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Citation	Gutchess, Angela H. and Daniel L. Schacter. 2012. The neural correlates of gist-based true and false recognition. <i>NeuroImage</i> 59(4): 3418–3426.
Published Version	doi:10.1016/j.neuroimage.2011.11.078
Accessed	February 19, 2015 12:04:05 PM EST
Citable Link	http://nrs.harvard.edu/urn-3:HUL.InstRepos:11829085
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Gutchess, A.H. & Schacter, D.L. (2012). The neural correlates of gist-based true and false recognition. *NeuroImage*, 59, 3418-3426.

The neural correlates of gist-based true and false recognition

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Abstract

When information is thematically related to previously studied information, gist-based processes contribute to false recognition. Using functional MRI, we examined the neural correlates of gist-based recognition as a function of increasing numbers of studied exemplars. Sixteen participants incidentally encoded small, medium, and large sets of pictures, and we compared the neural response at recognition using parametric modulation analyses. For hits, regions in middle occipital, middle temporal, and posterior parietal cortex linearly modulated their activity according to the number of related encoded items. For false alarms, visual, parietal, and hippocampal regions were modulated as a function of the encoded set size. The present results are consistent with prior work in that the neural regions supporting veridical memory also contribute to false memory for related information. The results also reveal that these regions respond to the degree of relatedness among similar items, and implicate perceptual and constructive processes in gist-based false memory.

Keywords: memory, false recognition, gist, fMRI, hippocampus

1. Introduction

Memory is a constructive process that is sometimes prone to error and distortion (e.g., Bartlett, 1932; Loftus, 1979; Neisser, 1967; Schacter, 2001; Schacter & Addis, 2007; Schacter, Norman, & Koutstaal, 1998). The notion that memory distortions are a byproduct of a constructive memory system is supported by a wealth of behavioral data revealing the nature of these errors (e.g., Brainerd & Reyna, 2002; Deese, 1959; Mather, Henkel, & Johnson, 1997; Roediger & McDermott, 1995, 2000; Schacter, Israel, & Racine, 1999) (for reviews see Gallo, 2006, 2010; Newman & Lindsay, 2009; Schacter, Guerin, & St. Jacques, 2011). For example, in his classic studies, Bartlett (1932) provided evidence that errors in story recall were frequently attributable to the operation of schemas that help to organize experiences and guide retrieval processes. Other memory errors reflect the operation of associative memory processes that play a key role in organizing memory or related gist-based processes that promote the retention of thematic information (Deese, 1959; Reyna & Brainerd, 1995; Roediger & McDermott, 1995). These kinds of findings have provided empirical support for the claim that a range of memory distortions are based on the operation of adaptive cognitive processes that contribute to the efficient and flexible functioning of memory (for further discussion, see Newman & Lindsay, 2009; Schacter & Addis, 2007; Schacter, et al., 2011).

Neuroimaging studies of *false recognition*, where individuals incorrectly claim that a novel item has been encountered previously, reveal a striking overlap between the brain regions activated during true and false recognition (e.g., Abe et al., 2008; Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Dennis et al., 2008; Garoff-Eaton, Slotnick, & Schacter, 2006; Johnson et al., 1997; Kensinger & Schacter, 2006; Okado & Stark, 2003;

Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997; Schacter et al., 1996; Slotnick & Schacter, 2004); (see review by Schacter, Chamberlain, Gaesser, & Gerlach, in press; Schacter & Slotnick, 2004). Such observations are consistent with the idea that when memory errors occur, there is a high degree of overlap in the subprocesses that contribute to true and false memory (Mitchell & Johnson, 2009), and provide additional evidence supporting claims of adaptive memory distortions (Schacter et al., 2011).

Previous fMRI studies examining false recognition of novel items that are related to previously studied items indicates the types of overlapping processes that can lead to false recognition. In a comparison of true recognition, related false recognition (e.g., of perceptually similar novel shapes), and unrelated false recognition (e.g., perceptually dissimilar novel shapes), Garoff-Eaton and colleagues (2006) noted that a wide array of regions, including prefrontal, lateral and medial temporal, parietal, and occipital cortices, were activated by both identical true and related false recognition. These findings suggest that related false recognition engages many of the same processes as accurate recognition, including semantic and visual processes. Studies of associative memory errors also suggest that semantic processes contribute to false memory, with heightened engagement of inferior frontal gyrus during encoding (Kim & Cabeza, 2007) and retrieval (Garoff-Eaton, Kensinger, & Schacter, 2007), and a possible role for anterior temporal regions that subserves semantic processing (Gallate, Chi, Ellwood, & Snyder, 2009). Perceptual regions implicated in false memory include late visual regions, which respond to both true and false memory (Kim & Cabeza, 2007; Slotnick & Schacter, 2004), and a midtemporal region responding more for false than true memories for rhyming or orthographically similar words (Garoff-Eaton, et al., 2007).

The paradigms employed thus far, however, have not investigated false recognition based on the *degree* or *amount* of related information that is available at the time of retrieval (see Kim & Cabeza, 2007, and Dennis et al., 2007, for studies of encoding activity based on the extent of false recognition of categorized words). While several neural regions are engaged when there is some degree of overlap between novel and familiar exemplars, there may only be a subset of regions that are increasingly engaged as the gist-based representation is strengthened. Characterizing and understanding these regions is particularly relevant to the claim that memory distortions often reflect the operation of adaptive cognitive processes (Schacter et al., 2011). In this study, we explore the neural regions that respond during true and false recognition as a function of the number of related items. Furthermore, the present paradigm incorporates visually and conceptually rich pictures, which should draw on both perceptual and semantic processes, in contrast to previous studies (see Dennis, et al., 2008, Dennis, Kim, & Cabeza, 2007, and Kim & Cabeza, 2007 for comparisons of categorically-related words).

To investigate the effects of the degree of relatedness on neural activity during false recognition, we focus on a memory error known as *gist-based false recognition*. Gist-based errors occurs when people extract the gist, or general information about thematic content, but fail to encode or retrieve verbatim, item-specific distinguishing details (Brainerd & Reyna, 2002; Koutstaal & Schacter, 1997). Strengthening gist representations by encountering multiple exemplars of a class of objects can lead to false recognition of items thematically related to studied exemplars (Koutstaal & Schacter, 1997). Importantly, the number of memory errors seem to be driven by the amount of

related information; as the number of related studied items increases, so too does the percentage of items falsely recognized (Koutstaal & Schacter, 1997). For example, studying a dozen pictures of cats leads one to remember quite well that cats were studied, but can hinder one's ability to recall perceptual details of particular cats and thus to discriminate novel pictures of cats from studied pictures of cats. Stimulus characteristics, instructions, and test conditions all can influence reliance on gist-based responding (Guerin, Robbins, Gilmore, & Schacter, in press; Koutstaal & Cavendish, 2006; Koutstaal et al., 2003; Koutstaal, Schacter, Galluccio, & Stofer, 1999; Tun, Wingfield, Rosen, & Blanchard, 1998).

A number of cognitive processes have been proposed to contribute to gist-based memory errors. The semantic categorization account maintains that pre-existing semantic associations can overshadow the use of item-specific features, and is predicated on the finding that studying sets of concrete, but not abstract, pictures increases levels of false recognition (Koutstaal, et al., 2003). Retrieval processes contribute substantially to gist-based errors (Guerin et al., in press), as disambiguating perceptual information is adequately encoded to at least some extent (Koutstaal, 2003), and can be made accessible under appropriate retrieval conditions (Guerin et al., in press). In addition, encountering many overlapping perceptual features can reinforce the representation of prototypical features (e.g., the shape features that are generally shared across exemplars from the category "chair") which then, as a result of flexible recombination or binding of features by a constructive memory system, could seem familiar in a novel exemplar that shares those same prototypical features.

In addition to semantic and perceptual processes, retrieval also relies on reconstructive processes to combine information from various sources, and the hippocampus appears to contribute in this role. For example, the hippocampus is engaged more by the correct recognition of a previously encountered word than by a novel recombination of parts of the word in young adults, and is implicated in age-related failures to correctly bind features together (Giovanello, Kensinger, Wong, & Schacter, 2010; Mitchell, Johnson, Raye, & D'Esposito, 2000). Recent work suggests that the region's role in connecting information together also contributes to imagination. The hippocampus is engaged both by imagining a future scenario and retrieving a memory of the past (e.g., Addis, Wong, & Schacter, 2007). Constructing future scenarios can even drive the region more than retrieving memories of the past (Schacter & Addis, 2007), particularly engaging anterior hippocampal regions when constructed events contain high levels of detail (Addis & Schacter, 2008) and reflect specific, rather than general, scenarios (Addis, Cheng, Roberts, & Schacter, 2011). This role for the hippocampus is thought to reflect the relational processing demands of integrating and recombining information from a variety of sources to imagine and encode a new scenario (Addis, Pan, Vu, Laiser, & Schacter, 2009; Addis, et al., 2007; Hassabis, Kumaran, Vann, & Maguire, 2007; Martin, Schacter, Corballis, & Addis, 2011); (for review and discussion, see Buckner, 2010; Schacter & Addis, 2009).

Consistent with prior studies of false recognition of related information, we expect that gist-based errors will occur due to the engagement of semantic, perceptual, and constructive processes. However, investigating false recognition as a function of gist strength, based on having encountered previously varying numbers of related items,

allows for the investigation of false memory across gradations of relatedness. While previous studies have begun to identify shared neural substrates for accurate memory and erroneous memory for related information, relatedness has been treated in an all-or-none fashion. It may be that a minimal level of relatedness is all that is required to invoke similar processes to support true and false recognition, in which case we should find that perceptual, semantic, and constructive processes are no more engaged as gist strength increases. However, behavioral data indicating higher levels of gist-based false recognition as a function of the number of related items studied (Koutstaal & Schacter, 1997) suggest that these processes and their corresponding neural regions should be increasingly engaged as function of gist strength.

Our approach based on manipulating gist strength should be particularly useful for shedding light on the mixed results in the literature thus far, with some studies indicating that the hippocampus and other regions are engaged equally by true and false memories (e.g., Addis, et al., 2007; Garoff-Eaton, et al., 2006; Schacter, et al., 1997), while some suggest that the regions are engaged more by true than false memories (e.g., Cabeza, et al., 2001; Giovanello, et al., 2010; Kensinger & Schacter, 2005; Schacter, et al., 1996), or even more by imaginary than true memories, as in the research on future event simulation (e.g., Addis, et al., 2007; Schacter & Addis, 2007). One possibility is that the hippocampus responds to the *degree* of relatedness among similar items, such that false memories that have more information in common with true ones implicate these regions more than those false memories with less in common with true memories. We tested the response of the hippocampus and other regions by manipulating the strength of the gist-based representation for conceptually and perceptually rich information. Using a

parametric modulation approach, we identify the neural regions that respond as the number of related items increases, allowing us to selectively identify those cognitive processes leading to increased levels of gist-based recognition.

2. Methods

2.1 Participants. Sixteen participants (8 male) between the ages of 19-33 ($M = 24.13$, $SD = 4.57$) were recruited to take part in the study. Seven additional participants were excluded from the study for failing to respond to large numbers of trials (1 participant; > 40% no responses), failure to follow instructions (1 participant), or too few false alarms in at least one condition (5 participants; < 8 items). The final sample of participants averaged 16.41 years of education ($SD = 2.85$), and all participants had some college education. Eligibility criteria included right handedness, English as a native language, absence from medications known to affect the central nervous system, and the absence of neurological, psychological, or physical conditions contraindicated for MRI scanning. Participants provided written informed consent for a protocol approved by Harvard University and Partners Institutional Review Board.

2.2 Materials and Procedures. Participants incidentally encoded 468 pictures of single objects by making a yes/no button press to denote whether the type of object depicted is something they would use or interact with during an average day. Pictures were drawn from 54 sets of objects (e.g., umbrellas, chairs, cats), with 18 categories assigned to each condition. Multiple exemplars of each object were encoded with small study sets containing four studied exemplars (e.g., four umbrellas), medium study sets containing eight studied exemplars (e.g., eight chairs), and large studied sets containing fourteen exemplars (e.g., fourteen cats). Exemplars from each category were distributed

across three encoding runs (e.g., the four umbrellas or fourteen cats would be distributed as evenly as possible across encoding runs). Across three encoding runs, participants viewed 72 pictures that would ultimately comprise the small condition, 144 medium set pictures, and 252 large set pictures. Each picture was presented for one second followed by a 1-second blank interval. On average, participants responded to 94.24% of the trials during encoding (SD = 8.20%).

After an approximately ten minute delay during which time structural images were acquired, participants received a surprise recognition test. Participants' memory was assessed for a total of 456 pictures (216 studied items and 240 lures). Each studied small, medium, and large object category (e.g., cats) was tested with four studied exemplars and four novel lure exemplars, randomly selected from the studied and unstudied items for each category. Thus, there was a total of 72 items in each of the conditions, with items from each specific category from each condition evenly distributed across four runs. In addition, twenty-four novel pictures were presented from distinct object classes not studied previously in order to provide a baseline false alarm rate. Example stimuli are displayed in Figure 1. Counterbalancing of the assignment of object classes to each of the four studied set sizes (i.e., zero, small, medium, and large) and assignment of tested items as either lures or studied targets was accomplished across participants using eight different recognition orders. Participants had four seconds in which to decide whether or not they had previously seen the picture and to press a button corresponding to "yes" or "no". Pictures were selected from photo CDs (Hemera Technologies, Gatineau, Quebec).

Both encoding and recognition trials were randomly ordered in a jittered design (Dale, 1999) containing fixation cross trials that participants passively viewed for times

varying from 2000 to 10000 msec. Trials were presented and behavioral data acquired with E-Prime software (Psychology Software Tools, Pittsburgh, PA).

2.3 Functional MRI Data Acquisition. Images were acquired using a Siemens Avanto 1.5 Tesla whole-body scanner (Siemens, Erlangen, Germany). Thirty-two slices 3.2mm thick with a .3mm skip between slices were acquired with an echo-planar imaging (EPI) sequence (TR = 2000 msec, TE = 30, FOV = 200mm, and a flip angle = 90°). During each of the three encoding runs, 212 measurements were collected; each of the four recognition runs consisted of 304 measurements. Encoding data are intended for a separate investigation and will not be discussed further.

2.4 Functional MRI Analyses. Analyses were conducted in SPM2 (Wellcome Department of Cognitive Neurology, London, UK). Random effects analyses allowed for assessment of distinct and common patterns of activation, and parametric analyses were conducted to identify regions that modulate neural activity during hits or false alarms as an effect of the amount of gist. The random effects model included eight regressors: False alarms (FA)-large, FA-medium, FA-small, Hits-large, Hits-medium, Hits-small, Zero-Correct Rejections (novel lures), and Miscellaneous (i.e., all misses and remaining correct rejections; when applicable, false alarms to the Zero category and non-response trials). Results are thresholded at a voxel-level correction of $p < .01$ with a cluster-level threshold of 44 voxels in order to achieve an overall correction of $p < .05$ (Slotnick, Moo, Segal, & Hart, 2003). To assess the commonality, or overlap, across two comparisons, two separate contrasts were estimated. The map for the first contrast was thresholded at $p < .035$ (Fisher, 1950; Garoff-Eaton, et al., 2006) to create a mask in which the second contrast was tested at a threshold of $p < .035$ (for a conjoint p-value of approximately

$p=.001$) and a cluster extent = 44 voxels (for consistency with the difference analyses), for an overall correction surpassing $p<.05$.

The parametric modulation analyses were conducted at the fixed-effects level, entering set size (i.e., small, medium, and large) as a covariate of interest, to test for linear trends across set sizes separately for hits and false alarms. These analyses allowed for the identification of regions whose activity correlated positively (i.e., increasing as set size increased) and negatively (i.e., increasing as set size decreased) modulations across the different levels of set size for either hits or false alarms. Because the parametric modulation responses could differ depending on whether recognition was true or false, we directly compared the slope of the parametric responses across these two conditions by entering the positive contrast images from the fixed-effects models into random-effects paired samples t-tests in SPM (i.e., testing whether the positive modulation effect differed between true and false recognition, and whether the negative modulation effect differed between true and false recognition) (as in Addis & Schacter, 2008). Any slope differences identified between conditions could reflect: (1) slopes of the same sign that differ significantly in magnitude across conditions (e.g., the parametric effect is strongly positive for true recognition and weakly positive for false recognition); or (2) slopes of opposite sign (e.g., the parametric effect is positive for true recognition and negative for false recognition). Moreover, it is possible that even when there are significant differences in slope across conditions in a particular voxel, the parametric effects themselves may not be significantly different from zero (e.g., a non-significant positive effect for true recognition and a weak non-significant negative for false recognition). Thus, in order to fully explore all these possibilities, we computed a random-effects one-sample t-test for the parametric effect in each condition. The values in the resultant beta images from these one-sample t-tests reflect the average estimated slope of the regression line in each condition; these beta images could then be probed (in regions identified by the paired sample t-test as showing a differing

parametric effect across condition) to examine the nature of the parametric effect (sign; significance; see Table 3).

For the purposes of illustration, activations are displayed on a canonical single subject's brain. Estimates for bar graphs are based on random effects analyses with values extracted with MarsBar (Brett, 2002). Labels of regions are approximate, based on Talairach (Talairach & Tournoux, 1988) and AAL labels (Tzourio-Mazoyer et al., 2002), as implemented in mricron (Rorden, Karnath, & Bonilha, 2007).

3. Results

3.1 Behavioral recognition data. Participants showed the expected pattern of greater false alarms as a function of increasing set size, as tested in a univariate ANOVA of false alarm rates across the three previously studied set sizes $F(2, 30) = 17.67, p < .001$, partial $\eta^2 = .54$. Each set size differed significantly from the others, with more false alarms to large than medium set sizes, $F(1, 15) = 11.07, p < .01$, partial $\eta^2 = .43$, and to medium than small, $F(1, 15) = 8.90, p < .01$, partial $\eta^2 = .37$. Participants made fewer false alarms to the entirely novel zero items than to any other set, $t(30) = 11.28, p < .001$ (for the comparison against the small set). In contrast to the false alarm rate data, set size did not influence hit rates across the three different set sizes when tested in a univariate ANOVA, $F(1, 15) = 1.78, p = .19$, partial $\eta^2 = .11$.

3.2 Functional data: Random Effects Analyses

3.2.1 Common activity for true and false recognition. We first assessed the overlap of the activations for hits and false alarms as a baseline comparison of whether the overlap reported in previous studies for true and false recognition was also true for our study. The conjunction of the hits minus novel items (i.e., encoded set size of zero) contrast and the false alarms minus novel items contrast resulted in several regions of

activation, including bilateral inferior parietal, bilateral inferior and middle frontal, bilateral precuneus, and occipital gyri, as well as right hippocampus. A subset of these regions is displayed in Figure 2A (the full set of coordinates is available as Supplementary Table 1).

3.2.2 Differences in the activity for true and false recognition. In a comparison collapsing across set sizes, we tested for differences in the activity underlying true and false recognition. Representative slices from these comparisons are displayed in Figure 2B (the full set of coordinates is available as Supplementary Table 2). Hits tended to recruit visual, parahippocampal, and temporal regions more than false alarms, whereas false alarms recruited regions of frontal cortex, including anterior cingulate, and right dorsal and ventral regions of middle frontal gyri, to a greater extent than do hits.

3.3 Functional data: Parametric Modulations

Parametric modulation analyses reveal regions that show an increasing (or decreasing) response as set size increases (or decreases). Such a pattern indicates that the regions contribute not only to true or false memory for items related to those studied previously (as shown with the random effects analyses), but show a graded responses as set size increases.

3.3.1 Modulation with set size for false recognition. Activations associated with false alarms to increasing (Table 2A) or decreasing (Table 2B) set sizes are displayed in Figure 3. For false recognition, as set size increased, activity increased in visual regions (fusiform and calcarine gyri) and the hippocampus.

3.3.2 Modulation with set size for true recognition. Activations associated with hits to increasing (Table 2C) or decreasing set sizes (Table 2D) are displayed in Figure 3.

In contrast to the pattern for false recognition, as set size increased for true recognition, activity decreased in visual regions (fusiform and middle occipital). In contrast, angular gyrus exhibits greater deactivation as set size decreases.

As noted in Table 2, many of the regions emerging in the parametric modulation analyses also reached significance in the random effects analyses, suggesting there is consistency in the results from the two analyses.

3.3.3 Differences in modulation across true and false recognition. Because parametric modulation responses were analyzed separately for true and false recognition, we directly compared the patterns of responses across the two types of memory using paired samples t-tests in SPM, as described in Section 2.4). Mean betas (see Table 3) reflect the average estimated slope of the regression line extracted from each condition; we then tested whether the betas differed significantly from zero. Regions in Table 3a exhibited positive modulations to false alarms (i.e., a stronger response as the amount of gist increases) and negative modulations (i.e., a stronger response as the amount of gist decreases) to hits (Table 3a), and included right hippocampus, parahippocampal gyrus, bilateral fusiform gyri, and occipital regions. Table 3b indicates regions showing positive modulations to hits and negative modulations to false alarms, and included temporal, frontal, and occipital regions.

4. Discussion

The findings of the present study are generally consistent with previous literature (e.g., (Garoff-Eaton, et al., 2006; Slotnick & Schacter, 2004) in underscoring the extensive overlap in the sensory and reconstructive processes that support true and false recognition (Johnson, Hashtroudi, & Lindsay, 1993; Mitchell & Johnson, 2009; Schacter & Addis,

2007; Schacter, et al., in press; Schacter & Slotnick, 2004). The results are novel because they provide information regarding the response of the hippocampus and other regions across levels of relatedness and degree of gist. While previous studies of true and false recognition treated relatedness in an all-or-none fashion, the present study investigated true and false recognition as a function of the degree of relatedness, finding that many of the relevant processes and corresponding neural regions respond in a graded fashion. As the gist representation is strengthened for false memories, the hippocampus and visual regions respond to a greater extent, indicating roles for constructive and perceptual processes as the degree of gist increases for false memory. This finding is consistent with behavioral studies of gist-based based false recognition (Koutstaal & Schacter, 1997) in suggesting that the processes underlying false recognition are engaged to a greater extent as more related information has been encountered. For true memories, however, multimodal association regions track increasing amount of gist, perhaps playing a role in integrating sensory information and representing the outputs of retrieval processes in order to inform decision processes (Wagner, Shannon, Kahn, & Buckner, 2005), but perceptual regions respond to the individuation of objects (as gist decreases). Throughout the remainder of the discussion, we consider these component processes and their contribution to true and false recognition as gist strength increases and decreases.

The results implicate a number of processes as shared across true and false recognition, consistent with prior work (Garoff-Eaton, et al., 2006). For the comparison of true vs. false recognition, regardless of the degree of gist, the engagement of visual regions, including occipital cortex and fusiform gyrus, suggest that perceptual processes are invoked as gist information increases for both true and false memories. This activity

could reflect the shared visual features across exemplars in a set (e.g., the shape of a chair). The activity of the hippocampus, in turn, could underlie the combination of perceptual, as well as semantic, features through the kinds of constructive memory processes discussed earlier (e.g., Schacter & Addis, 2007).

In terms of overall differences across true and false memories regardless of the level of gist, recognition is associated with the greater recruitment of visual, parahippocampal, posterior parietal, and temporal regions, likely reflecting increased access to sensory information for true than false recognition (e.g., Cabeza et al., 2001; Slotnick & Schacter, 2004). In contrast, false recognition is associated with greater engagement of frontal cortex, including anterior cingulate and right middle frontal gyrus, likely reflecting increased monitoring of retrieved memories (e.g., Cabeza et al., 2001; Slotnick & Schacter, 2004; Schacter et al., 1996; Schacter et al., 1997). These findings fit generally with the source monitoring framework in that true memories tend, on average, to have more perceptual details than false memories (Johnson, et al., 1993; Mitchell & Johnson, 2009). A number of results are consistent with this framework (e.g., Cabeza, et al., 2001; Gonsalves & Paller, 2000; Hashtroudi, Chrosniak, & Johnson, 1990; Schacter, et al., 1997; Schacter, et al., 1996; Slotnick & Schacter, 2004). In contrast, frontal areas are more active when more monitoring is required (see Mitchell & Johnson, 2009 for a review), suggesting that in the present study, category-related lures may have generated more uncertainty than old items, engaging more frontally-based monitoring processes.

For true recognition, multimodal association areas were more engaged as gist strength increased. Activity linearly increased in regions including supramarginal and inferior parietal cortex as the number of related items increased. These parietal regions

play a role in integrating information across modalities, reflecting the number of modalities engaged by objects (Wagner, et al., 2005). The involvement of these regions suggests that integration of information drawn from multiple senses, in conjunction with semantic and linguistic processes (e.g., Binder, Desai, Graves, & Conant, 2009), play important roles in supporting accurate memory as more items were studied. As gist strength decreased, visual regions (with distinct peaks from those that modulated false alarms) were engaged, suggesting individuation of exemplars based on their unique perceptual features. For example, regions involved in visual analysis of objects (e.g., fusiform and middle occipital gyri) may contribute to individuating objects. These regions linearly increase their activity for hits as the number of related items decrease, suggesting a response to the visual properties of specific exemplars.

In terms of false memory, participants committed more false alarms as gist strength increased with larger set sizes at encoding, consistent with previous research (Koutstaal & Schacter, 1997). For false alarms, several regions were also associated with correct recognition (despite differences in peaks between true and false recognition), such as the fusiform gyrus, calcarine gyrus, and hippocampus, exhibited a larger response as the set size increased. Prior work has noted a role for these regions in accurate memory and false recognition of related items (Cabeza, et al., 2001; Garoff-Eaton, et al., 2006; Schacter & Slotnick, 2004; Slotnick & Schacter, 2004), and we will further consider the contributions of the hippocampus and visual regions.

Specifically, the hippocampus exhibited linear increases as encoding set size increased. Our data are consistent with the idea that the hippocampus contributes to constructive memory in that it flexibly binds elements together in memory, sometimes

resulting in false memories through erroneous recombinations (Cabeza, et al., 2001; Giovanello, et al., 2010; Schacter & Addis, 2007; Schacter & Slotnick, 2004; Slotnick & Schacter, 2004). The direct comparison of modulations for true and false memory suggests that the differential hippocampal activity tended to be the strongest for hits with small set size vs. large set size. The complex pattern of hippocampal engagement suggests reasons why previous studies have found an inconsistent role for the hippocampus in true and false memories. The engagement of the hippocampus could reflect the amount of information that needs to be bound together (captured here, but not in all previous studies, as the modulation across set size) as well as the content of that information (illustrated here through the differential effects of set size across hits and false alarms). For example, the hippocampus could be engaged by binding together more veridical details for small set size hits but more erroneous and gist-based details in the case of large set size false alarms.

An alternative explanation is that hippocampal activity reflects pattern separation mechanisms such as the greater demands of assigning a distinct representation to the lure stimulus (Bakker, Kirwan, Miller, & Stark, 2008; Norman & O'Reilly, 2003). This interpretation fits well with prior data in that pattern separation, represented by engagement of areas in the CA3/dentate gyrus field of the hippocampus, is most required for novel information and similar lures, but less engaged for repeated information (Bakker, et al., 2008; Lacy, Yassa, Stark, Muftuler, & Stark, 2011). While it may seem counterintuitive to find a region more engaged for high amounts of gist for false, but not true, memory, it could reflect different contributions of pattern separation mechanisms to true vs. false memory. For example, greater hippocampal activity could be required in the

case of true memories when few, specific veridical details were encoded (e.g., when distinct, nonoverlapping representations to novel stimuli were rapidly assigned) and in the case of false memory, when prototypical features are falsely recalled (e.g., overlapping representations were assigned to similar stimuli, and high levels of overlap occur). In contrast, true memory influenced by high amounts of gist could depend on pattern completion mechanisms. Further work is needed because the pattern here is somewhat at odds with Norman and O'Reilly's (2003) model (simulation 3), and because the contribution and failures of pattern separation and pattern completion mechanisms are not well understood across true and false memories sharing large amounts of gist.

Our results for greater involvement of visual regions as gist-based false recognition increases is consistent with the idea that people commit gist-based memory errors in this task due to mistakenly retrieving perceptual information (e.g., Mitchell & Johnson, 2009; Schacter, et al., in press; Schacter & Slotnick, 2004). For false memories, retrieving perceptual information is erroneous, leading individuals to falsely endorse novel items as familiar, based on their subjective experience (Johnson, et al., 1993). Interestingly, distinct visual regions are implicated for false alarms to new exemplars from large sets of encoded items. Specifically, activity in regions of the fusiform gyrus and calcarine cortex linearly increase as a function of increasing encoded set size. While prior work showed that early visual regions tend to be engaged by true more than false memories but respond to both types of memories to some degree (Slotnick & Schacter, 2004), our results suggest that these regions can be modulated by the strength of the gist component. Notably, these visual regions responded to the amount of gist information for both true and false recognition. This finding suggests that visual processes can benefit

recognition by individuating small set exemplars but can also impair memory, perhaps by accentuating the prototypical visual features (e.g., the overall shape of a glove) common to novel and studied exemplars from large sets. The perceptual processes engaged could reflect a response to specific features viewed previously (e.g., the straight-back of a studied chair) or the strength of a pictorial representation of a prototypical, but unstudied, member of the relevant category. The potential importance of prototypical features is consistent with Koutstaal et al. (2003), who observed that semantic knowledge contributes to gist-based memory; in the present study, semantic knowledge of typical shape and perceptual properties could account for false memories. The potential importance of global shape information, likely to be shared across exemplars in a set, is also consistent with some work in perception (Sampanes, Tseng, & Bridgeman, 2008). Future research is needed to better distinguish the component visual processes implicated in gist-based memory, particularly to address the question of whether the visual response is to specific features vs. prototypes and, importantly, whether the same vs. different visual processes engage the overlapping neural regions for true and false memory in this task.

In contrast to previous work (e.g., Dennis, et al., 2008; Dennis, et al., 2007; Garoff-Eaton, et al., 2007; Kim & Cabeza, 2007), temporal activations and the left inferior frontal activity that purportedly reflect semantic processing do not emerge in the present study as regions that respond as the amount of gist increases across true and false recognition. While it is possible that this divergence from prior literature reflects the fact that semantic processes per se do not contribute to false memories in a graded fashion (note that semantic processes could also engage perceptual processes, as discussed

above), other explanations may account for this pattern. The engagement of temporal and inferior frontal regions in previous studies could reflect specific processes evoked by associative memories that have been implicated in DRM paradigms, rather than gist memory in the present paradigm. It is also possible that our use of pictures of nameable objects that tended to share both rich perceptual and conceptual information across exemplars evoked distinct processes than previous studies of related false recognition that used perceptually similar abstract shapes (e.g., Garoff-Eaton, et al., 2006; Slotnick & Schacter, 2004) or semantically related words (Dennis, et al., 2008; Dennis, et al., 2007; Garoff-Eaton, et al., 2007; Kim & Cabeza, 2007; Schacter, et al., 1997; Schacter, et al., 1996). We also implicate additional regions in false recognition that have not been emphasized in prior studies, with inferior parietal and middle and inferior prefrontal activity possibly tracking the amount of recollected information (Wagner, et al., 2005) and the engagement of monitoring processes (e.g., was this perceptual feature actually perceived, or was it invoked by studying other exemplars?) during the memory search (Schacter & Slotnick, 2004). Further work is needed to directly compare the activity evoked in this study with other false memory paradigms.

While the present study investigated the veridical and erroneous memory processes during the retrieval stage, it would also be of interest to consider the processes during encoding that lead to the formation of true and false memories, as well as those that contribute to the formation of gist representations. The majority of previous studies (e.g., Kim & Cabeza, 2007; Okado & Stark, 2005; Dennis et al., 2007; Dennis et al., 2008; Garoff-Eaton et al., 2007; Slotnick & Schacter, 2004; Kensinger & Schacter, 2005, Kensinger & Schacter, 2006) investigated the stages of memory separately, but the joint

investigation of encoding and retrieval would allow for investigation into the interplay of processes across these stages. For example, it is possible that similar perceptual processes are invoked during encoding and retrieval, which would allow for a direct test of the sensory reactivation hypothesis such that robust engagement of sensory regions during encoding is mirrored by reactivation of the same regions at recognition. However, it is also possible that robust activation of later perceptual regions during encoding could support the formation of false memories due to shared higher-level features across many exemplars in a category.

In conclusion, our results converge with prior work in that false memories engage many of the same regions as true memory. However, we also find that perceptual and constructive, or binding, processes contribute as the degree of relatedness increases, thereby providing initial insights into the processes that are involved in the building of false memories that are based on the encoding and retrieval of gist information and further advancing our understanding of how erroneous memories can arise from otherwise adaptive cognitive processes.

Acknowledgments

The authors gratefully acknowledge support from the National Institutes of Health, grants NIMH R01 MH60941 (to DLS) and NIA F32 AG026920 (to AHG). Portions of this research were conducted when A.H.G. was a fellow of the American Federation for Aging Research. The Athinoula A. Martinos Center for Biomedical Imaging is supported by the National Center for Research Resources (grant P41 RR14075) and by the MIND Institute. We thank Elizabeth Kensinger and Rachel Garoff Eaton for helpful discussions, and Donna Rose Addis for generously sharing her expertise and insights. Correspondence concerning this article should be addressed to: Angela H. Gutchess, Department of Psychology, Brandeis University, MS 062 P.O. Box 549110, Waltham, MA 02454. E-mail: gutchess@brandeis.edu.

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Table 1

This table summarizes the behavioral data (means and standard deviations) for hit and false alarm rates for each set size.

	<i>Zero</i>	<i>Small</i>	<i>Medium</i>	<i>Large</i>
Hits	N/A	.60 (.14)	.63 (.15)	.63 (.12)
False Alarms	.04 (.07)	.19 (.09)	.24 (.13)	.30 (.10)

Table 2

The table lists regions modulating hit or false alarm activity that surpass a voxel threshold of $p > .01$ and a cluster extent threshold > 44 to achieve an overall correction of $p < .05$. The top peak of each cluster is listed, and an asterix (*) denotes regions that also emerge in the random effects analysis of large vs. small set sizes.

Region	BA	MNI coordinates of Activation Peak (x, y, z)			# voxels	t value
A. False alarms: positive modulations (Lrg > Med > Small)						
* R fusiform	37	36	-38	-26	111	6.03
* R hippocampus	N/A	38	-10	-18	73	4.34
* L lingual/calcarine gyrus	17	2	-64	10	77	4.13
* R calcarine	17	16	-70	12	134	3.70
B. False alarms: negative modulations (Small > Med > Lrg)						
* R precentral	4	34	-24	58	97	4.80
* R caudate	25	14	24	0	113	4.04
* L superior parietal	7	-26	-48	58	53	4.03
C. Hits: positive modulations (Lrg > Med > Small)						
* R angular gyrus	39/40	58	-56	30	198	4.95
* L supramarginal gyrus	40/39	-60	-54	30	161	4.58
*L middle temporal/occipital	37/19	-54	-76	12	80	3.62
L inferior parietal	40/39	-48	-58	50	54	3.33
D. Hits: negative modulations (Small > Med > Lrg)						
*R inferior/middle occipital	19/18	38	-90	-2	333	5.39
*R middle occipital	19	32	-76	32	156	5.09

*L middle occipital	18	-30	-92	10	134	4.66
*R fusiform	37	38	-60	-14	205	4.27
*L putamen	N/A	-16	12	0	58	5.07
*L putamen	N/A	-28	-12	12	62	4.17
*L putamen	N/A	-24	14	12	53	4.12
*R cerebellum	37	36	-52	-24	50	4.44
*N/A	N/A	-18	40	14	49	4.37
*Vermis	N/A	0	-42	-16	61	3.86
*L midcingulate/ paracentral	4	-14	-32	52	57	3.82
N/A	47	28	38	4	68	3.27

Table 3. Regions showing different patterns of modulation across false alarms (FA) and hits. An overall correction of $p < .05$ is achieved using a voxel extent threshold of $p < .01$ and a cluster extent threshold of 44 voxels. The mean beta indicates the direction of the effect for hits and false alarms. * indicates whether the positive or negative mean beta for hits or FA differs significantly from 0 at a threshold of $p < .01$.

Region	BA	MNI coordinates of Activation Peak (x, y, z)			# voxels	t value	<u>Mean beta</u>	
		Hits	FA					
A. False Alarms > Hits								
R fusiform	37	34	-38	-26	1044	5.51	-.81	1.67*
R inferior occipital	19	44	-74	-12		5.34	-1.25*	1.57*
R cerebellum		34	-52	-24		5.30	-1.96*	.55
R fusiform/ parahippocampal gyrus	20	38	-16	-24	87	3.92	-1.22*	.92*
R hippocampus	N/A	42	-18	-16		3.26	-.78*	.53
L fusiform	19	-34	-70	-16	45	3.33	-.98	.51
L middle occipital	18	-28	-92	8	70	3.67	-1.86*	.83
“	“	-28	-86	2		3.10	-.59	.71
R mid-cingulate	23	10	-10	32	87	4.44	-.77*	.59
Midline	N/A	-4	-20	-8	48	4.06	-.62	.69*
Ventricle	N/A	-14	-34	26	108	6.69	-.56	.68*
white matter	N/A	-24	-28	24		3.58	-.51	.47
B. Hits > False alarms								
L sup temporal pole	38	-44	20	-12	56	5.07	.77	-1.12*
L inferior orbitofrontal	47	-34	22	-12		3.21	.61	-.82
L superior frontal	10	-16	60	20	47	4.55	.32	-.59
R precentral	4	34	-24	56	63	4.28	.57	-.86*

R superior temporal	22	64	-58	24	76	4.18	.91	-1.14*
R angular	40/39	64	-54	34		3.41	.84	-.72
L middle occipital	37	-44	-66	6	69	4.18	.97	-.96*
L middle temporal	37/19	-54	-72	14		3.18	1.75*	-1.11
R middle temporal	39	46	-66	20	64	4.06	.76*	-.61
“	37	52	-68	14		3.00	.91	-.49

Figure captions

Figure 1. Example stimuli are displayed for a medium set size. Participants encoded eight exemplars (outlined in yellow). At the time of recognition, they were tested on four of the previously presented exemplars (middle row, outlined in yellow and green) as well as four new lure exemplars (bottom row, outlined in green). Four old and four new exemplars were tested at recognition for all set sizes, although the number of encoded exemplars ranged from four (i.e., small sets) to fourteen (i.e., large sets).

Figure 2A. Overlap between true and false recognition (compared to novel items) occurs in a variety of regions. The selected slices (from left to right) display activations in left middle occipital (peak = -20, -92, 10), bilateral inferior parietal (right peak = 28, -50, 48; left peak = -28, -46, 48), right hippocampal (26, -26, -10), and bilateral inferior frontal (right peak = 42, 30, 20; left peak = -42, 24, 30) regions.

Figure 2B. Differences between true and false recognition (collapsed across set size) occur in predominantly sensory regions for the comparison of hits – false alarms and in predominantly frontal control regions for the comparison of false alarms – hits (bottom row). Activations for the comparison of true minus false recognition (displayed on the top row) include right middle occipital (peak = 32, -80, 26), left parahippocampal (-26, -40, -6), left middle temporal (-50, -10, -8) and left posterior parietal (peak = 4, -20, 46) cortex. Activations for the false alarms minus hits comparison (displayed on the bottom row) include right anterior cingulate (peak = 16, 20, 34), two regions of right middle frontal gyrus (ventral peak = 30, 40, -4; dorsal peak = 36, 52, 18).

Figure 3. Parametric modulations across set sizes. For false memories (left panel), fusiform (peak: 36, -38, -26) and calcarine (16, -70, 12) gyri activations reflect the role of visual regions in perceiving and recollecting prototypical features, and hippocampal (38, -10, -18) activations reflect the constructive nature of memory processes. These regions are more engaged for stronger gist representations. For true memories (right panel), the visual regions (fusiform [38, -60, -14] and left middle occipital [-30, -92, 10] gyri) are more engaged for more distinct items, reflecting a response to the visual properties of individual items, whereas angular gyrus (58, -56, 30) activations increase with set size, suggesting greater abstraction of conceptual and multimodal information as gist increases.

Figure 1



Figure 2

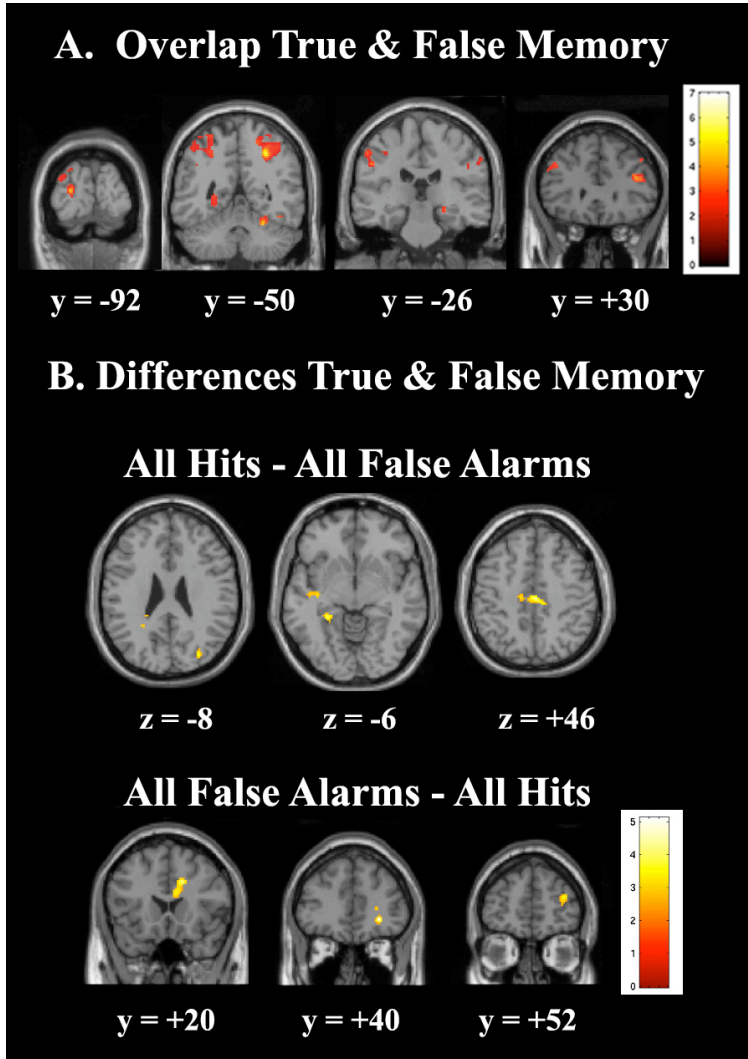
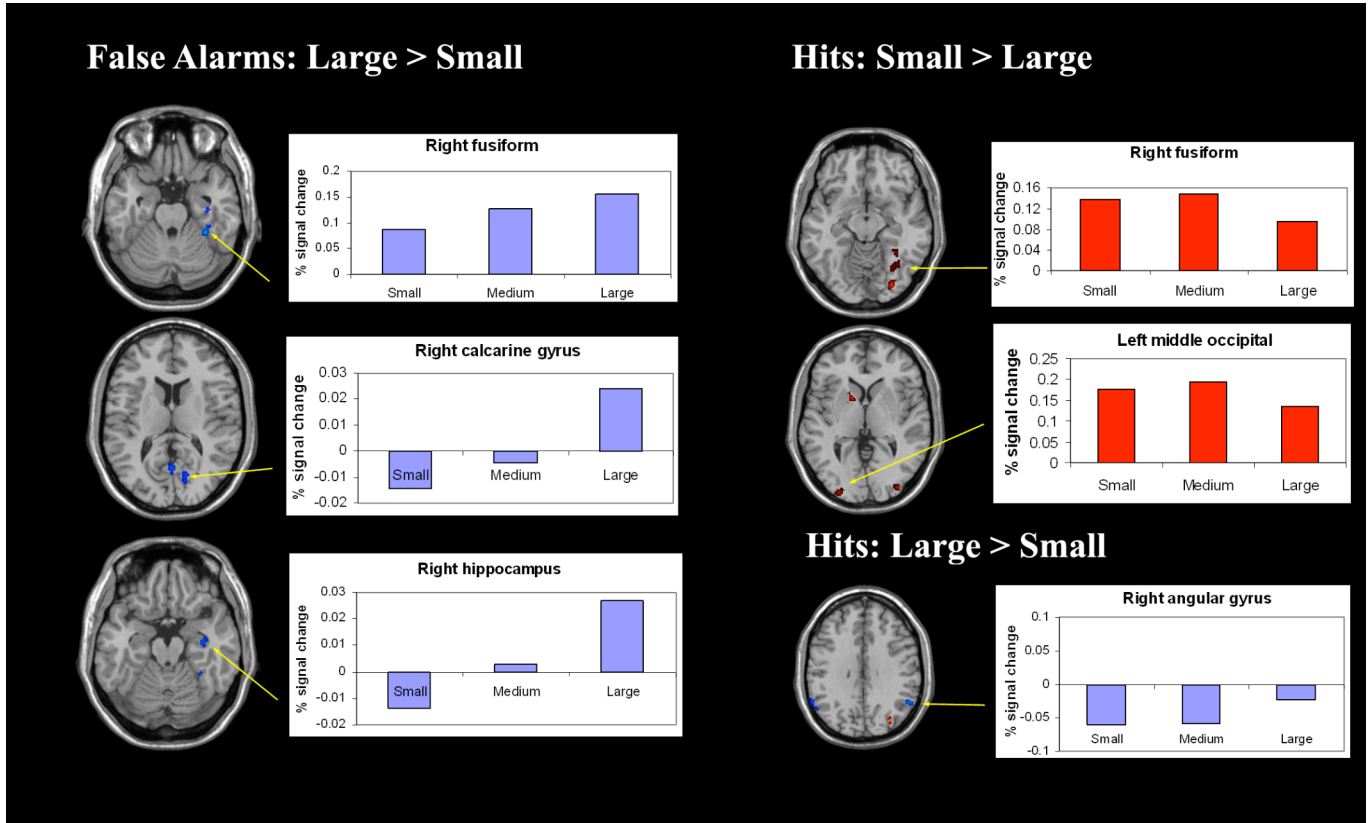


Figure 3



Supplementary Table 1. Conjunction of Hits minus Novel and False Alarms minus Novel. Both contrasts were tested with a voxel threshold of $p < .035$ for a conjoined $p = .001$. An overall correction of $p < .05$ is achieved using a cluster extent threshold > 44 .

Region	BA	MNI coordinates			# voxels	t value
		of Activation				
		Peak (x, y, z)				
Left middle frontal	6	-26	10	44	61	6.99
Left superior frontal	8	-20	18	48		2.96
Right inferior parietal	7	28	-50	48	1474	5.48
Right angular gyrus	7	36	-60	44		4.53
Right precuneus	7	12	-72	52		3.69
Right cerebellum	N/A	26	-52	-24	133	5.35
Right cerebellum	N/A	32	-44	-22		4.27
Right fusiform	37	44	-52	-16		3.67
Left cerebellum	N/A	-22	-32	-32	68	4.85
Left cerebellum	N/A	-20	-48	-24		2.90
Left cerebellum	N/A	-30	-40	-30		2.75
Right cerebellum	N/A	24	-38	-20	59	4.72
Right hippocampus	N/A	26	-26	-10		3.24
Left middle occipital	18	-20	-92	10	111	4.47
Right precentral	6	54	10	44	316	4.17
Right postcentral	6	58	2	34		3.69
Right inferior frontal	48	42	4	22		3.50
Right suppl motor/medial prefrontal	8/32	8	26	48	183	4.15
Right suppl motor	6	14	0	54		3.91

Left mid-cingulate	32	-8	14	42		3.58
Left inferior frontal	48	-42	24	30	77	4.12
Left inferior frontal	44	-54	22	32		3.32
Right inferior frontal	48	42	30	20	763	4.10
Right middle frontal	46	42	48	28		4.04
Right inferior frontal	48	34	32	26		3.98
Right precentral	6	38	-6	50	143	4.00
Right precentral	6	30	-10	48		2.57
Right precentral	6	42	6	52		2.28
N/A	N/A	-14	-12	34	47	3.99
N/A	N/A	-4	0	6	99	3.99
N/A	N/A	4	-2	6		3.78
Left pallidum	N/A	-12	4	6		3.54
Right supramarginal	1	64	-22	38	108	3.82
Right supramarginal	48	64	-20	28		3.44
Right supramarginal	40	64	-30	42		3.12
Left supramarginal	2	-50	-26	36	215	3.66
Left inferior parietal	3	-56	-20	46		3.36
Left inferior parietal	40	-28	-46	48	770	3.53
Left inferior parietal	40	-44	-42	38		3.40
N/A	N/A	-26	-56	32		3.35
Left middle frontal	44	-42	12	40	144	3.53
Left precentral	6	-42	0	40		3.34

Left middle frontal	44	-50	10	36		2.81
Left cerebellum	N/A	10	-56	-22	126	3.38
Vermis	N/A	2	-62	-20		3.35
Right cerebellum	N/A	12	-70	-18		2.82
Right middle frontal	44	42	24	40	54	3.31
Right middle frontal	9	38	24	48		2.38
Right middle frontal	9	46	18	50		2.12
Left lingual	19	-24	-58	-10	116	3.31
Left precuneus	19	-24	-52	4		3.22
Left cerebellum	N/A	-14	-62	-20	50	3.22
Left cerebellum	N/A	-14	-64	-12		2.55
Left cuneus	18	-18	-76	36	54	3.19
Right pallidum	N/A	28	-8	-4	54	3.08
Right hippocampus	N/A	24	-8	-14		2.09
Right cerebellum	N/A	30	-62	-20	48	2.96
Right postcentral	48/3	50	-18	32	56	2.77
Right supramarginal	48	48	-30	28		2.17
Left precuneus	7	-14	-76	60	126	2.73
Left precuneus	7	-8	-68	58		2.57
Left precuneus	5	-14	-60	60		2.51
Left middle occipital	19	-28	-90	24	65	2.61
Left superior occipital	18	-20	-92	32		2.06

Supplementary Table 2. Random effects analyses of all hits vs. all false alarms. Activations are listed that surpass a voxel threshold of $p > .01$ and a cluster extent threshold > 44 to achieve an overall correction of $p < .05$.

Region	BA	MNI coordinates			# voxels	t value
		of Activation				
		Peak (x, y, z)				
A. All Hits – All False Alarms						
Left cerebellum	N/A	-16	-42	-26	64	5.13
Left mid-cingulate	23	4	-20	46	166	4.41
Left mid-cingulate	N/A	-10	-18	50		3.81
N/A	N/A	-16	-20	40		3.78
N/A	N/A	-26	-40	16	65	4.11
N/A	N/A	-26	-48	24		3.20
N/A	48	-22	-38	24		3.04
Left parahippocampal gyrus	37	-26	-40	-6	44	3.85
Right middle occipital	19	32	-80	26	44	3.62
Left middle temporal	22/48	-50	-10	-8	50	3.51
Left hippocampus	N/A	-36	-16	-8		3.33
Left superior temporal	48	-44	-16	-6		2.95
B. All False Alarms – All Hits						
R middle frontal (ventral)	10	30	40	-4	44	5.37
Right anterior cingulate	32	16	20	34	126	4.21
Right anterior cingulate	32	10	18	24		3.70
R middle frontal (dorsal)	46	36	52	18	85	3.81

R middle frontal (dorsal)	10	34	48	10		3.64
R middle frontal (dorsal)	47	28	42	6		3.03
N/A	48	40	-16	30	49	3.70
N/A	48	28	-12	34		2.94
N/A	48	46	-10	26		2.91