal reports) and correct rejections (new items correctly judged as *new*). The resulting six conditions (object, word, and face source hits and correct rejections) formed the bases of the analyses. Blink artifacts were minimized by estimating and correcting their contribution to the ERP waveforms via a standard regression technique (Rugg, Mark, Gilchrist, & Roberts, 1997). Trials with horizontal and nonblink vertical movements were excluded, as were trials containing drifts (± 50 μV), amplifier saturation, or muscle artifacts. ERPs were based on a minimum of 15 artifact-free trials. On average, ERP waveforms for object, word, and face source hits were based on 63, 57, and 40 trials, respectively. Waveforms for correct rejections were based on 62, 61, and 58 trials, respectively.

Experiment 2

The procedures of Experiment 2 were identical to those of Experiment 1, with the following exceptions. Twenty-four healthy adults (mean age = 21.5 years, range = 19–26, 12 men), none of whom had participated in Experiment 1, served as volunteers. Participants were sampled from the same student population as in Experiment 1, and the two experiments were run in close temporal succession.[1] Two additional participants failed to provide enough source hits for faces, and were excluded from the analyses. As in Experiment 1, all subjects gave written informed consent and reported to be right-handed, native English speaking, and to be without neurological and psychiatric history. The crucial difference was that in Experiment 2, stimuli belonging to the three categories were presented in separate study–test blocks. Experiment 2 included an additional study–test block (24 instead of 23) to accommodate equal numbers of blocks for each stimulus type. The blocks were composed of 197 objects, 197 words, 197 faces, and 369 locations. Eight of the study–test blocks contained objects, eight words, and eight faces. Blocks belonging to the same stimulus category were presented sequentially, and the order of blocks was balanced across participants. On average, 59, 53, and 34 trials contributed to ERPs for object, word, and face source hits, respectively, and 65, 64, and 60 trials to ERPs for object, word, and face correct rejections.

RESULTS

Task Performance

Source Memory Test

Table 1 shows memory performance in each experiment. The accuracy with which recognition judgments were made was initially assessed with the discrimination measure $P_{\text{hits}} - P_{\text{false alarms}}$ (Snodgrass & Corwin, 1988), where P_{hit} denotes the probability of correctly identifying an item as old, irrespective of whether the source accompanying the item at study was recollected. Discrimination values and standard deviations for objects, words, and faces were 0.97 (0.03), 0.91 (0.07), and 0.76 (0.11), respectively in Experiment 1, and 0.90 (0.10), 0.83 (0.11), and 0.63 (0.15), respectively, in Experiment 2. Thus, accuracy was higher for objects than either words or faces, and higher for words than faces. A mixed-model analysis of variance (ANOVA) using factors of stimulus material and experiment confirmed that this pattern was statistically significant [Greenhouse–Geisser corrected $F(1.4, 63.8) = 145.7$, $p < .001$; subsequent pairwise comparisons, $p < .001$]. This pattern did not differ across experiments, but item recognition was, on the whole, better in Experiment 1 [$F(1, 46) = 13.9$, $p = .001$].

The accuracy with which source judgments were made was computed as the probability of a source hit (accompanied by correct verbal report), given that the item had already correctly been classified as old. An ANOVA confirmed that source accuracy differed significantly depending on type of stimulus material [$F(1.7, 79.4) = 54.5$, $p < .001$]. In both experiments, source information was more often recollected for objects than words or faces, and for words than faces (pairwise comparisons, $p < .001$). No significant main effect of experiment or interaction between type of stimulus material and experiment emerged. The time taken to make accurate source judgments also differed across experiments and stimulus materials. A between-subjects ANOVA showed that source judgments were generally made faster in Experiment 1 [$F(1, 46) = 16.1$, $p < .001$] and, regardless of experiment, made fastest for objects, then words, and then faces [$F(1.6, 72.7) = 32.0$, $p < .001$; subsequent pairwise comparisons, $p < .001$]. Again, no interaction between type of stimulus material and experiment was observed.

ERPs

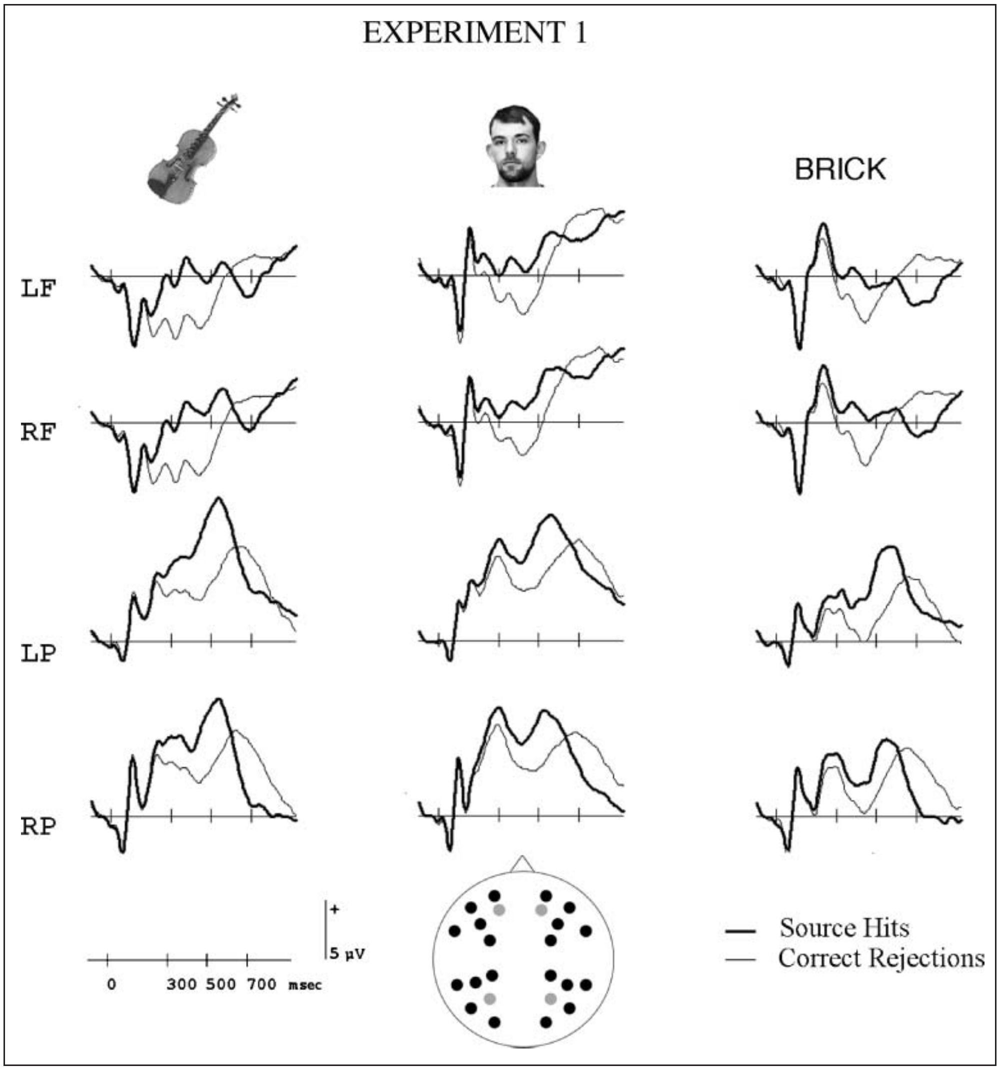
Figure 2 illustrates the group-averaged ERP waveforms elicited by source hits and correct rejections for objects, faces, and words in Experiment 1. Figure 3 shows the same comparison for Experiment 2. Waveforms are shown for representative frontal and parietal electrode sites (whole-head data available on request). As typically observed, recollected items in all three stimulus categories give rise to more positive-going waveforms as new items over large portions of the epoch. This old/new effect starts just before 300 msec and persists until at least 700 msec. At first glance, effects appear similar across stimulus materials, apart from the well-known overall variations in wave shapes associated with the perceptual processing of objects, faces, and words. Memory-related differences across stimulus categories are best seen in the voltage spline maps displayed in Figures 4 and 5. Early in the epoch,

Table 1. Memory Performance

	Experiment 1			*Experiment 2*		
	Objects	*Words*	*Faces*	*Objects*	*Words*	*Faces*
Proportion						
Source hits	0.60 (0.2)	0.54 (0.2)	0.38 (0.1)	0.53 (0.2)	0.47 (0.1)	0.30 (0.1)
Source misses	0.35 (0.2)	0.37 (0.2)	0.46 (0.1)	0.35 (0.1)	0.35 (0.1)	0.41 (0.1)
Misses	0.02 (0.0)	0.06 (0.0)	0.14 (0.1)	0.06 (0.1)	0.11 (0.0)	0.24 (0.1)
Correct rejections	0.99 (0.0)	0.97 (0.0)	0.90 (0.1)	0.97 (0.0)	0.94 (0.1)	0.87 (0.1)
Response Time (msec)						
Source hits	1306 (264)	1448 (310)	1526 (315)	1771 (502)	1972 (590)	2138 (734)
Source misses	1731 (337)	1795 (335)	1832 (395)	2885 (1433)	2855 (1303)	2865 (1279)
Misses	1428 (384)	1575 (658)	1396 (306)	1968 (840)	1852 (537)	1718 (571)
Correct rejections	929 (181)	969 (173)	1072 (191)	1147 (441)	1299 (356)	1455 (442)

Standard deviations are displayed in parentheses. The proportions of source hits and source misses are computed relative to the total number of old items. Source hit probabilities do not incorporate trials given an incorrect verbal response (i.e., when participants reported an incorrect location).

Figure 2. Group-averaged ERP waveforms from Experiment 1 at representative frontal and parietal electrodes (sites 34, 21, 29, 26 from montage 10; www.easycap.de/easycap/e/electrodes/13_M10.htm). Displayed are ERPs elicited by recollected and new objects, faces, and words.



old/new effects for objects and faces have a more anterior scalp distribution than those for words. Later on, all stimulus categories give rise to effects that are largest over left parietal sites. In addition, however, effects for objects and faces extend to more anterior sites. This later effect is especially pronounced when stimulus categories were blocked (i.e., in Experiment 2). No differences in the onset or duration of old/new effects are apparent across categories.

To quantify recollection-related effects, mean amplitudes were measured in the 300–500 and 500–700 msec latency intervals. These are typical intervals used in previous ERP old/new studies (e.g., MacKenzie & Donaldson, 2007, 2009; Curran & Hancock, 2007; Wilding & Herron, 2006; Yovel & Paller, 2004; Rugg & Wilding, 2000), and capture effects in all three stimulus categories in both of the current experiments. The analyses were performed on 24 electrode sites, partitioned to allow contrasts between the left and right, and anterior and posterior, scalp locations known to show old/new effects. For both time windows, a mixed-model ANOVA was computed on the amplitude differences between old and new items, using factors of stimulus material (objects/words/faces), site (six locations along the ventral-to-midline axis), location (anterior/posterior), hemisphere (left/right), and experiment (intermixed/blocked design). Analyses were also performed on data scaled with the max/min procedure (McCarthy & Wood, 1985), so that effects related to scalp topography were not confounded by amplitude differences. Greenhouse–Geisser corrections were applied to all factors with more than two levels to remedy violations of sphericity (Keselman & Rogan, 1980). Significant interactions involving stimulus material were followed up with subsidiary ANOVAs within each stimulus category.

In the 300–500 msec time window, the mixed-model ANOVA showed a significant main effect of stimulus material [$F(1.7, 77.6) = 9.8, p < .001$]. This reflected the fact that objects generally elicited larger old/new effects than either words or faces. More importantly, a significant Stimulus material × Location interaction pointed to scalp distribution differences across categories [$F(1.6, 74.9) = 13.9, p < .001$]. This interaction remained significant after scaling [$F(1.9, 90.0) = 4.9, p = .01$]. Separate ANOVAs within each category indicated that the difference between source hits and correct rejections was larger at anterior than posterior locations for objects and faces [main effects of location: $F(1, 47) = 56.2$, $p < .001$ and $F(1, 47) = 5.2$, $p = .028$, respectively], but not words ($p = .6$). None of the scalp distribution differences interacted with type of experimental design ($p > .2$).

The ANOVA on the data from the 500–700 msec interval showed a significant four-way interaction between stimulus material, location, hemisphere, and experiment [$F(1.6, 76.2) = 4.9$, $p = .014$]. The same interaction in the analysis of the scaled data [$F(1.9, 85.2) = 3.2$, $p = .048$] indicated that material-specific old/new effects differed in their scalp topography across experiments. In Experiment 1, effects were largest over left posterior electrodes for all three stimulus materials [$F(1, 23)$ for the interaction between location and hemisphere within each stimulus category ranged between 12.7 and 35.2, all $p < .003$]. In Experiment 2, only words displayed a typical left parietal old/new effect, whereas objects and faces had effects with a widespread scalp distribution [main effect of location: $F(1, 23) = 17.6$, $p < .001$ for words, $F(1, 23) = 2.4$, $p = .13$ for objects, $F(1, 23) = 0.3$, $p = .60$ for faces]. A direct test across the two time windows on the frontal scalp sites revealed that the anterior effect observed for objects and faces was larger in the 300–500 than in the 500–700 msec interval [main effect of time window: $F(1, 46) = 64.1$, $p < .001$], especially in the intermixed experiment [interaction between time window and experiment: $F(1, 46) = 8.6$, $p = .005$].

DISCUSSION

The present study had two primary aims. The first was to assess whether electrical brain activity differs depending on the type of information that is recollected. The second was to determine whether, in addition, recollection-related activity is influenced by study–test list composition. To address these issues, we contrasted ERPs for the retrieval of objects, faces, and words in a source memory task in situations where categories were intermixed within experimental lists (Experiment 1) or separated across lists (Experiment 2). From around 300 msec, recollection-related

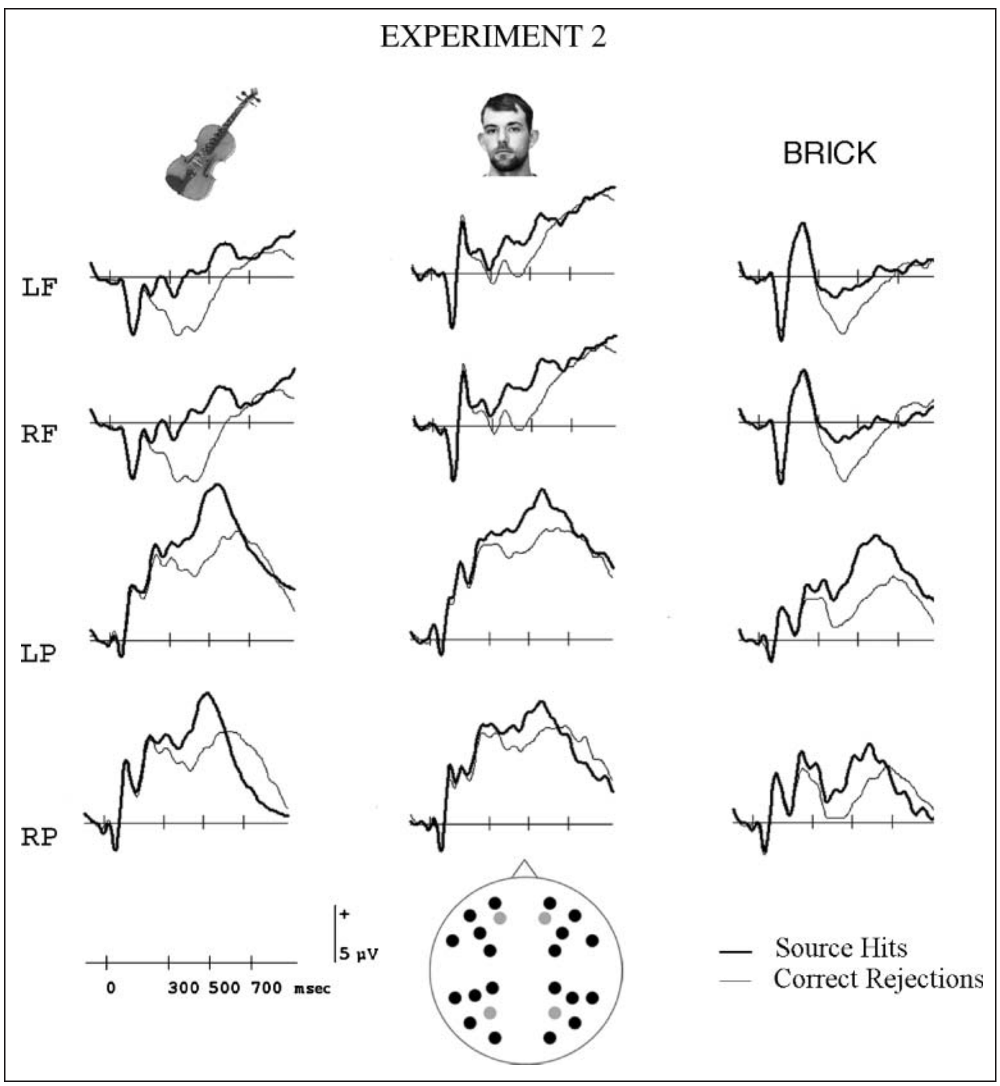


Figure 3. As in Figure 2, but data from Experiment 2.

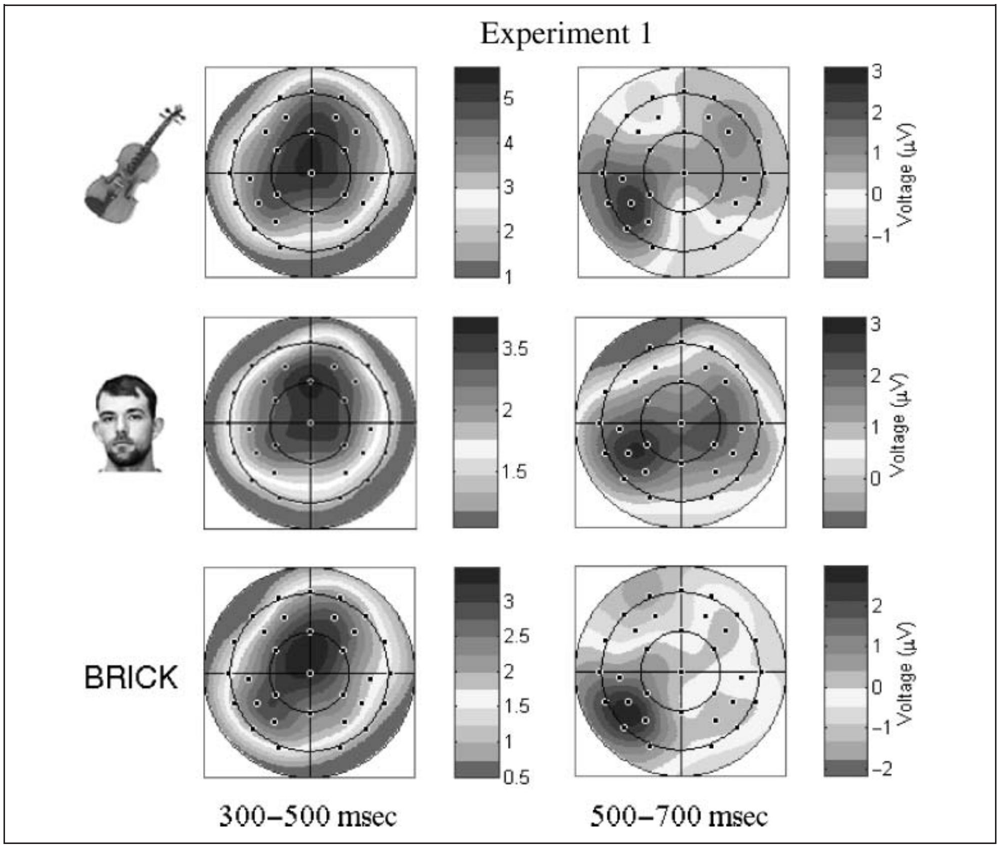


Figure 4. Voltage spline maps showing the scalp distribution of recollection effects (difference between source hits and correct rejections) in Experiment 1. Maps are range scaled.

activity had a more anterior scalp distribution for objects and faces than words. A similar pattern was observed later on. All three stimulus categories gave rise to effects over left posterior sites. However, these effects extended more anteriorly for objects and faces, especially when stimulus categories were blocked.

The fact that old/new effects for different stimulus categories did not just differ in their amplitude, but also in their

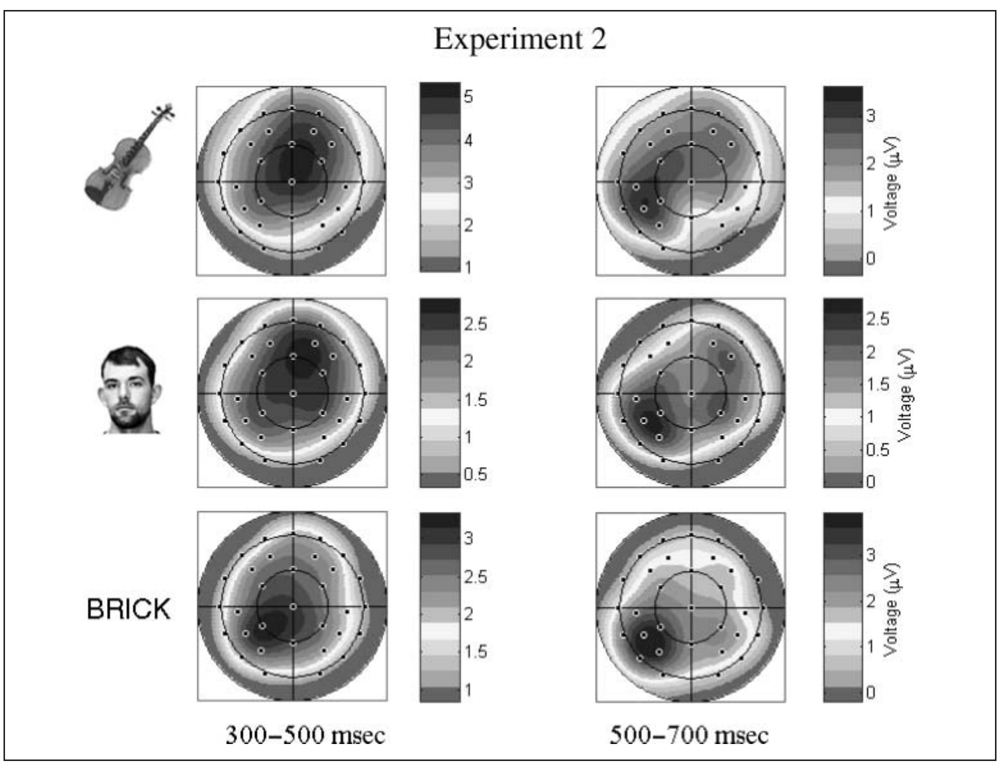


Figure 5. As in Figure 4, but data from Experiment 2.

scalp distribution, indicates that there are qualitative differences in the neural correlates of recollection contingent upon the contents of the retrieved event (see Otten & Rugg, 2004, for an introduction on how to interpret ERPs). This conclusion is consistent with cognitive theories of source memory (Mitchell & Johnson, 2009; Johnson et al., 1993), and with neuroimaging and neuropsychological studies that have shown that the successful retrieval of different stimulus materials is associated with distinct brain regions (e.g., Guerin & Miller, 2009; Woodruff et al., 2005; Moscovitch & McAndrews, 2002; Vaidya et al., 2002; Simons et al., 2001; Kim et al., 1999; McDermott et al., 1999; Jones-Gotman et al., 1997). Importantly, the high temporal resolution of electrical brain activity pinpoints material-specific effects to a time at which processes related to the search for, and recovery of, stored information are known to operate (cf. Johnson et al., 2008; Wilding & Herron, 2006; Rugg & Wilding, 2000). These early differences were identified by contrasting materials within the same experiment, in circumstances where it is certain that contextual information is retrieved for each item (Tulving, 1983; Mandler, 1980). Thus, the present findings provide strong evidence for the idea that material-specific neural correlates of recollection play a direct role in episodic memory retrieval. One possibility is that the details of a new event, such as its stimulus modality, are encoded into the representation of the event in memory. These details, and the neural activity associated with them, may then be used to retrieve the episode later on (Norman & O'Reilly, 2003; Rolls, 2000).

Because we used three stimulus categories, it is possible to determine what kind(s) of stimulus material triggers distinct neural correlates of recollection. The old/new effects we observed for words are generally consistent with previous findings in the literature (Wilding & Herron, 2006; Rugg & Wilding, 2000). By contrast, pictures of nameable objects and pictures of unfamiliar faces both elicited effects with more anterior scalp distributions. No differences emerged between the two types of pictorial information. More anteriorly distributed effects for objects and faces have also been found in previous studies in which old/new effects were compared across objects and words (Ally & Budson, 2007; Schloerscheidt & Rugg, 1997), across faces and words (MacKenzie & Donaldson, 2009; Yick & Wilding, 2008), and for objects in isolation (Kuo & Van Petten, 2006; Duarte et al., 2004; Johansson et al., 2002; Ranganath & Paller, 2000). Together, these findings indicate that material-dependent retrieval responses mainly reflect the difference between pictorial and verbal information. Although electrical brain activity does not pick up all types of brain activity (Nunez, 1981), this may imply that not every type of stimulus feature is encoded into a memory representation and used during retrieval. Faces, at least the kind used here, do not appear to have a special status. The old/new effects we found for faces closely resemble those found previously with a similar paradigm (MacKenzie & Donaldson, 2007, 2009; Yovel & Paller, 2004). A general pattern therefore seems to be emerging that the recollection of faces gives rise to qualitatively different old/new effects. This may even be consistent with the data shown in Curran and Hancock (2007), even though the authors did not explicitly test this possibility.

What cognitive processes might be associated with the anteriorly distributed ERP effect for recollected objects and faces? Any such processes must be common to the two types of pictorial information, and not shared with words. At first glance, it may not seem surprising to find a contribution of anterior regions to the recovery of information from episodic memory considering findings from neuroimaging experiments (e.g., Rugg, Fletcher, Chua, & Dolan, 1999). However, frontally distributed ERP effects do not necessarily arise from frontal brain regions (Scherg, 1990), and ERP studies suggest that frontal brain activity may reflect postretrieval processes (Hayama & Rugg, 2009; Henson, Rugg, Shallice, & Dolan, 2000). Early frontal ERP effects have traditionally been linked to familiarity (Woodruff et al., 2006; Curran, 2000). One possibility is that the recognition of pictorial information benefits more from familiarity-related processes than verbal information. However, we restricted the analyses to source hits, which primarily rely on recollection. Although a proportion of recollected trials will also be familiar under the assumption of independence (Yonelinas, 2002), it is not immediately clear why objects and faces, which differed substantially in source accuracy, would engender exactly the same level of familiarity. In addition, a functional interpretation of the early frontal ERP effect in terms of familiarity is, especially for faces, controversial (Voss & Paller, 2008).

Alternatively, the frontal effect may be a reflection of reinstatement processes leading to successful recollection. Johnson et al. (2008) recently demonstrated a content-dependent, anterior recollection-related effect similar to that found here. The authors interpreted this effect in the light of the earlier mentioned neural models of episodic memory (Norman & O'Reilly, 2003; Rolls, 2000), hypothesizing that the effect might reflect the reinstatement of processes engaged during encoding. Applying these ideas here, the associative study task in the present experiment may involve a greater amount of perceptual analysis or visual imagery for pictorial than verbal stimulus events. The subsequent recollection of pictorial information may then rely on the retrieval of the specific perceptual attributes encoded during study (cf. Yick & Wilding, 2008; Ranganath & Paller, 2000). This is in line with cognitive models of source memory (Mitchell & Johnson, 2009; Johnson et al., 1993), which characterize memory representations on the basis of the types of features incorporated into them. Representations of pictorial events may have more differentiated perceptual features than verbal events, and thus, involve qualitatively different memories. This may, in turn, be reflected in material-specific ERP effects. It is noteworthy that a recollection-related anterior ERP effect was absent in retrieval studies that used line drawings instead of photographs (compare Curran & Cleary, 2003 with Duarte et al., 2004, and Schloerscheidt & Rugg, 1997). The information provided by a perceptually less complex line drawing differs from that conveyed by a real picture. This accentuates the relationship between the anterior ERP effect and the retrieval of perceptual attributes, and warrants investigations separating recollection effects for stimuli varying in perceptual configuration. The idea that the frontal old/new effect for pictorial material reflects the reinstatement of perceptual processes is further corroborated by considering the timing of the effect. Interestingly, the effect was more prominent in the earlier (300–500 msec) than later (500–700 msec) time interval. This may reflect the recovery of perceptual attributes in the early stages of a retrieval attempt. Recent fMRI work suggests that frontal brain regions may be involved in such a process. For example, Thomas et al. (2008) showed that during face retrieval, peak activity in prefrontal cortex precedes activity in the fusiform face area.

In addition to type of stimulus material, study–test list composition affected the neural correlates of recollection. The anterior effect for objects and faces in the early time interval was observed in both experiments. However, the effect only extended into the later interval when stimulus categories were presented in different task blocks. Importantly, study–test list composition did not alter the qualitative nature of the effects elicited by each stimulus category. Rather, it accentuated the separation between pictorial and verbal information late in the epoch. The sensitivity of old/new effects to not only type of stimulus material, but also study–test composition, strongly suggests that higher-level control processes interact with material-specific processes when retrieving information from episodic memory.

Blocked designs offer the opportunity to maintain cognitive operations across successive trials, as there is no risk that a different category needs to be processed next (Donaldson, 2004; Otten, Henson, & Rugg, 2002; Wilding & Nobre, 2001). Blocked designs also increase list homogeneity. It seems unlikely that changes in list homogeneity underlie the observed differences across experiments. Objects are inherently easier to discriminate from one another than unfamiliar faces (Ally & Budson, 2007; Nelson, Reed, & Walling, 1976), and changes in list homogeneity would therefore be expected to affect objects and faces differentially. In contrast, blocked versus intermixed designs affected ERPs for recollected objects and faces to the same degree. Being able to maintain cognitive operations across trials may well explain the prolonged effects in blocked sequences. If there are qualitative differences in the retrieval of pictorial and verbal information, any such differences are likely to be emphasized when one or the other category is recollected in isolation. In that case, material-specific processes can be maintained for longer on each trial, as there is no need to abort such processes in favor of superseding preparatory or switching processes in service of the upcoming trial. One might expect that memory performance would be better in such circumstances. In contrast, performance was generally observed to be better with intermixed sequences. This may simply be a consequence of participants being more alert during the more varied intermixed sequences.

An important remark about the differences between the two experimental designs is that the effects of study–test list composition may originate at encoding, retrieval, or both. The fact that differences emerge at retrieval implies that retrieval-related processes must have been affected. It is not clear, however, whether these processes interacted with differences in earlier stages of memory. The two experiments may involve different encoding strategies, and this may, in turn, affect the way stimuli are recollected. Another, more general, remark is that the material-specific ERP old/new effects may have arisen because of differences in the processing of source hits, correct rejections, or both. Because faces, objects, and words engage different perceptual pathways and, therefore, generate fundamentally different ERP waveforms, memory-related processes can only be isolated by contrasting activity elicited by old and new items. This inherent limitation, which not only affects ERPs and the current study, leaves open the possibility that new as well as old items are processed in qualitatively different ways across stimulus categories and experimental designs.

Finally, we should note that not only ERPs but also task performance varied as a function of stimulus category and type of experimental design. It is therefore important to consider whether the more anterior recollection-related effects for objects and faces are merely a side effect of different levels of task performance. Specifically, it could be argued that the anterior effect—in both the early and late time intervals—reflects different degrees of retrieval success and/or retrieval effort across materials. This account is inconsistent with the behavioral data, however. In both experiments, recognition performance was better for objects than words, and in turn, better for words than faces. If the anterior effect observed here was a mere artifact of task difficulty, its amplitude would be expected to be graded across objects, words, and faces. This was not observed. In addition, when we split participants into those who performed well and not so well in the memory tasks, both groups exhibited the same material-specific recollection effects. An interpretation in terms of task difficulty is therefore not feasible. It is also unlikely that the frontal ERP effect reflects different degrees of pre-experimental familiarity. Unlike faces, objects and words have verbalizable features and preexisting representations in memory. This may have led to a richer encoding context and enhanced recollection. However, if pre-experimental familiarity caused the different ERP responses, we should have observed similar effects across objects and words, not objects and faces.

In conclusion, the present findings indicate that neural activity leading up to successful recollection is material specific, the crucial difference being between pictorial and verbal information. Recollection-related activity is further influenced by the distribution of stimulus categories within or across experimental lists. Material-specific processes thus seem to interact with higher-level control processes. Although we focused here on the processes underlying recollection, material-specific influences on retrieval may well generalize to other kinds of memory processes, such as familiarity. This issue will be important to address in future experiments. In addition, it will be of interest to test the proposal that more anteriorly distributed ERP effects may relate to the reinstatement of perceptual processes in aid of recovery of an episode.

APPENDIX: SPOKEN LOCATIONS USED IN THE STUDY PHASE

abbey	cafeteria	dentist's	guest room	luggage office	power plant
airport	cage	desert	gulf	mall	prison
airstrip	camp	desk	gym	manor house	promenade
alley	campus	dining room	hairdresser	mansion	pub
almond grove	canal	disco	hamlet	meadow	pyramids
alpine refuge	canteen	ditch	harbour	mechanic's	quarry
apartment	car park	dock	hardware store	mews	racetrack
aquarium	car wash	doctor's	hatchery	mill	ranch
aqueduct	carvery	dome	hay stack	mobile home	reading room
arcade	casino	dormitory	herbalist's	monastery	reception
arch	castle	dressing room	high school	mosque	refectory
archives	cathedral	drive-in	hill	motel	rental shop
arena	cattery	dump	holiday home	motor show	repair shop
art gallery	cavern	dungeon	hospice	motorway	reserve
attic	cellar	embankment	hospital	mountains	resort
auction house	chalet	embassy	hostel	museum	restaurant
auditorium	chapel	emporium	hot spring	newsagent's	restroom
avenue	check-in desk	engine room	hotel	night club	riding ground
bakery	chemist's	entrance	house boat	nunnery	river
balcony	china shop	equator	hut	nursery	rock
bank	church	escalator	ice rink	nuthouse	roof
banquet	cinema	exhibition	infirmary	ocean	ropeway
bar	circus	factory	inn	off-licence	running track
barber's	classroom	farmhouse	institute	opera house	runway
barn	clinic	fence	island	optician's	salt marsh
barracks	cloakroom	ferryboat	jail	orchard	sanctuary
bathroom	cloister	field	jeweler's	orchestra pit	sauna
bay	closet	fire station	jungle	orphanage	sawmill
bazaar	club	fishmonger's	kennel	oyster bar	schoolyard
beach	coast	fitting room	kindergarten	paddy	scooter
bedroom	cockpit	flat	kitchen	palace	seafood shop
bench	coffee shop	flea market	laboratory	parlour	seashore
billiard room	college	football field	lake	path	secretariat
boiler room	common room	forest	lane	patio	shed
book store	confectioner's	fortress	laundry	patisserie	sheep pen
boot camp	confessional	fountain	law court	penthouse	ship
booth	conservatory	frontier post	lawn	pet shop	shipyard
boutique	consulate	funfair	leather shop	pharmacy	showroom
box	convent	furniture shop	library	pier	shrine
boxing ring	cornfield	gallery	lift	pigsty	sickroom
brasserie	cot	gambling house	lighthouse	pinewood	synagogue
brewery	cottage	garage	linen room	planetarium	ski slope
brickworks	country house	garden	liquor store	platform	skyscraper
bridge	courthouse	gate	loan office	playroom	sleeping car
brothel	cowshed	glade	lobby	police station	slum
bungalow	crag	golf course	lock	pond	solarium
bunk bed	crematorium	gorge	locksmith's	porch	solicitor's
bus stop	crypt	grammar school	lodge	port	spa
butcher's	dam	graveyard	loft	post office	sports shop
cabin	dance-hall	greengrocery	lookout	post room	square
cable car	delicatessen	greenhouse	lounge	pottery	squash court

APPENDIX *(continued)*

stable	suite	tent	trailer park	villa	wine shop
stadium	sun deck	terrace	train	village	wood
stage	supermarket	theatre	travel agency	vineyard	workhouse
stalls	swamp	till	tree house	volcano	workroom
stationer's	swimming pool	tobacconist	tribunal	waiting room	yacht
store	tailor's	toilet	tube	ward	youth club
storeroom	tavern	tollbooth	tunnel	warehouse	zebra crossing
strand	tea house	tower	typing office	watchmaker's	zoo
street	telephone box	town hall	underpass	waterfall	
studio	temple	toy shop	valley	waterpark	
suburbs	tennis field	trading centre	veranda	wharf	

Acknowledgments

L. J. O. was supported in part by a Wellcome Trust Research Career Development Fellowship (WT073147). Stimulus presentation was programmed with the Cogent2000 software of the physics group of the Wellcome Trust Centre for Neuroimaging.

Reprint requests should be sent to Giulia Galli, Institute of Cognitive Neuroscience, 17 Queen Square, London, WC1N 3AR, UK, or via e-mail: g.galli@ucl.ac.uk.

Note

1. The close temporal separation and similarity in sampling populations make it unlikely that uncontrolled variables can account for the observed differences across experiments. However, as an anonymous reviewer pointed out, we cannot exclude this possibility.

REFERENCES

Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception: I. Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex, 9,* 415–430.

Ally, B. A., & Budson, A. E. (2007). The worth of pictures: Using high density event-related potentials to understand the memorial power of pictures and the dynamics of recognition memory. *Neuroimage, 35,* 378–395.

Curran, T. (2000). Brain potentials of recollection and familiarity. *Memory & Cognition, 28,* 923–938.

Curran, T., & Cleary, A. M. (2003). Using ERPs to dissociate recollection from familiarity in picture recognition. *Cognitive Brain Research, 15,* 191–205.

Curran, T., & Hancock, J. (2007). The FN400 indexes familiarity-based recognition of faces. *Neuroimage, 36,* 464–471.

Donaldson, D. I. (2004). Parsing brain activity with fMRI and mixed designs: What kind of a state is neuroimaging in? *Trends in Neurosciences, 27,* 442–444.

Donaldson, D. I., & Rugg, M. D. (1999). Event-related potential studies of associative recognition and recall: Electrophysiological evidence for context dependent retrieval processes. *Cognitive Brain Research, 8,* 1–16.

Duarte, A., Ranganath, C., Winward, L., Hayward, D., & Knight, R. T. (2004). Dissociable neural correlates for familiarity and recollection during the encoding and retrieval of pictures. *Cognitive Brain Research, 18,* 255–272.

Düzel, E., Yonelinas, A. P., Mangun, G. R. Heinze, H. J., & Tulving, E. (1997). Event-related brain potential correlates of two state of conscious awareness in memory. *Proceedings of the National Academy of Sciences, U.S.A., 94,* 5973–5978.

Friedman, D., & Johnson, R. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research and Technique, 51,* 6–28.

Guerin, S. A., & Miller, M. B. (2009). Lateralization of the parietal old/new effect: An event-related fMRI study comparing recognition memory for words and faces. *Neuroimage, 44,* 232–242.

Hayama, H. R., & Rugg, M. D. (2009). Right dorsolateral prefrontal cortex is engaged during post-retrieval processing of both episodic and semantic information. *Neuropsychologia, 47,* 2409–2416.

Henson, R. N., Rugg, M. D., Shallice, T., & Dolan, R. J. (2000). Confidence in recognition memory for words: Dissociating right prefrontal roles in episodic retrieval. *Journal of Cognitive Neuroscience, 12,* 913–923.

Johansson, M., Stenberg, G., Lindgren, M., & Rosén, I. (2002). Memory for perceived and imagined pictures: An event-related potential study. *Neuropsychologia, 40,* 986–1002.

Johnson, J. D., Minton, B. R., & Rugg, M. D. (2008). Content dependence of the electrophysiological correlates of recollection. *Neuroimage, 39,* 406–416.

Johnson, M. K. (2005). The relation between source memory and episodic memory: Comment on Siedlecki et al. (2005). *Psychology and Aging, 20,* 529–531.

Johnson, M. K., Hashtroudi, S., & Lindsay, D. S. (1993). Source monitoring. *Psychological Bulletin, 114*, 3–28.

Jones-Gotman, M., Zatorre, R. J., Olivier, A., Andermann, F., Cendes, F., Staunton, H., et al. (1997). Learning and retention of words and designs following excision from medial or lateral temporal-lobe structures. *Neuropsychologia, 35,* 963–973.

Kahana, M. J., & Sekuler, R. (2002). Recognizing spatial patterns: A noisy exemplar approach. *Vision Research, 42,* 2177–2192.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17,* 4302–4311.

Keselman, H. J., & Rogan, J. C. (1980). Repeated measures F tests and psychophysiological research: Controlling the number of false positives. *Psychophysiology, 17,* 499–503.

Kim, J. J., Andreasen, N. C., O'Leary, D. S., Wiser, A. K., Ponto, L. L., Watkins, G. L., et al. (1999). Direct comparison of the neural substrates of recognition memory for words and faces. *Brain, 122,* 1069–1083.

Kučera, H., & Francis, W. N. (1967). *Computational analysis of present-day American English*. Providence, RI: Brown University Press.

Kuo, T. Y., & Van Petten, C. (2006). Prefrontal engagement during source memory retrieval depends on the prior encoding task. *Journal of Cognitive Neuroscience, 18,* 1133–1146.

MacKenzie, G., & Donaldson, D. I. (2007). Dissociating recollection from familiarity: Electrophysiological evidence that familiarity for faces is associated with a posterior old/new effect. *Neuroimage, 36,* 454–463.

MacKenzie, G., & Donaldson, D. I. (2009). Examining the neural basis of episodic memory: ERP evidence that faces are recollected differently from names. *Neuropsychologia, 47,* 2756–2765.

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A., 29,* 8135–8139.

Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review, 87,* 252–271.

McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology, 62,* 203–208.

McDermott, K. B., Buckner, R. L., Petersen, S. E., Kelley, W. M., & Sanders, A. L. (1999). Set- and code-specific activation in frontal cortex: An fMRI study of encoding and retrieval of faces and words. *Journal of Cognitive Neuroscience, 11,* 631–640.

Mecklinger, A. (2000). Interfacing mind and brain: A neurocognitive model of recognition memory. *Psychophysiology, 37,* 565–582.

Minear, M., & Park, D. C. (2004). A lifespan database of adult facial stimuli. *Behavior Research Methods, Instruments & Computers, 36,* 630–633.

Mitchell, K. J., & Johnson, M. K. (2009). Source monitoring 15 years later: What have we learned from fMRI about the neural mechanisms of source memory? *Psychological Bulletin, 135,* 638–677.

Moscovitch, D. A., & McAndrews, M. P. (2002). Material-specific deficits in "remembering" in patients with unilateral temporal lobe epilepsy and excisions. *Neuropsychologia, 40,* 1335–1342.

Nelson, D. L., Reed, V. S., & Walling, J. R. (1976). Pictorial superiority effect. *Journal of Experimental Psychology: Human Learning and Memory, 2,* 523–528.

Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Reviews, 100,* 611–646.

Nunez, P. L. (1981). *Electrical fields of the brain: The neurophysics of EEG*. New York: Oxford University Press.

Otten, L. J., Henson, R. N., & Rugg, M. D. (2002). State-related and item-related neural correlates of successful memory encoding. *Nature Neuroscience, 5,* 1339–1344.

Otten, L. J., & Rugg, M. D. (2004). Interpreting event-related brain potentials. In T. C. Handy (Ed.), *Event-related potentials: A methods handbook* (pp. 3–16). Cambridge, MA: MIT Press.

Ranganath, C., & Paller, K. A. (2000). Neural correlates of memory retrieval and evaluation. *Brain Research, Cognitive Brain Research, 9,* 209–222.

Rolls, E. T. (2000). Hippocampo-cortical and cortico-cortical backprojections. *Hippocampus, 10,* 380–388.

Rugg, M. D., Fletcher, P. C., Chua, P. M., & Dolan, R. J. (1999). The role of the prefrontal cortex in recognition memory and memory for source: An fMRI study. *Neuroimage, 10,* 520–529.

Rugg, M. D., Mark, R. E., Gilchrist, J., & Roberts, R. C. (1997). ERP repetition effects in indirect and direct tasks: Effects of age and interitem lag. *Psychophysiology, 45,* 572–586.

Rugg, M. D., Mark, R. E., Walla, P., Schloerscheidt, A. M., Birch, C. S., & Allan, K. (1998). Dissociation of the neural correlates of implicit and explicit memory. *Nature, 392,* 595–598.

Rugg, M. D., & Wilding, E. L. (2000). Retrieval processing and episodic memory. *Trends in Cognitive Sciences, 4,* 108–115.

Scherg, M. (1990). Fundamentals of dipole source potential analysis. In F. Grandori, M. Hoke, & G. L. Romani (Eds.), *Auditory evoked magnetic fields and electric potentials* (pp. 40–69). Basel: Karger.

Schloerscheidt, A. M., & Rugg, M. D. (1997). Recognition memory for words and pictures: An event-related potential study. *NeuroReport, 20,* 3281–3285.

Simons, J. S., Graham, K. S., Owen, A. M., Patterson, K., & Hodges, J. R. (2001). Perceptual and semantic components of memory for objects and faces: A PET study. *Journal of Cognitive Neuroscience, 13,* 430–443.

Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: Applications to dementia and amnesia. *Journal of Experimental Psychology: General, 117,* 34–50.

Thomas, C., Moya, L., Avidan, G., Humphreys, K., Jung, K. J., Peterson, M. A., et al. (2008). Reduction in white matter connectivity, revealed by diffusion tensor imaging, may account for age-related changes in face perception. *Journal of Cognitive Neuroscience, 20,* 268–284.

Tulving, E. (1983). *Elements of episodic memory*. New York: Oxford University Press.

Vaidya, C. J., Zhao, M., Desmond, J. E., & Gabrieli, J. D. (2002). Evidence for cortical encoding specificity in episodic memory: Memory-induced re-activation of picture processing areas. *Neuropsychologia, 40,* 2136–2143.

Viggiano, M. P., & Vannucci, M. (2002). Drawing and identifying objects in relation to semantic category and handedness. *Neuropsychologia, 40,* 1482–1487.

Viggiano, M. P., Vannucci, M., & Righi, S. (2004). A new standardized set of ecological pictures for experimental and clinical research on visual object processing. *Cortex, 40,* 491–509.

Voss, J. L., & Paller, K. A. (2008). Brain substrates of implicit and explicit memory: The importance of concurrently acquired neural signals of both memory types. *Neuropsychologia, 46,* 3021–3029.

Wilding, E. L., & Herron, J. E. (2006). Electrophysiological measures of episodic memory control and memory retrieval. *Clinical EEG & Neuroscience, 37,* 315–321.

Wilding, E. L., & Nobre, A. C. (2001). Task-switching and memory retrieval processing: Electrophysiological evidence. *NeuroReport, 16,* 3613–3617.

Wilding, E. L., & Rugg, M. D. (1996). An event-related potential study of recognition memory with and without retrieval of source. *Brain, 119,* 889–905.

Woodruff, C. C., Hayama, H. R., & Rugg, M. D. (2006). Electrophysiological dissociation of the neural correlates of recollection and familiarity. *Brain Research, 1100,* 125–135.

Woodruff, C. C., Johnson, J. D., Uncapher, M. R., & Rugg, M. D. (2005). Content-specificity of the neural correlates of recollection. *Neuropsychologia, 43,* 1022–1032.

Yick, Y. Y., & Wilding, E. L. (2008). Material-specific neural correlates of memory retrieval. *NeuroReport, 19,* 1463–1467.

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language, 46,* 441–517.

Yovel, G., & Paller, K. A. (2004). The neural basis of the butcher-on-the-bus phenomenon: When a face seems familiar but is not remembered. *Neuroimage, 21,* 789–800.