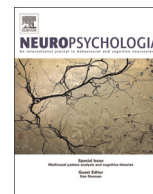




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Maintaining a cautious state of mind during a recognition test: A large-scale fMRI study

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ABSTRACT

Decision criterion is an important factor in recognition memory, determining the amount of evidence required to judge an item as previously encountered. For a typical recognition memory test involving the prior study of a set of items, a conservative criterion establishes a higher standard of evidence for recognition and designates fewer items as previously studied. In contrast, a liberal criterion establishes a lower standard of evidence and designates more items as previously studied. Therefore, the hit rate and the correct rejection rate on a recognition memory test can be affected by both the memory strength of the studied items and the criterion used to make that judgment. Yet most neuroimaging studies of the successful retrieval effect (a contrast between hits and correct rejections) fail to measure or consider decision criterion. The goal of the current fMRI study with ninety-five participants was to directly manipulate decision criteria on two tests of recognition memory by varying the likelihood of an item's prior occurrence. Our results indicate that regions of the lateral prefrontal and parietal cortex associated with successful retrieval are significantly more active when using conservative criteria than liberal criteria. Furthermore, our results reveal that activity in these regions associated with successful retrieval can be accounted for by individual differences in the conservativeness of the decision criterion above and beyond any differences in memory strength. These results expound on the role of cognitive control in recognition memory and the neural mechanisms that mediate this processing.

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1. Introduction

Neural investigations into memory processing have often compared the response associated with correctly recognizing old items (hits) relative to the response associated with correctly rejecting new items (correct rejections), commonly referred to as the successful retrieval effect. This contrast has a robust neural signature spanning large regions of the frontal and parietal cortex (see Wagner et al., 2005). The functional significance of this pattern of activity has been intensely investigated, and has been linked to different aspects of the retrieval process, including those specifically related to the memory content and other aspects such as the control of attention and retrieval orienting (see Miller and Dobbins, in press). In this study, we examined a specific decision

process in recognition memory that is often neglected in neuroimaging studies: the maintenance of a decision criterion used to evaluate memory retrieval across a period of time. In a large-scale fMRI study of 95 participants, we examined the sensitivity of successful retrieval brain activity when at times a conservative criterion was engaged and at other times a liberal criterion was engaged on two tests of recognition memory. The results from this study provide new insight into the role of decision criterion in memory retrieval mechanisms.

The outcome of the recognition judgment in a memory test is dependent on both the sensitivity in discriminating old items (targets) from new items (distractors) and the placement of a decision criterion (see Fig. 1A). In a Signal Detection Theory framework (Green and Swets, 1966; Macmillan and Creelman, 2005), both targets and distractors will be normally distributed along an axis of memory strength. Sensitivity, as measured by d' , is the distance between the mean of the target distribution from the mean of the distractor distribution. Decision criterion is the point

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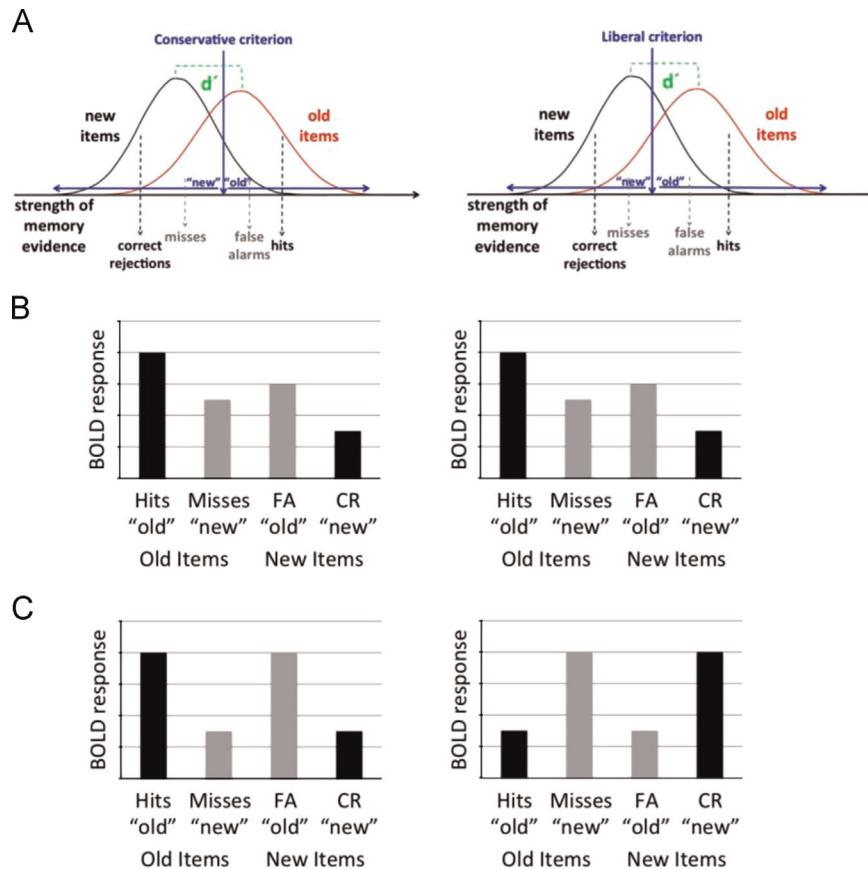


Fig. 1. (A) Model of Signal Detection Theory. (B) A memory strength account of the pattern of neural activity in the successful retrieval effect. (C) A response bias account of the pattern of neural activity in the successful retrieval effect.

along a continuum of memory strength that is used to determine whether there is enough evidence to consider an item as previously encountered. Test items with less memory strength than the decision criterion would be judged as new. The more conservative a criterion, the more evidence, i.e., memory strength, is needed to respond “old” on a recognition test. A decision criterion is typically set with respect to a certain strategy such that optimal decision-making may require individuals to flexibly adapt criterion in response to changing information (e.g., base rate probability) (Green and Swets, 1966; Macmillan and Creelman, 2005; Hockley, 2011; Aminoff et al., 2012).

Neuroimaging studies of recognition memory have typically focused on the contrast between successfully retrieved old items and successfully rejected new items (Wagner et al., 2005). This commonly became known as the “successful retrieval effect.” In this study, we will simply refer to this contrast in neural activity as the H > CR effect. Although the H > CR contrast has been used as the hallmark of studying successful memory retrieval, this contrast is rarely considered in behavioral studies of recognition memory. In a behavioral sense, the processes involved in this contrast would necessarily depend on both discrimination of targets from distractors (as measured by d') and the placement of the decision criterion. However, brain activity associated with H > CR can be related to discrimination only, criterion only, or some combination of both. Yet, criterion placement is often not considered in interpretations of neuroimaging studies of recognition memory. In fact, criterion measures are rarely manipulated or even reported in neuroimaging studies.

Many previous neuroimaging studies have claimed that the H > CR contrast represents the mnemonic contents of successfully retrieving a studied item, which would be affected by varying

levels of discrimination (Wheeler and Buckner, 2003; Kahn et al., 2004; Wagner et al., 2005; Vilberg and Rugg, 2008; Shimamura, 2011; Yu et al., 2012; Criss et al., 2013). For example, the neural activity of the H > CR contrast could arise from hits having greater memory strength than correct rejections, regardless of where the decision criterion lies along an axis of memory strength. However, recent studies have demonstrated that H > CR activity represents non-mnemonic cognitive processes, such as attention and decision-making related to the recognition judgment, rather than the memory content, per se, which may be affected by variations in criterion placement (Cabeza et al., 2008; Ciaramelli et al., 2008; O'Connor et al., 2010; Jaeger et al., 2013; Miller and Dobbins, in press). In this alternative, the brain signal of the H > CR contrast could arise simply from hits having memory strength that exceeds the decision criterion and thus yielding an “old” response, whereas correct rejections do not. Therefore, the H > CR contrast could be an effect of the cognitive processes used for a particular response type as determined by a decision criterion rather than differences in memory strength. Alternatively, the H > CR effect could be the result of both. Unfortunately, most neuroimaging studies utilizing an H > CR contrast report measures of memory strength but not measures of decision criteria. A memory test paradigm where the H > CR effect was measured across differing decision criteria could assess these various alternatives. The goal of this study is to directly examine the extent to which maintaining a particular decision criterion affects the brain activity associated with the contrast between hits and correct rejections.

A memory strength account of the H > CR effect, such as the accumulation of mnemonic evidence associated with hits but not with correct rejections (Kahn et al., 2004; Wagner et al., 2005; Wheeler and Buckner, 2003; Yonelinas et al., 2005), or the

buffering of retrieved information associated with hits but not with correct rejections (Vilberg and Rugg, 2008; Wagner et al., 2005), would claim that brain activity is tracking with the difference in memory strength between hits and correct rejections. When comparing the memory strength for all memory response types (hits, false alarms, misses, and correct rejections) the mean memory strength for hits should be the strongest (i.e., responded “old” to an old item); the mean memory strength for false alarms (i.e., responding “old” to a new item) should be greater than the mean memory strength for misses (i.e., responding “new” to an old item); and the mean strength of misses should be greater than the mean memory strength for correct rejections (i.e., responding “new” to a new item). Indeed, this pattern of brain activity (hits > false alarms > misses > correct rejections, Fig. 1B) has been reported previously providing evidence for a strength-based account (Kahn et al., 2004; Wheeler and Buckner, 2003). However, these studies did not manipulate the decision criterion. Thus, it is not clear to what extent the placement of the criterion may also be affecting the activity associated with hits minus correction rejections. According to a memory strength account, a change in decision criterion may slightly affect the signal strength of particular trial types, but the relative order of the trial types in signal strength will always be the same (i.e., hits > false alarms > misses > correct rejections) (Macmillan and Creelman, 2005).

Alternatively, the $H > CR$ effect could be due exclusively to biasing an “old” or a “new” response (i.e., the placement of a decision criterion) and have little to do with a difference in memory strength and item history (see Miller and Dobbins, *in press*) (Fig. 1C). For example, in a condition in which participants are being conservative with their decision criteria, and thus require a high level of memory evidence for judging an item as old, they are biasing a “new” response (Green and Swets, 1966; Macmillan and Creelman, 2005). In this case, brain activity in certain regions of the prefrontal and parietal cortex may be more active when responding “old” to old items (hits), i.e., away from the biased response, than when responding “new” to new items, i.e. toward the biased response. Although the outcome is the same (i.e. more brain activity to hits than to correct rejections) the driving force behind this differential activity is due to a movement away from a proclivity in response type, not to a difference in memory strength. Under this framework, when participants are being liberal with their decision criterion, the opposite effect in brain activity may occur with activity being greater when responding “new” (now responding away from the biased response) to new items (correct rejections) than when responding “old” (toward the biased response) to old items (hits). Historically, only hits greater than correct rejections ($H > CR$ effect) have been robust, rather than an effect of correct rejections greater than hits (but see also Jaeger et al., 2013, O’Connor et al., 2010). This may be due to general conservativeness of participants in a memory experiment being conducted within an MRI scanner (Gutchess and Park, 2006), though criterion measures are rarely reported.

If response bias were driving the $H > CR$ effect, then this would indicate that the brain activity reflects decision processing rather than memory content. This view is supported by a recent neuroimaging study by Jaeger et al. (2013) that examined the relationship between expectancy violations and memory evidence using a trial-by-trial cue validity paradigm. In this study, an explicit memory cueing paradigm was used wherein participants were first shown a cue on each trial (Likely New or Likely Old) and then shown a test item (target or distractor). Cues were valid 80% of the time. Similar to spatial cuing on a visual target detection paradigm, the cue in this case (e.g., Likely New) sets up the expectation that the next trial will be of a certain type (e.g., a new item), biasing the response of the participant. Critically, in support of the bias account, the large portions of the prefrontal cortex and

the parietal cortex tracked with the validity of the trials and not the successful memory of the trial (Jaeger et al., 2013). In other words, the activity in these regions was greater for hits than for correct rejections, but only when participants were expecting a new item as indicated by the cue (Likely New); however in the case where novelty was unexpected (Likely Old), there was greater activity for correct rejections than for hits. This is an effect predicted by a bias account but not by a strength-based account of the $H > CR$ effect. The authors framed this effect in terms of memory orienting similar to spatial orienting. For example, during a trial that is cued as “likely new,” an unexpectedly familiar test probe may reorient the individual’s attention and/or strategy to the probe. As Jaeger and colleagues noted, this activity represents executive processing needed to respond in the opposite direction of the participant’s expectations.

There are two critical differences between the predictions of the memory strength account and the predictions of the response bias account of the $H > CR$ effect (Fig. 1). One of these differences occurs when using a conservative decision criterion. According to the bias account, the activity associated with making an “old” response should be greater than the activity associated with making a “new” response, which is the same prediction made by a memory strength account for hits versus correct rejections. However, a strict bias account would also predict that responding “old” to new items (false alarms) should be just as active as hits, and that responding “new” to old items (misses) should not be any more active than correct rejections. The second difference between the predictions of the two accounts occurs when using a liberal decision criterion – meaning when the level for memory strength necessary to respond “old” is low, and thus more items are judged as “old”. In this case, participants are now biased to respond “old.” Therefore, if the $H > CR$ effect were only related to executive processing needed to make a response away from the expected or biased response, then it would predict brain activity would be greater for responding “new” than for responding “old” (the biased response). This would produce activity that is greater for correct rejections than for hits within a liberal condition, a pattern that could not be accounted for by a memory strength account.

The plausibility of a bias account of the $H > CR$ effect is supported by neuropsychological data as well. Neuropsychological evidence showed regions of the brain associated with the $H > CR$ effect (the prefrontal cortex and the parietal cortex) can be damaged with little effect on recognition memory, but can affect response biases, causing many patients to respond more liberally than matched controls (Ally et al., 2008; Ciaramelli et al., 2010; Dobbins et al., 2012; Simons et al., 2009).

However, an important distinction between the bias account described above (see Fig. 1C) and the results reported by Jaeger et al. (2013) is that their reported effects due to the expectancy of the test item interacted significantly with the memory strength of the old items. As they suggested, the effects of memory orienting depend on the ability of the participants to discriminate old items from new items (i.e., d'). The higher the d' the more an incongruent cue (e.g., Likely Old for a distractor) would affect their expectations. In contrast, the bias account (Fig. 1C) would not predict this correlation with d' or any interaction with the presentation history of the item. Any brain activation that is based purely on the biasing of a particular response should not be affected by whether or not the item was old. In addition, Jaeger and colleagues varied the expectation of the target, and thus the bias of the participant, on a trial-by-trial basis. It is unknown if a similar effect would be found if the bias, or criterion, was maintained across a block of trials.

The purpose of our study was to examine the nature of the $H > CR$ effect and to investigate whether maintaining a response

bias could account for the brain activity associated with memory retrieval. To this end, we used a memory test paradigm that directly manipulated decision criterion by employing a cue indicating the probability that the test item was viewed during the study session (either 70% or 30%). We used this paradigm in two study/test sessions with each participant, one with word stimuli and the other with face stimuli. We utilized three general techniques to examine the relationship between response bias and the $H > CR$ effect. First, we made the recognition tests difficult enough so that discriminating between old and new items would not be easy. A moderately low d' also ensures that most participants will affectively shift their criterion in response to the probability information of the cue (see Aminoff et al., 2012). Second, we utilized a blockwise paradigm that required participants to maintain a criterion across a block of trials. Third, we included a large number of participants ($N=95$). By contrast, the Jaeger et al. (2013) study had 18 subjects. This large sample gave us significant power to carefully examine the relationship between $H > CR$ brain activity and individual differences in d' and criterion placement. Our goal was to determine whether any of the $H > CR$ effect could be explained purely on the basis of a response bias.

In a full investigation of the behavioral results of this study, Aminoff et al. (2012) found that changes in target probability significantly affected participants' criteria. Participants used a liberal criterion for blocks of trials with a 70% target probability, and they used a conservative criterion for blocks of trials with a 30% target probability. The current study examined the brain mechanisms underlying these behavioral effects.

2. Materials and methods

2.1. Participants

One hundred and thirty three individuals were recruited to participate in this study. However, 38 of the participants were not used in the final analysis due to the following reasons: 8 did not pass MRI safety screening measures; 4 were claustrophobic; 5 had a technical error in data collection; 20 participants did not respond to more than 40 trials (over 10% of the trials) in either the Words or the Faces test (some of these participants reported falling asleep); and 1 did not follow instructions on the task.

Data were analyzed from 95 participants: ages 27–47 ($M=35$); 5 females; 12 left-handed. This study was part of a larger project investigating the individual variability in the structure and function of brain activity in combat-experienced Army officers – therefore the participants were either a combat-experienced Army officer ($N=68$) or an individual from the Santa Barbara community ($N=27$), a majority of who were graduate students or postdoctoral researchers ($n=21/27$). Informed written consent was obtained from each participant prior to the experimental sessions. All procedures were approved by the University of California, Santa Barbara Human Subjects Committee.

2.2. Stimuli

Three hundred and sixty faces and three hundred and sixty words were used as stimuli in this experiment. Faces of varying ethnicity were depicted in black and white photographs. Words were four to eight letters in length. Words in the target and distractor lists were matched for imageability (range 502–655) and frequency (range 1–382; Kucera–Francis written frequency count) as evaluated through the MRC Psycholinguistic Database (http://www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). Words were presented in Arial font with a font size of 40. Faces were 2.78 in. by 3.33 in. Stimuli were counter-balanced across participants and conditions.

2.3. Experimental procedure

Overall Procedure – To familiarize participants with the task prior to entering the MRI scanner, each individual participated in a short practice session. The practice included separate study sessions of 15 words and 15 faces, and separate test sessions of 30 words and 30 faces, respectively. Once comfortable with the task, participants were placed in the MRI scanner. Participants were reminded of the instructions and began the first study session (either faces or words), during which imaging data was not collected. Once completed, a high-resolution anatomical scan was acquired, which lasted nine minutes, during which a screen saver was presented on the screen. Participants were then reminded of the instructions for the test session and performed the recognition memory test (either the faces or words stimuli depending on the preceding study session) while functional MRI scans were collected. Immediately following the first study–test session, they participated in the second study–test session. The delay between the second study and test session was also around 9 min during which a diffusion tensor imaging scan was acquired. Each participant had separate study and test sessions for each set of stimuli (either faces or words) in which the order (first or second study/test) was counter-balanced across participants. In addition, participants filled out a number of questionnaires assessing factors that could account for individual differences in behavior (e.g., cognitive style, personality, and mental health), which is beyond the scope of the current paper. A full analysis of these individual differences can be found in Aminoff et al. (2012).

2.3.1. Study session (not scanned)

One hundred and eighty stimuli (either faces or words) were presented sequentially in the center of the screen on a white background. Words were presented in black font and faces were presented without a frame. Stimuli were shown for 1 s (words) or 1.5 s (faces) and both were separated by a 1 s inter-trial-interval. Participants were instructed to remember each stimulus for a later memory test. To facilitate deep encoding of the faces, which were harder to remember, participants judged whether each face was pleasant or unpleasant via a button press. The words were passively viewed.

2.3.2. Test session (scanned approximately 9 min after the study session)

Each test consisted of the 180 stimuli previously studied, and 180 novel stimuli. Test stimuli were divided into two conditions: a high probability condition in which the stimulus had a 70% probability of being old (i.e., studied previously), or a low probability condition, in which there was a 30% probability of being old. Probability condition was cued via font color for words (red or green) or a colored, rectangular frame around the picture for faces (red or green). The association between color and condition was counter-balanced. Stimuli were presented in the same size and location as the study session for 1.5 s with a 1 s inter-trial-interval.

Participants were instructed to determine whether the stimulus was previously studied, and to press the respective button for an old or new response. Instructions to the participants included explicit information about the color cue, which indicated the probability that the stimulus was old. Participants were told which color indicated a 70% likelihood that the stimulus was old, and thus highly likely that it was seen during the study session and which color indicated a 30% likelihood that the stimulus was old, and was therefore mostly likely a new stimulus not presented at study. Participants were told that these were accurate probabilities and there was no deception. However, the instructions did not explicitly tell the participant to incorporate the probability into the memory judgment. Stimuli were presented in a pseudo-block

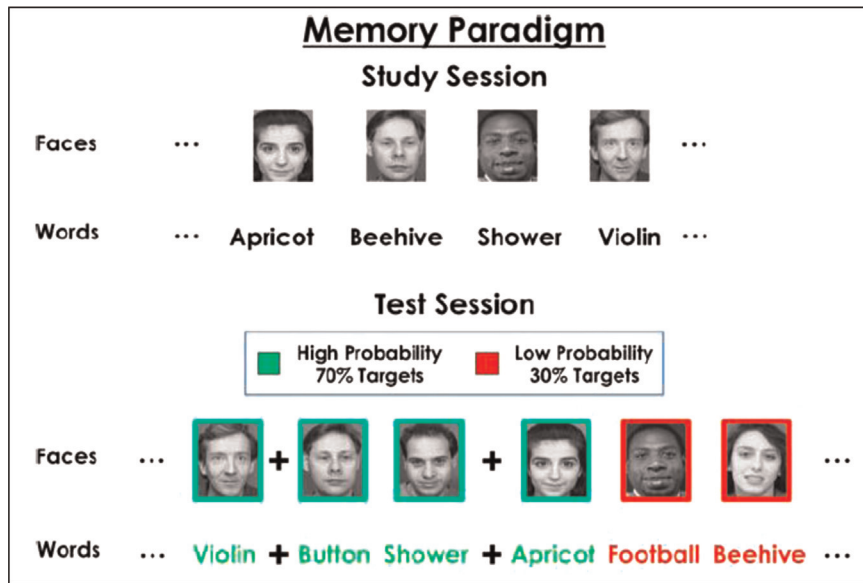


Fig. 2. Figure and portions of the caption are from Aminoff et al. (2012). Participants studied 180 of each stimulus set. Studied stimuli were presented in black font and without a colored frame (top). Stimuli at test ($N=360$) were presented with a color cue via the font or a frame around the picture that indicated the probability that the item had been presented during the study session (bottom). Intermixed with stimulus trials were fixation trials on which a “+” was presented, and there was no task performed on these trials. Trials were presented in blocks of six to nine trials of the same probability before the probability switched. The figure depicts only a portion of each block: only the last four trials (out of the six to nine possible) in the block for the high-probability condition (i.e., green) and the beginning two trials (out of the six to nine possible) in the block for the low-probability condition (i.e., red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

format: six to nine trials of the same probability were presented before the probability switched. Old and new stimuli were intermixed within these blocks. The probability indicated by the color cue did not necessarily correspond to the proportion of old and new stimuli within each mini-block (i.e., the 6–9 trials in a row) but rather to the distribution within the overall test session. 180 fixation trials were intermixed throughout the entire test session, and consisted of a black “+” symbol presented at the center of the screen for 2.5 s. Refer to Fig. 2 for an illustration of the trial sequence.

This procedure and parameters were used for the majority of our participants (participants 31–133), however the first 30 participants (only 20 of which were used in the final analysis) had a slight variation of the sequence of events (regarding the delay between study and test) and durations of study presentation. These procedural variations of the study session were done in an attempt (unsuccessfully) to equalize the memory strength of face and word stimuli. A one-way ANOVA determined there were no significant differences in criterion or d' due to procedural variations.

2.4. Memory behavioral data analysis

A full behavioral analysis of this dataset has been reported previously (Aminoff et al., 2012). For the purposes of this study, sensitivity and criterion were calculated for each participant separately for the low and high probability conditions in each test (separately for words and faces). Sensitivity (or accuracy) was calculated using the formula: $d' = z(\text{hits}) - z(\text{false alarms})$. Criterion was calculated using the formula: $c = -.5(z(\text{hits}) + z(\text{false alarms}))$. Trials that received either no response or multiple responses were not included in any of the analyses.

2.4.1. Reliance on the cue information

Subjective assessments of the degree to which participants relied on the probability cues in making their recognition judgments were obtained in post-experiment questionnaires using

both free responses and a rating scale describing whether the memory judgment at test typically relied on probability information or memory strength (scale was 1–10, with 1 being least and 10 being most). Two raters scored the free response questions with high consistency (words $r=.84$; faces $r=.84$). The free response ratings between the two raters were then averaged together. The final strategy score was an average of the averaged free response ratings and the ratings given by the participant in the questionnaire (consistency for words $r=.65$; for faces $r=.61$).

2.5. MRI data acquisition

Participants were scanned at the UCSB Brain Imaging Center using a 3 T Siemens TIM Trio with a standard 12-channel head coil. Cushions were placed around the head to minimize head motion. Participants held a MRI compatible response box with two buttons in their right hand and a squeeze ball for emergency purposes in their left hand. Stimuli for the experiment were projected on a screen behind the participant when lying in the scanner. A mirror mounted on the head coil reflected the images from the screen for the participant to view. Functional runs consisted of a T2* - weighted single shot gradient echo, echo-planar sequence sensitive to BOLD contrast (TR=2.5 s, TE=30 ms, FA=90°) with generalized autocalibrating partially parallel acquisitions (GRAPPA). Each volume consisted of 37 slices acquired parallel to the AC–PC plane, although the angle was slightly adjusted to optimize for frontal acquisition if necessary (interleaved, 3 mm thickness with .5 mm gap; 3 mm × 3 mm in-plane resolution). A total of 540 volumes were acquired for each test run (two total: faces and words), which consisted of 360 stimulus trials and 180 fixation trials. A high-resolution anatomical image was collected at the beginning of the scan session for each participant using an MPRAGE sequence (TR=2300; TE=2.98 ms; FA=9°; 160 slices; 1.10 mm thickness).

In addition to the functional and high-resolution anatomical scans, a diffusion-tensor, a resting state, and two additional functional scans (at the end of the session) were collected for a

separate experiment (Hermunstad et al., 2013; Hermunstad et al., 2014) and were not used in the present analysis.

2.6. fMRI data analysis

2.6.1. Preprocessing

Standard preprocessing was conducted using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>). Images were realigned to correct for minor head motion by registering all images to the first image of the series. Functional images were coregistered to the anatomical image. The anatomical image was normalized using combined segmentation and normalization to conform to the MNI-152 template. The parameters of this transformation were applied to the functional images, which were re-sampled to 2 mm isotropic voxels. Functional images were then smoothed using an isotropic Gaussian kernel (FWHM=8 mm).

2.6.2. General linear model and second level analysis

fMRI data were analyzed in an event-related paradigm using a canonical hemodynamic response function separately for the words and the faces test dataset. Each event was modeled within a 16 s time window. A high-pass filter using 128 s was implemented. The general linear model incorporated a robust weighted least squares (rWLS) algorithm (Diedrichsen and Shadmehr, 2005). The purpose of the rWLS algorithm was to weight each image by the noise in the image, so that images with a large amount of noise (e.g., due to movement) would be weighted less in the final model compared to an image with relatively less noise. The rWLS method used a covariance model that estimated the noise in each image of the un-smoothed data. Afterwards, those estimates were applied as weights in a second pass on the smoothed data. The model simultaneously estimated the noise covariates and temporal auto-correlation for later use as nuisance regressors. These covariates were then modeled within the design matrix.

Trials were presented in an event-related design that optimized the extraction of BOLD signal related to the contrasts of interest. The intermixed order of fixation, old, and new items, as well as a range in the length of the block (6–9 trials) enabled the use of an event-related analysis despite the probability cues being presented in mini-blocks. For both the faces and words tasks, a memory retrieval analysis modeled eight conditions: hits, misses, false alarms, and correct rejections, separately for the trials in the high probability condition and the low probability condition. A critical contrast examining differential beta estimates was constructed using hits versus correct rejections to examine the neural correlates of “successful retrieval” (separately for high and low probability conditions). These contrast maps were then passed to a second-level random effects analysis that consisted of testing the contrast against zero using a voxel-wise single-sample *t*-test. All group maps presented are whole-brain analyses using an FDR correction of $q=.05$. For visualization purposes, group *t* maps, corrected for multiple comparisons, were rendered onto 3D inflated brains using the CARET software (Van Essen et al., 2001).

2.6.3. Regional brain analyses

The goal of this analysis was to determine whether or not the

brain activity elicited by $H > CR$ could be attributed to a particular criterion placement or the strength of the memory. We functionally derived ROIs from the peak voxels of the $H > CR$ contrast (collapsed across probability conditions) directly from each task (see Table 2 for a listing of the peak voxels). These ROIs were defined irrespective of the participants' criteria or sensitivity since the neural activity associated with $H > CR$ could be affected by *c* alone, *d'* alone, or both. The peak voxels defined the center of each 10 mm spherical ROI. ROI data extraction was performed using the MarsBaR toolbox (<http://marsbar.sourceforge.net/index.html>; Brett et al., 2002) in which weighted parameter estimates (i.e. beta values) from the contrasts of interest were averaged across all voxels within each 10 mm spherical ROI and extracted. This resulted in a single beta value for each contrast for each ROI. These beta values were used for all subsequent analyses. The ROIs were corrected for multiple comparisons using a Bonferroni correction. These values were then submitted to a hierarchical multiple regression analyses for each ROI that first partialled out any variance that could be accounted for by individual differences in *d'* or reaction time. This was done to determine whether any portion of the variance in brain activity could be due exclusively to the criterion of the participant.

3. Results

Our main goal was to evaluate whether decision criterion modulated the $H > CR$ effect, thereby directly testing the response bias account against the memory strength account. A response bias account had three predictions: (1) a $H > CR$ effect would be found when using a conservative criterion, as in the low probability condition, but would not be found when using a liberal criterion, as in the high probability condition, since “new” is no longer the biased response - in fact, a bias account would predict in this condition that activity would be greater for correct rejections than for hits when using a liberal criterion; (2) individual differences in the extent of the criterion (i.e., the more conservative in the low probability condition and the more liberal in the high probability condition) would correlate with the $H > CR$ effect but not individual differences in *d'*, whereas the memory strength account would predict the opposite; and (3) the pattern of brain activity for hits, false alarms, misses, and correct rejections could be explained by the response type (i.e., “old” versus “new”) and not by item history (i.e., old items versus new items) (see Fig. 1C).

3.1. Behavioral results

Table 1 summarizes the behavioral performance in terms of criterion (*c*), sensitivity or accuracy (*d'*), reaction time, and reliance on the cue information. The main manipulation of target probability was successful: on average, participants applied a more liberal criterion for the high probability condition and a more conservative criterion in the low probability condition confirmed by a significant main effect of the probability condition on criterion across both tasks ($F(1,94)=243.24$, $p < 10^{-28}$, $MSE=.37$) in a

Table 1
Behavioral data for each memory test. Standard error in parentheses.

	Criterion (<i>c</i>)		Sensitivity (<i>d'</i>)		Reaction time		Reliance on cues
	Low prob.	High prob.	Low prob.	High prob.	Low prob.	High prob.	
Words	.30 (.04)	-.32 (.04)	.83 (.05)	.73 (.05)	1.03 (.01)	1.02 (.01)	2.42 (.09)
Faces	.28 (.04)	-.31 (.04)	.60 (.04)	.59 (.04)	1.10 (.01)	1.09 (.01)	2.73 (.10)

repeated measures ANOVA. Also, there was no significant main effect of task stimuli (words or faces) on criterion ($F(1,94)=0.03$, n.s., $MSE=.19$). A full behavioral analysis of this variation in the tendency to shift a decision criterion has been reported previously (Aminoff et al., 2012). The degree to which an individual shifted a criterion was used in a later fMRI analysis.

While sensitivity and criterion are theoretically independent (Green and Swets, 1966; Macmillan and Creelman, 2005), it is known that movements in criterion can be affected by varying levels of sensitivity (Hirshman, 1995; Macmillan and Creelman, 2005; Aminoff et al., 2012). For example, Aminoff et al. (2012) demonstrated that the more an individual remembers the studied items the less they need to shift a decision criterion in response to changes in target probability. The end result of that relationship may be that the magnitude of the criterion is less for those individuals with a higher d' . As reported in Aminoff et al. (2012), we found that the higher the individual d' the less liberal the individual criterion in the high target probability condition (words, $r=.29$, $p=.004$; faces, $r=.29$, $p=.005$), while the higher the individual d' the less conservative the individual criterion in the low target probability condition (words, $r=-.13$, n.s.; faces, $r=-.20$, $p=.056$). Further, while reaction time was not significantly correlated with criterion in any of the conditions, the participant's self-reported reliance on the probability cue was significantly correlated with criterion in the low target probability conditions using words (low probability, $r=.23$, $p=.022$; high probability, $r=-.065$, n.s.) and with criterion in the high target probability condition using faces (low probability, $r=.098$, n.s.; high probability, $r=-.21$, $p=.037$). Since any of these three factors may moderate the relationship between the magnitude of a criterion and $H > CR$ brain activity, we partialled out these relationships in the subsequent hierarchical regression analyses.

3.1.1. Task stimuli

Separate analyses were carried out across two independent memory tests (words and faces) within the same individuals. There was no main effect of stimuli with respect to the criterion used ($F(1,94)=0.03$, n.s., $MSE=.19$). However, despite our early attempts to equalize the sensitivity performance (as measured by d') between the task with word stimuli and the task with face stimuli, a repeated-measures ANOVA revealed a significant main effect of task ($F(1,94)=12.08$, $p < .001$, $MSE=.66$), with the word stimuli being better remembered than the face stimuli. After testing, several participants reported that the recognition test with the face stimuli was more difficult than the words. Reaction time was also different between the two test stimuli. As shown in Table 1, participants were significantly slower for faces than for words ($F(1,94)=70.21$, $p < 10^{-13}$, $MSE=.016$). Lastly, a self-reported measure of how much the participant relied on the cue information to make their recognition judgment showed a higher score for face stimuli than it did for word stimuli ($t(94)=-3.35$, $p < .001$), which may be attributed to the difficulty of the face task. However, even though differences exist across the two tasks, all fMRI comparisons are made within test, and only examined across the two tests for consistency.

3.2. fMRI results

3.2.1. Prediction 1: $H > CR$ would be evident in the low probability condition but not in the high probability condition

One of the primary aims of this study was to examine whether the brain activity associated with $H > CR$ could be modulated by changes in decision criterion. To this end, two contrasts of interest were analyzed: $H > CR$ in the high probability condition and $H > CR$ in the low probability condition. As illustrated in Fig. 1, the memory strength account and the response bias account make

different predictions about the resulting contrast of brain activity. If memory strength accounts for the difference in brain activity between hits and correct rejections, then greater activity should be observed for hits than for correct rejections across both probability conditions equally. However, if response bias accounts for the difference in neural activity, then greater activity should be observed for hits than for correct rejections in the low probability condition but not in the high probability condition. Furthermore, a bias account would predict that in the high probability condition brain activity should actually be greater for correct rejections than for hits because the bias is now to respond "old".

As shown in Fig. 3 and in Table 2, the $H > CR$ contrasts yielded significant differential activity throughout the lateral prefrontal cortex, the anterior insula, superior parietal cortex above the intraparietal sulcus, and regions of the lateral parietal cortex lying below the intraparietal sulcus, in both the left and right hemisphere. This effect was most evident in the low probability condition, in which old items were less likely to occur than new items and the criterion placement by the participants was conservative. These patterns of brain activity were almost identical between the recognition test with word stimuli and the recognition test with face stimuli, with the word stimuli producing slightly more significant activity than face stimuli. As shown in Fig. 4, the differences between the two probability conditions were directly analyzed by contrasting the $H > CR$ contrast in the low probability condition with the $H > CR$ contrast in the high probability condition. This analysis confirmed significantly more $H > CR$ activity in the low probability condition than in the high probability condition. Critically, there was no difference in sensitivity (d') between the two probability conditions. These results could not be predicted by a memory-strength based account of the $H > CR$ effect. Thus, the first prediction of the bias account was confirmed: greater BOLD signal was associated with hits than with correct rejections in the low probability condition, where a conservative criterion was used, than in the high probability condition, where a liberal criterion was used.

However, it should be noted that, when an "old" response was biased, as in the high probability condition, the pattern of differential BOLD signal in the contrast of hits versus correct rejections (Figs. 3 and 4) did not exhibit a change in the direction of activations (with CR being greater than H) as would be predicted by the bias account in Fig. 1. That is, when participants were biased to respond "old" (liberal) when the probability of a target was high, there were no significant activations related to correct rejections that was greater than activations related to hits, nor were that any differences found in this direction between the high probability and the low probability conditions. While this would not be predicted by a memory-strength account of the $H > CR$ effect, it would also not be predicted by the bias account. We next turn to an analysis of individual differences to investigate this point further.

Individuals varied the extent to which their decision criteria shifted in response to the change in probability information, which correlated with the magnitude of the criterion used in each condition. As reported by Aminoff et al. (2012), there was enormous individual variability in criterion shifting, with some individuals shifting their criterion to the extreme while others did not shift at all. To examine this, a tertiary split of the participants according to the degree to which they shifted their criterion between the two probability conditions was conducted, such that high shifters were compared to the low shifters. Behavioral analyses of the criterion difference between the two groups confirmed that the high shifters were significantly more conservative in the low probability condition than the low shifters (words; $t(62)=5.20$, $p < .001$: faces; $t(62)=4.20$, $p < .001$) and they were significantly more liberal in the high probability condition (words; $t(62)=-5.27$, $p < .001$: faces; $t(62)=-7.95$, $p < .001$). Aminoff et al. (2012) attributed this

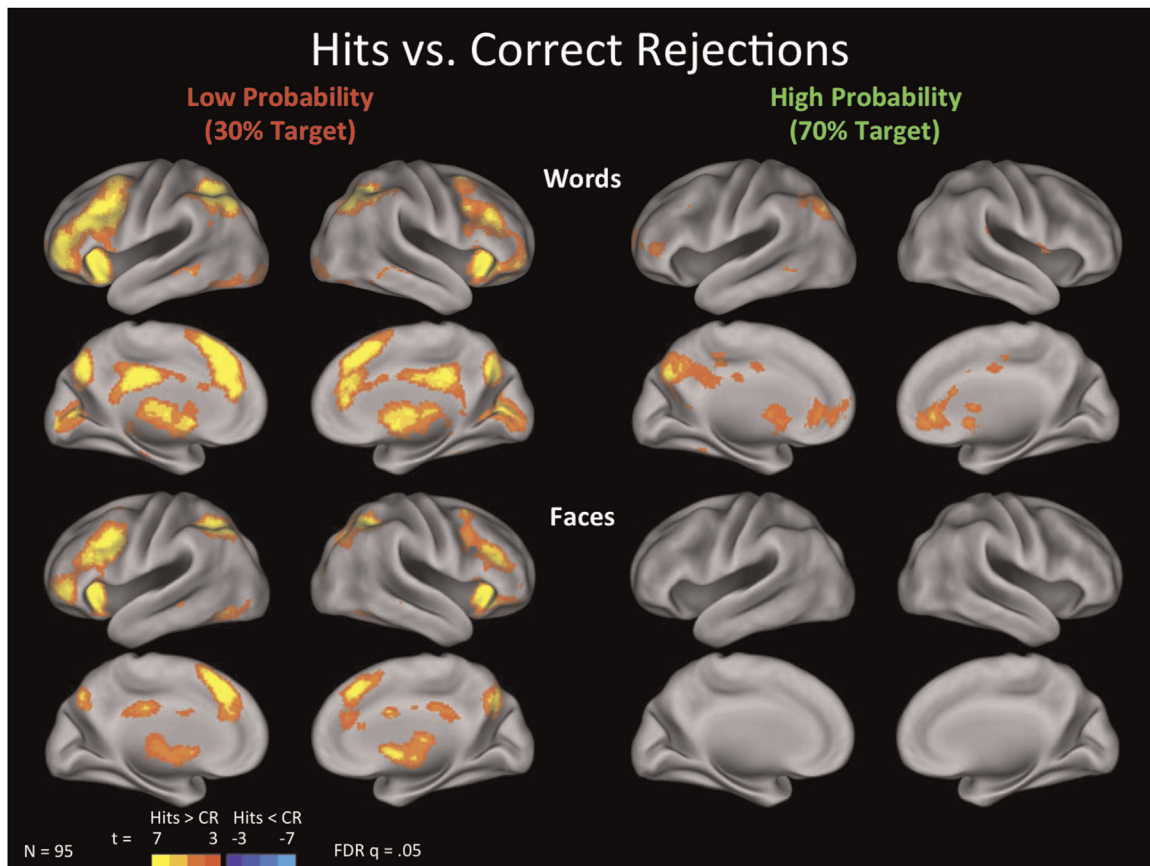


Fig. 3. Whole-brain statistical parametric group average maps for the words and faces datasets, FDR corrected, $q=.05$, with $N=95$, in both the low target probability condition when participants utilized a conservative criterion and the high target probability condition when participants utilized a liberal criterion.

Table 2

Peak activations for the $H > CR$ contrast (low target probability condition only). IPL=inferior parietal lobule; SPL=superior parietal lobule; Pc=precuneus; IFG=inferior frontal gyrus; MeFG=medial frontal gyrus; MFG=middle frontal gyrus; PoC=posterior cingulate; Ins=insula.

Brain regions		Words					Faces				
		BA	x	y	z	t-Value	BA	x	y	z	t-Value
L. Superior parietal	IPL	40	-38	-56	46	11.81	40	-32	-56	44	10.08
R. Superior parietal	IPL	40	44	-64	40	7.93	40	40	-54	52	8.69
	SPL/Pc	7	36	-68	48	10.26	19	34	-70	40	7.21
R. Medial parietal	Pc	7	14	-64	36	8.76	7	12	-66	40	6.62
L. Medial parietal	PoC	23	-2	-30	32	8.96	-	-	-	-	-
L. Ventral prefrontal	Ins-IFG	47	-34	20	-4	12.18	47	-30	22	-2	10.04
R. Ventral prefrontal	Ins-IFG	47	34	22	-4	10.29	47	32	24	-2	10.40
L. Dorsal prefrontal	MFG	9	-48	24	28	9.05	46	-46	28	22	7.06
	MFG	9	-50	14	34	8.05	9	-44	8	32	9.13
R. Dorsal prefrontal	MFG	46	50	32	24	7.14	46	44	32	18	6.76
L. Anterior prefrontal	IFG	10	-40	52	0	8.80	10	-44	46	-2	8.18
L. Medial prefrontal	MeFG	6	-6	32	38	10.72	9	-6	30	36	8.70
R. Thalamus	-	-	14	10	-4	9.33	-	10	10	0	8.19

variability between individuals to a willingness to make the extra effort necessary to shift a decision criterion while continuing to make a old/new judgment, a tendency of the individual that was consistent across both recognition tests ($r=.581$, $p<.001$). Therefore, individuals that were willing to shift their decision criterion in response to changes in the target probability may exhibit more extreme criterion than those that were not willing to shift, and that may be evident in their pattern of $H > CR$ activity as well. Fig. 5 shows the results of the tertiary split. Indeed, the top third criterion shifters showed significant $H > CR$ activity in the low probability condition but not in the high probability condition, but the bottom third criterion shifters showed little significant

activity in either condition. This suggests that when an individual shifts their criterion, more extreme criterion is applied (i.e., being more conservative), which elicited greater differential BOLD signal in $H > CR$ due to the more extreme response bias. These results support a response bias account of the $H > CR$ effect.

3.2.2. Prediction 2: individual differences in the extent of the criterion would correlate with the $H > CR$ effect but not individual differences in d'

Up until this point, analyses have been conducted by examining group averages. The next step was to examine the relationship between the individual performance measures and the BOLD signal

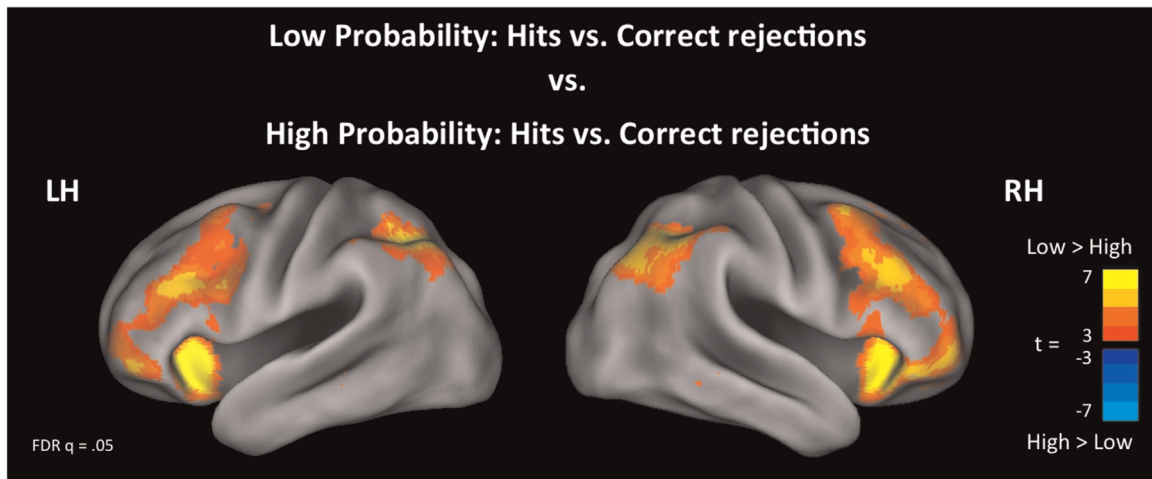


Fig. 4. Increased H > CR effect associated with using a more conservative criterion in the low probability condition for the word dataset (similar pattern of results for the faces dataset).

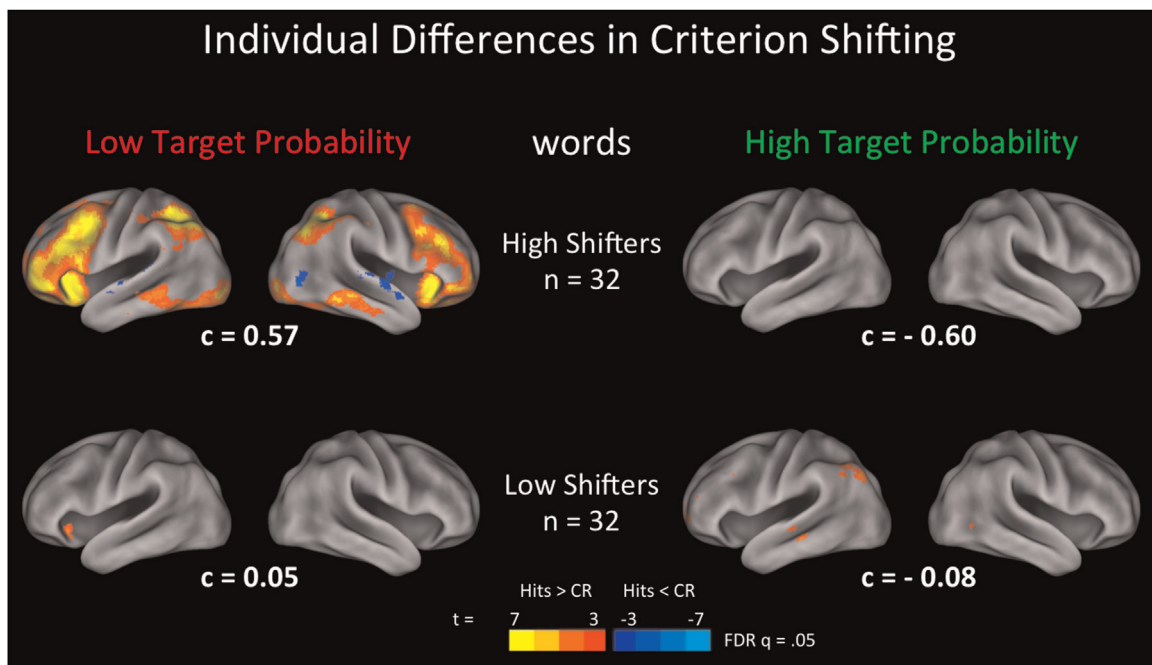


Fig. 5. Individuals that shifted their criteria the most between the low and high target probability conditions exhibited the most extreme criteria while individuals that shifted the least exhibited criteria close to neutral. Average criterion values for each group for each of the probability conditions are listed below the brain maps. Only those individuals who became quite conservative in the low probability condition had significant H > CR activity.

related to H > CR. The bias account would predict that the more conservative the criterion (i.e., positive criterion) the greater the H > CR activity, whereas the memory-strength account would predict that H > CR activity would only be modulated by memory sensitivity (d'), but not criterion. As shown in Table 3 the relationship between criterion placement and H > CR activity was strongly positive in 8 out of the 11 brain regions (direct effect) in the low target probability condition above and beyond any relationship with reaction time, attention to the probability cues, and d' . The thalamus was excluded from all ROI analyses, as was the left medial parietal cortex due to the significant activity being limited to the words dataset. The three brain regions that did not show this effect were the anterior and posterior portion of the right superior parietal lobe ROI and the right medial parietal lobe. The strongest relationship between H > CR activity and criterion were observed in the right and left ventrolateral prefrontal cortex and the left medial prefrontal cortex. These results support the response bias account and not a memory-strength account of the H > CR effect.

The bias account described in Fig. 1 would also predict a strongly negative relationship between criterion and the H > CR effect in the high probability condition. Meaning, in the high probability condition a more extreme liberal criterion would be used – which is represented by a more negative number as measured by c – and the more liberal criterion, the more biased is the “old” response, which would predict that correct rejections should elicit more BOLD signal than hits. However, instead we found a positive relationship between criterion and the H > CR effect. In the high probability condition, the more conservative the criterion the greater the H > CR activity, and this was significant above and beyond any differences in memory sensitivity in four of the ROIs (see Table 3). Even though group activity related to H > CR in the high probability condition was greatly attenuated in these ROIs in the whole-brain map, there was still evidence on an individual basis that more conservative criterion were related to stronger H > CR activity. This suggests that the H > CR effect might not be driven by response bias in general, but rather a response bias specifically related to the cautiousness of

responding “old” and not necessarily to the cautiousness of responding “new”. This is a critical qualification of the bias account that will be addressed in the discussion section.

The memory-strength account of the $H > CR$ effect would predict that the greater the sensitivity (d') to old items the greater the $H > CR$ activity should be in the individual. It should be noted that individual differences in d' (i.e., sensitivity) were significantly correlated with $H > CR$ activity in 5 out of the 11 brain regions in the low target probability condition, above and beyond any differences in criterion placement (see Table 3). This pattern would be predicted by memory strength accounts of the $H > CR$ effect. However, this relationship was only evident in the low target probability condition and not the high target probability condition, which would not be predicted by a memory content explanation. The interactions between criterion and sensitivity will be further explored using a trial type analysis (Section 3.2.3) in different regions associated with the $H > CR$ effect.

3.2.3. Prediction 3: the pattern of neural activity could be explained by the response type (i.e., “old” versus “new”) and not by item history (i.e., old items versus new items)

To further understand the effects of response bias versus memory strength (and possible interactions) on the $H > CR$ effect, we conducted a trial-type analysis for all possible memory trial types: hits, misses, false alarms, and correct rejections across the target probability conditions. Previously, we were examining the $H > CR$ effect, which only takes into account hits and correct rejections. However, if the BOLD signal in these regions tracks with response bias, then we should see BOLD signal increase for trials that were given an “old” response regardless of whether the item was presented before, i.e., for both hits and false alarms in the low probability condition, and BOLD signal increase for trials that were given a “new” response in the high probability condition. In contrast, if the increase in activity we observe were related to memory strength, we would expect the BOLD signal to track with item

history (i.e., activity greater for hits than for false alarms and activity greater for misses than for correct rejections) regardless of probability condition.

To examine this, we ran a $2 \times 2 \times 2$ repeated-measures ANOVA looking at the main effects and interaction of response type (“old” or “new”), item history (old items or new items), and criterion condition (low probability or high probability) on BOLD signal in each of the 11 $H > CR$ ROIs listed in Table 2 (excluding the thalamus and left medial parietal cortex). The results of the ANOVA are detailed in Table 4, which reports the effect sizes for each main effect and two-way interaction for all 11 ROIs. The three-way interactions were not significant for any ROI, and therefore are not reported. The main effect of response type was significant across all ROIs. The effects for response type were particularly robust ($> .25$) in the left superior parietal cortex, right superior posterior parietal cortex, left ventral prefrontal cortex, right ventral prefrontal cortex, left dorsal anterior and posterior prefrontal cortex, left anterior prefrontal cortex, and the left medial prefrontal cortex. In all 11 ROIs, there was a significant response type \times probability condition interaction such that responding “old” produced significantly greater activity than responding “new” in the low probability condition but not in the high probability condition (left superior parietal ROI, $F(1,94)=34.63$, $p < 10^{-8}$, $MSE=1.38$; left ventral prefrontal ROI, $F(1,94)=62.22$, $p < 10^{-11}$, $MSE=1.29$) (Fig. 6). In contrast, the main effect of item history (old versus new) was significant in only 4 of the 11 ROIs, including the left superior parietal cortex, the left dorsal anterior and posterior prefrontal cortex, and the left anterior prefrontal cortex. In all 4 of the significant ROIs, the effect sizes for item history were smaller than for response type. Item history did not significantly interact with probability condition in any of the ROIs. However, item history did significantly interact with response type in two of these four regions (left superior parietal, $F(1,94)=22.65$, $p < 10^{-5}$, $MSE=1.14$; left anterior prefrontal, $F(1,94)=8.73$, $p=.004$, $MSE=1.18$).

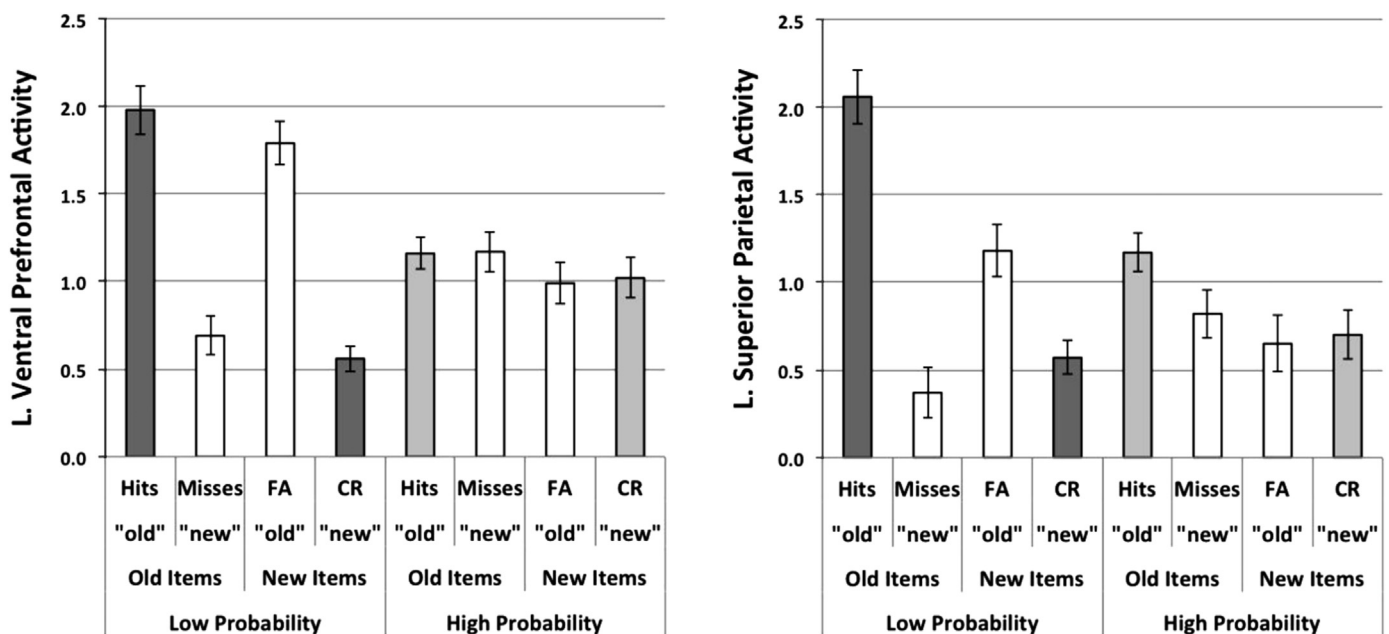


Fig. 6. Beta values for each trial type in two representative $H > CR$ ROIs. For a complete set of these graphs for each ROI please see Supplemental materials. The left panel is activity from the left ventral prefrontal cortex. In the conservative condition (low target probability), the typical “successful retrieval” contrast (hits versus correct rejections, both represented by the dark gray bars) was driven by the response type (“old” or “new”) and not by item history (present or not present at study). In the liberal condition (high target probability), there were no significant differences in activity between item types, which explains the lack of a $H > CR$ effect (represented by the light gray bars; see Table 4 for the effect sizes). The right panel illustrates $H > CR$ activity in the left superior parietal cortex. In this case, the $H > CR$ effect was driven by an interaction between response type and item history, but much more so in the conservative condition than in the liberal condition (see Table 4 for the effect sizes).

Table 3
Results of the hierarchical multiple linear regression of H > CR activity ROIs, criterion, and *d'*. **Bold** type indicates significant effects at $p < .05$ with a Bonferroni correction for multiple comparisons.

Criterion (c)	Low probability condition			High probability condition				
	Total effect	Mediating effects		Total effect	Mediating effects		Direct effect	
		RT&cue	<i>d'</i>		RT&cue	<i>d'</i>		
Brain regions								
L. Superior parietal	0.324	-0.009	-0.024	0.357	0.409	-0.008	0.021	0.396
R. Superior parietal (ant.)	0.164	-0.036	-0.022	0.222	0.229	-0.012	0.045	0.196
R. Superior parietal (post.)	0.112	-0.039	-0.017	0.168	0.223	-0.009	0.038	0.194
R. Medial parietal	-0.002	-0.016	-0.013	0.027	0.1	-0.005	0.022	0.083
L. Ventral prefrontal	0.474	0.002	-0.016	0.488	0.509	-0.02	-0.016	0.545
R. Ventral prefrontal	0.538	-0.015	-0.012	0.565	0.472	-0.013	-0.017	0.502
L. Dorsal prefrontal (ant.)	0.382	0.017	-0.014	0.379	0.257	-0.008	-0.034	0.299
L. Dorsal prefrontal (post.)	0.375	0	-0.003	0.378	0.266	-0.007	-0.016	0.289
R. Dorsal prefrontal	0.373	-0.015	-0.006	0.394	0.205	-0.016	-0.06	0.281
L. Anterior prefrontal	0.274	-0.019	-0.022	0.315	0.234	0.005	0.017	0.212
L. Medial prefrontal	0.476	0.013	-0.012	0.475	0.43	-0.011	-0.008	0.449
Sensitivity (<i>d'</i>)								
	Low probability condition			High probability condition				
	Total effect	Mediating effects		Total effect	Mediating effects		Direct effect	
		RT&cue	<i>c</i>		RT&cue	<i>c</i>		
Brain regions								
L. Superior parietal	0.357	-0.049	-0.021	0.427	0.173	-0.025	0.121	0.077
R. Superior parietal (ant.)	0.379	-0.001	-0.013	0.393	0.19	-0.028	0.059	0.159
R. Superior parietal (post.)	0.321	0.013	-0.01	0.318	0.166	-0.029	0.059	0.136
R. Medial parietal	0.236	0	-0.001	0.237	0.101	-0.001	0.025	0.077
L. Ventral prefrontal	0.203	-0.069	-0.028	0.3	0.107	-0.003	0.166	-0.056
R. Ventral prefrontal	0.121	-0.053	-0.033	0.207	0.088	-0.004	0.153	-0.061
L. Dorsal prefrontal (ant.)	0.147	-0.08	-0.022	0.249	-0.044	-0.014	0.091	-0.121
L. Dorsal prefrontal (post.)	0.156	-0.059	-0.022	0.237	0.005	-0.028	0.088	-0.055
R. Dorsal prefrontal	0.062	-0.022	-0.023	0.107	-0.153	-0.027	0.086	-0.212
L. Anterior prefrontal	0.334	-0.038	-0.018	0.39	0.078	-0.047	0.065	0.06
L. Medial prefrontal	0.121	-0.07	-0.028	0.219	0.084	-0.022	0.137	-0.031

Table 4
The effect of item history and response type of H > CR activity in 11 ROIs. Values indicate the effect sizes (η^2) across trial types. **Bold** type indicates significant effects at $p < .05$ with Bonferroni correction for multiple comparisons.

Brain regions	Probability condition	Response type	Item history	Prob. \times resp.	Prob. \times hist.	Resp. \times hist.
L. Superior parietal	0.111	0.415	0.225	0.269	0	0.194
R. Superior parietal (ant.)	0.027	0.108	0.032	0.297	0	0.161
R. Superior parietal (post.)	0.228	0.449	0.029	0.209	0.055	0.333
R. Medial parietal	0.028	0.23	0.043	0.139	0.014	0.072
L. Ventral prefrontal	0.113	0.413	0.073	0.398	0	0.001
R. Ventral prefrontal	0.011	0.272	0.031	0.42	0.008	0.001
L. Dorsal prefrontal (ant.)	0.137	0.226	0.148	0.243	0.01	0.026
L. Dorsal prefrontal (post.)	0.135	0.274	0.093	0.271	0.034	0.032
R. Dorsal prefrontal	0.006	0.131	0.004	0.355	0.027	0.058
L. Anterior prefrontal	0.044	0.276	0.086	0.147	0	0.085
L. Medial prefrontal	0.056	0.309	0.05	0.351	0.007	0.021

Fig. 6 illustrates these relationships across trial types in two representative ROIs, see [Supplementary material](#) for the remaining ROIs. In the left ventral prefrontal cortex, the H > CR effect is largely driven by the “old” response in the low probability condition but not in the high probability condition. In this region, item history has no apparent effect on H > CR activity. In the left superior parietal cortex, the relationships were more complex. In this case, the contrast between hits and correct rejections was being driven by a combination of “old” responses and previously presented items, again more so in the low probability condition than in the high probability condition. The effect of item history on activity in this region indicates that memory content may be contributing to H > CR activity in select brain regions in limited conditions (low target probability but not in a high target probability condition), suggesting that memory orienting (O'Connor et al., 2010; Jaeger et al., 2013) may be playing a role in H > CR

activity within these regions. However, the overall pattern of activity across trial types and across all regions of the H > CR effect strongly suggests that activity was mainly being driven by “old” responses in a conservative state of mind.

4. Discussion

The purpose of the present study was to determine the extent to which brain activity associated with H > CR could be accounted for by the maintenance of a response bias rather than memory strength as measured by sensitivity. This large-scale fMRI study (95 participants) took advantage of the wide variance between individuals in criterion placement and memory strength on two recognition tests that included shifts in target probability. Overall, we had three key findings: (1) a significant portion of the brain

activity associated with the $H > CR$ effect could be accounted for by individual differences in the conservativeness of the decision criterion above and beyond individual differences in memory strength; (2) many regions of the $H > CR$ effect showed a main effect of response type (greater activity for responding “old” than for responding “new”) rather than item history in the low probability condition only; and (3) individual differences in memory strength could also account for a significant portion of the brain activity in several parietal regions associated with $H > CR$, but again, only in the low probability condition. We suggest that these findings indicate that much of the brain activity during “successful retrieval” is actually due to the cautiousness, or conservativeness, of the recognition judgment.

The current study used a memory paradigm that varied the probability that the test item was previously studied in order to test whether the response bias or memory strength could account for the $H > CR$ effect. The paradigm was specifically designed to induce many trials in which the participant's criterion shifted in response to changes in target probability and to facilitate criterion shifting by making the discrimination between old and new items difficult, yielding relatively low d' values (see Aminoff et al., 2012, for a full account of the behavioral results). When the probability of a target shifts, the new probability is subsequently incorporated into the recognition judgment. This entails updating the decision rule used for determining whether an item was previously studied. Assuming the goal is to maximize correct responses, when the decision is uncertain and the probability of previous item occurrence is high, a rule should designate more items as old, and when the probability is low, a rule should designate more items as new (Green and Swets, 1966; Macmillan and Creelman, 2005; Aminoff et al., 2012).

4.1. $H > CR$ activity tracks with the cautiousness of the recognition response

The results of this study demonstrated that the activity associated with the $H > CR$ contrast could be accounted for, to a large extent, by the conservativeness of a decision criterion. Although the $H > CR$ effect is commonly associated with the memory strength of successfully recognized old items compared to correctly rejected new items, we found that these activations were more sensitive to changes in decision criterion than to changes in memory strength. For instance, we found that many regions of the prefrontal and parietal cortex that demonstrated significant $H > CR$ activity in the low probability condition, were not significantly active in the high probability condition of the same participants. Critically, this could not be accounted for by differences in d' between the two conditions. We also found in our multiple regression that individual differences in the conservativeness of the criterion was significantly related to increases in the activity of each region associated with the $H > CR$ effect. More importantly, the variance in brain activity accounted for by conservativeness was above and beyond the variance accounted for by any difference in reaction time, attention to the probability cues, or memory sensitivity. Our finding that the $H > CR$ effect depends, to a large extent, on the conservativeness of a decision criterion cannot be accounted for by a memory strength account of the $H > CR$ effect (as shown in Fig. 1). However, the finding also cannot be accounted for by a pure response bias account either, since the effect of response type occurred in the low probability condition (i.e., “old” responses eliciting greater activity than “new” responses) but not in the high probability condition (i.e., “new” responses eliciting greater activity than “old” responses).

If the $H > CR$ effect is based entirely on biasing a particular response in a probability condition, then one might expect more activity for “old” responses than “new” response in the low

probability condition, and more activity for “new” responses than “old” responses in the high probability condition. While we found that predicted pattern in the low probability condition, we did not find that predicted pattern in the high probability condition. In fact, we found that the average activity in the $H > CR$ effect across all participants was insensitive to either the response type or the item history in the liberal condition. Furthermore, in the analysis of individual differences, we found that the more conservative the participant was in the high probability condition, the more their pattern of brain activity resembled the pattern of activity in the low probability condition, i.e., more activity for “old” responses than for “new” responses. Therefore, we suggest that the effect observed was not necessarily due to working against any particular response bias, as suggested by a pure bias account (Fig. 1), but was due to participants being cautious to respond “old” on a recognition test.

Why would the $H > CR$ effect track with being cautious in only one direction - in making an “old” response, and not a “new” response? We predicted that in a condition with a low probability of a target participants would be cautious to respond “old” in order to avoid false alarms, but we also predicted that in a condition with a high probability of a target participants would be equally cautious to respond “new” in order to avoid misses. However, the pattern of brain activity that we observed suggests that the $H > CR$ effect only tracks with the cautiousness of the participants to avoid false alarms on a memory test. We suggest this is because the cognitive control engaged when being cautious about making an “old” response is different than that which is engaged when being cautious about making a “new” response. A liberal decision criterion allows the participants to be lenient or lax about responding “old,” - and therefore participants can respond “old” to any sense of oldness or familiarity in the test items. This requires less cognitive control since the participant just needs any sense of familiarity to make a decision that is in line with target probabilities. In contrast, a conservative criterion forces the participant to critically evaluate any evidence of familiarity since it is likely that the item is new. This is particularly difficult given that familiarity to previously encountered items is a potent and automatic response, and even new items will be normally distributed along some strength of familiarity axis, i.e., some new items will seem more familiar than others due to encounters and associations outside of the study context (Mandler, 1980; Yonelinas, 1997). Unlike the perceptual discrimination of targets and distractors, the recognition discrimination of targets and distractors must deal with varying levels of familiarity. To avoid a false alarm, one must resist the urge to respond to familiarity. To avoid a miss, one must simply go with the urge to respond to familiarity. This difference in the cognitive control of responding to familiarity, in particular, may be the underlying nature of the $H > CR$ effect.

If the underlying processes of the $H > CR$ effect were related to the cognitive control required when being cautious about making an old response, this would account for why the conservativeness of the criterion would track closely with the $H > CR$ effect regardless of the probability condition. As shown in Table 3, we observed that the conservativeness of the decision criterion accounted for the $H > CR$ effect above and beyond d' and other factors not only in the low probability condition but also in the high probability condition. Interestingly, averaged across all participants there were no BOLD differences found between hits and correct rejections (in either direction) in the high probability condition. As a group, the criterion was generally lax enough, such that cautiousness of an old response was not employed, yielding the $H > CR$ effect completely attenuated. Critically, however, some participants were still more conservative than others, and those participants showed an increased $H > CR$ effect in the same brain regions that were present in the low probability condition.

An explanation based on a cautious state of mind would converge with much of the decision-making literature showing that sustained cognitive control activates similar regions of the prefrontal cortex and dorsolateral regions of the parietal cortex (Bañich et al., 2000; Miller and Cohen, 2001; Gruber et al., 2002; Braver et al., 2003; Niendam et al., 2012). In other words, being cautious to respond “old” on a recognition test may be similar to the incongruent condition of the Stroop task, i.e., responding “red” to the word GREEN when that word is colored red. Braver (2012) describes this as a proactive control process that reflects sustained and anticipatory maintenance of goal-relevant information that is needed to optimize performance. Badre and Wagner (2007) suggested that these frontoparietal regions could operate on retrieved information to fit with decision criteria and response contingencies. Barredo et al. (2013) recently mapped out a pathway from the ventrolateral prefrontal cortex to the medial temporal lobe using a source-monitoring task that demonstrated how these prefrontal regions could control the sense of “oldness” that comes with episodic memory retrieval. However, the link between cautiousness to respond “old” on a recognition test and cognitive control mechanisms based on the brain regions that were activated must be qualified by the fact that we did not collect any direct measures of cognitive control. Hopefully, future studies can make this link more explicit.

4.2. Natural response tendency of the participant

It is possible that the effects we observed in this study were attenuated by the natural tendencies of our participants. For example, if our participants tended to be liberal, then placing them in a conservative condition in which they now have to be cautious to respond “old” may have been more effortful for them than it would be for participants that tended to be conservative. In other words, participants that are normally cautious in their recognition responses may not show the reported effects. Previous studies have reported that individuals seem to have a natural bias on recognition tests with neutral criterion conditions (e.g., 50/50 target ratio) that appears to be stable across a variety of tasks (Kantner and Lindsay, 2012). While we did not have a neutral condition in this study to measure participants’ natural tendencies, we did indeed find that, as reported in Aminoff et al. (2012), that participants tended to be slightly more liberal in the high probability condition ($C = -.32$ for the word stimuli and $C = -.31$ for the face stimuli) than conservative in the low probability condition ($C = +.30$ for the word stimuli and $C = +.28$ for the face stimuli). But that difference was quite small and may be due to some extreme liberal values in a small number of participants. In fact, an examination of the individuals within that study showed that they tended to skew more conservative than liberal for both recognition tests. Therefore, we believe these effects would be observed regardless of the natural tendencies of the participants, but to test this explicitly additional studies are needed.

Another stable tendency, however, that did have a noticeable effect on the results we report was the general tendency to shift a criterion between conditions (see Aminoff et al., 2012). Some participants shifted their criterion appropriately from one extreme to another, while other participants did not shift at all. Aminoff et al. (2012) explained this difference as a willingness to make the extra effort to adapt their decision criterion. The spread of decision criterion employed by participants who did not shift were equally conservative as they were liberal. However, we did find that if we split the participants into tertiary groups based on criterion shifting, participants with the lowest criterion shift scores did not show any attenuation of the $H > CR$ effect between the high or low probability conditions (see Fig. 5). We see this as further evidence that the $H > CR$ effect reflects the cautiousness of the recognition

response: regardless of the participants’ natural tendency to be liberal or conservative on a recognition test, these particular participants were not responding to changes in the target probability. Therefore, they were not being any more cautious to respond “old” in the low target probability condition than they were in the high target probability condition, and this is reflected in their measures of criterion (see Fig. 5). This analysis further demonstrated that the $H > CR$ effect was significantly affected by the willingness or ability of the individual to become cautious to respond “old”, beyond their natural tendency, on a recognition test.

Most neuroimaging studies of recognition memory do not attempt to manipulate criterion placement and often include experimental designs, such as a 50/50 target/distractor ratio, that should lead to a neutral bias. Yet these studies still report robust $H > CR$ activity in parietal and prefrontal regions (Wagner et al., 2005). However, it is difficult to know the actual criterion used by participants in these studies, despite the neutral designs, since criterion measures are rarely reported. It may be that participants are typically cautious to make “old” judgments even when the target probability is 50%, and they may be particularly cautious on a recognition test while having their brain scanned (Gutchess and Park, 2006). For example, in a Herron et al. (2004) study that varied target probability to examine the saliency of targets, the condition with a 50/50 target ratio actually produced more conservative responses ($Br = .40$) than the condition with a 25/75 target ratio ($Br = .49$). It is also not clear whether a criterion measure of zero is necessarily the absence of caution. For example, a measure of zero criterion may indicate that participants are as likely to avoid misses as they are to avoid false alarms, but is that still enough caution to produce a $H > CR$ effect? More systematic studies will be needed to explore these parameters and its effects on $H > CR$ activity.

4.3. Memory strength and the “successful retrieval” effect

With regard to a memory strength account of the $H > CR$ effect, several previous studies have shown $H > CR$ activity that is significantly modulated by the subjective memory experience (e.g., activity for false alarms is greater than misses) (Wheeler and Buckner, 2003; Kahn et al., 2004); recollection or familiarity (Henson et al., 1999; Wheeler and Buckner, 2004), the repetition of studied items (Guerin and Miller, 2011), and individual differences in confidence ratings (Yonelinas et al., 2005; Montaldi et al., 2006). Criss et al. (2013) recently showed separate regions of $H > CR$ activity, some that are correlated with individual differences in criterion (c) and not d' , and other regions with the opposite relationship. However, as Jaeger et al. (2013) demonstrated, the relationship with d' can be illusory. Other cognitive processes can become more engaged as the memory strength increases, including an unexpected familiarity response that increases with increased accuracy. We observed a similar effect such that there was a significant relationship between the $H > CR$ effect and individual differences in d' above and beyond c , but only in the conservative, low probability condition. If the $H > CR$ effect truly represents memory content as measured by d' , then one would expect that relationship to be significant above and beyond other cognitive factors such as criterion and to hold across criterion conditions. At the very least, any study that examines individual differences in brain activity needs to have a large enough sample size to carry out regression analyses that can account for possible interactions, individual differences and spurious correlations.

It should be noted that, given our participants’ relatively low discrimination between old and new items, that several studies using higher discrimination levels suggest that regions of the lateral parietal cortex more ventral to those reported here are sensitive to the amount of information recollected, including source

information related to recollection and strong familiarity responses (Vilberg and Rugg, 2008; Uncapher et al., 2010; Elman et al., 2013; Frithsen and Miller, 2014). Guerin and Miller (2011) manipulated the frequency of studied items (1, 2, 8, or 9 times) and did not find activity in any brain region that was modulated by the accumulated evidence of a frequency judgment (e.g., which of two studied items was presented more frequently?), but that a region of the angular gyrus was modulated linearly by the absolute frequency of the studied items in a frequency judgment. While $H > CR$ effects in more ventral portions of the angular gyrus and the supramarginal gyrus may be more directly linked to memory content and less susceptible to criterion effects, this needs to be tested more directly in the future. Indeed, we found that when we directly compared the low probability condition to the high probability condition, the activations extended more ventrally into the angular gyrus.

4.4. Previous studies of probability manipulation in recognition memory tests

Previous studies have manipulated the probability mixture of targets in order to observe the effect on activity associated with $H > CR$ (Herron et al., 2004; Vilberg and Rugg, 2009; O'Connor et al., 2010; Jaeger et al., 2013). A report by Herron et al. (2004) and a subsequent report by Vilberg and Rugg (2009) manipulated the ratio of old/new items (either 75/25% or 25/75%) on a recognition test. They reasoned that regions responsive to familiarity and recollection should not be sensitive to the saliency of targets through changes in the target ratios. Indeed, they found that many regions of the lateral parietal and prefrontal cortex showed an interaction between target ratio and “successful retrieval,” except for one region in the middle portion of the IPS that was not sensitive to target ratio, suggesting that it may indeed be sensitive to familiarity. However, our study showed that this same region in the IPS was sensitive to changes in target probability.

A critical difference between the Herron et al. (2004) and the Vilberg and Rugg (2009) studies and our study has to do with the behavioral effect of changing target probabilities. As we reported, changing the target probability significantly affected criterion (high old/new ratio $c = -.31$, low old/new ratio $c = +.28$ for words), whereas in the Vilberg and Rugg (2009) study the changes in target probability had no significant effect on response bias (high old/new ratio $Br = .47$, low old/new ratio $Br = -.36$). One difference is that participants in their study made a source judgment, while participants in our study made an item judgment. Alternatively, the lack of effect in the Vilberg and Rugg (2009) may also be due in part to the instructions they gave the participants. They specifically instructed the participants to respond to the test items on the basis of their memory for the item and to not make any guesses based on the apparent ratio of old/new items. Further, they did not explicitly cue the participants when changes occurred in the target ratios. Conscious awareness of target probability significantly affects the degree to which participants will shift their criterion (Estes and Maddox, 1995; Rhodes and Jacoby, 2007). Indeed, we found that the more participants were able to do this, the more $H > CR$ activity occurred in regions along the IPS. Even though Vilberg and Rugg (2009) did not find the middle portion of the IPS sensitive to differences in the target ratios, the overall conservativeness of the decision criterion could, nevertheless, have been driving the $H > CR$ activation if participants were equally conservative in both conditions regardless of the changes in target probability, as indicated by their behavioral results.

As discussed in the introduction, two other studies manipulated the probability mixture of targets, but in these cases did so on a trial-by-trial basis by cueing the participants prior to each test item as to whether the test item is likely old or likely new in order

to test the effect on $H > CR$ activity (O'Connor et al., 2010; Jaeger et al., 2013). The authors reasoned that $H > CR$ effects, particularly in lateral parietal cortex and prefrontal regions, reflect an orienting response similar to spatial orienting (Posner et al., 1980) and not a response due to processing the representation of mnemonic content. If a participant were expecting a new item on a test trial, then responding “old” to an old item would necessarily violate that expectation. They found that activity in the dorsal anterior angular gyrus, left lateral premotor, and anterior prefrontal cortex was greater for hits than correct rejections when the participants were expecting new items, but no difference between these conditions when they were expecting old items. Thus, a “hit” would represent a violation of an expected new item. Critical to their hypothesis, they also found the opposite pattern in separate regions, most notably in left anterior intraparietal sulcus and post-central gyrus, i.e., greater activity for correct rejections than for hits when expecting old items but not when expecting new items. Based on these results, the authors suggest that $H > CR$ activity during a recognition test is associated with participants orienting toward unexpected novelty or familiarity in the environment.

Both the memory orienting account (Jaeger et al., 2013) and a cautiousness to respond “old” account of the $H > CR$ effect would make the same prediction that higher BOLD signal would arise for hits than for correct rejections when using a conservative decision criterion (when test items are more likely to be new), but only the memory orienting account would predict higher BOLD signal for correct rejections than for hits when using a liberal decision criterion (when test items are more likely to be old). Another critical difference, though, between the two accounts is that the orienting account would predict a significant interaction with memory strength, and a cautiousness to respond “old” account would not. The memory orienting model depends on the ability to distinguish between old and new items. If it were difficult to distinguish between the two, then neither of the item types would be a violation of the expectancy that might be established by the probability cues. In fact, the Jaeger et al. (2013) study demonstrated that the expectancy violation response (in the likely new condition, i.e., unexpected familiarity) was significantly related to individual differences in d' . In our study, however, the $H > CR$ effect was quite robust in the likely new condition even though the overall d' was relatively low. We found that individual differences in the conservativeness of the criterion could account for variance in the $H > CR$ effect above and beyond any variance accounted for by differences in d' , supporting the response bias account. Furthermore, we found several regions of the prefrontal cortex that were sensitive to the response types within the conservative condition, but were not sensitive to the presentation history of the test items (Fig. 6). Thus, BOLD signal was similarly high for hits and false alarms, where the response was “old”, compared with the trials where the response was “new” (i.e., misses and correct rejections). Further, $H > CR$ activity in these prefrontal regions (except for the left anterior prefrontal cortex) were not significantly related to individual differences in d' . This would not be predicted by the memory orienting account. Although most of the parietal regions of the $H > CR$ effect interacted with memory strength in the low target probability condition, almost all of the prefrontal cortex regions did not. We suggest that all regions of the $H > CR$ effect are sensitive to caution to respond “old” on a recognition test that relies mostly on familiarity to make the discrimination, while the parietal regions of the $H > CR$ effect may also be sensitive to a memory orienting response that is dependent on the level of sensitivity.

4.5. Conclusion

Identifying a reliable neural marker of $H > CR$ activity that is unambiguously due to criterion versus one that is unambiguously

due to memory evidence could be enormously useful to recognition memory research. As Criss et al. (2013) recently demonstrated with the strength-based mirror effect, such neural markers could be used to adjudicate the source of several memory phenomena that currently cannot be resolved using behavioral measures alone. However, most studies examining the $H > CR$ effects do not take into account measures of criterion. As we have demonstrated in this study, large portions of the $H > CR$ effect may reflect a cautious approach to a recognition decision and not the successful output of episodic retrieval. This finding suggests that mechanisms associated decision criterion must be taken into account when exploring the psychological and neural mechanisms that mediate recognition memory. This study provides a foundation for examining the role of decision criterion in memory retrieval, which will aid in the exploration of memory retrieval, memory strategies, and optimal decision making.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2014.12.011>.

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