The Activation of the Caudate Is Associated with Correct Recollections in a Reward-Based Recollection Task

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Abstract: Although specific brain regions have been implicated in long-term memory processes, the brain function responsible for correctly recollecting information remains incompletely understood. This study used a remember–recollection–recognition task to explore brain activities specifically associated with correct recollection. Seventy-eight subjects were first asked to remember 40 items and recollect them in the scanner. Comparison of correctly recollected trials to incorrectly recollected trials (when participants mistakenly believed they had recollected information correctly) identified greater activation of the caudate bilaterally. The involvement of caudate activation appears important in recollecting information correctly. Potential explanations and implications are discussed. *Hum Brain Mapp* 37:3999–4005, 2016. © 2016 Wiley Periodicals, Inc.

Key words: recollection; caudate; memory; learning

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INTRODUCTION

The ability to retrieve correctly information from memory is important for human functioning [Karpicke and Roediger, 2008; King et al., 2015; Xue et al., 2013]. Recollection involves the conscious retrieval of contextual information about items or events based on previous encounters with them [Kahn et al., 2004]. Neuropsychological research has implicated multiple brain regions, including the medial temporal lobes, hippocampus and prefrontal cortex, in recollecting information or re-experiencing past events [Cabeza et al., 2008; Dolan and Fletcher, 1997; Ferbinteanu et al., 2006; Rutishauser et al., 2015; Tulving, 2002]. Regarding brain features associated with recollection, studies suggest that clearer category-specific representations are predictive of better memory formation [Kahn et al., 2004], and greater item-specific pattern similarity between encoding and decoding have been found in remembered as compared with forgotten items [Xue et al., 2010]. Questions remain regarding brain function specifically responsible for correct recollection [Xia et al., 2015].

Sometimes people correctly recollect information and at other times mistakenly believe they have recollected information correctly, and the neural processes underlying these differences have not been systematically examined. The current study sought to examine brain activities relating to correct versus incorrect recollections. Such information might be useful with respect to understanding the mechanisms underlying processing of accurately and inaccurately recollected information, which could have multiple implications (e.g., in targeting improved memory retrieval in efforts to enhance cognitive functioning).

Various tasks have been used in detecting brain activities associated with correct recollection. These include the subsequent memory [Wagner et al., 1998], remember/know [Angel et al., 2013], and cued recall/recognition [Cabeza et al., 2008; Rajah et al., 2010; Wang et al., 2015] tasks. While these studies have deepened our understanding of memory/recollection processes, they have specific characteristics that should be noted. First, most emphasize the analysis of old/new effects [Angel et al., 2013; McDonough et al., 2013; Xue et al., 2010], and these types of comparisons usually include two variables, familiarity and recollection, both of which may contribute to the correct identification of an old item [Cansino et al., 2015; Duverne et al., 2008; Dulas and Duarte, 2012]. Second, most of these tasks focus on the comparison between remembered and forgotten trials (correct/incorrect), and few permit the isolation of brain activity exclusively related to correct/“incorrect” recollections (i.e., “incorrect” recollections are ones that are believed to be correct when they are incorrect). Third, most of these studies focus on working memory (participants were asked to remember and recall information in the scanner), and few considered potential effects of long-term memory.

Studies focusing on brain responses associated with correct and incorrect responses revealed the caudate as being

involved in recollection. For example, one meta-analysis found that the caudate may support the satisfaction associated with target-detection, and with caudate activation linked to old/new effects in conditions associated with greater confidence in target-detection [Kim, 2013]. Another meta-analysis suggests that caudate activation relates to both objective recollection and objective > subjective recollection [Spaniol et al., 2009]. A recent review of imaging studies investigating memory processes proposed that the striatum plays an important role in declarative memory retrieval [Scimeca and Badre, 2012]. All of these studies suggest that the caudate contributes importantly to memory processing. However, most studies focus on old/new effects or correct/incorrect recollections, which leads to a relative deficit in studies that focus on correct recollections versus “incorrect” recollections. The comparison between these two conditions may be valuable in understanding which brain region contribute to correct recollections as well as those recollections mistakenly believed to be correct. Such information might be helpful in improving cognitive functioning and may provide insight into aspects of certain psychiatric illnesses; for example, with respect to erroneous cognitions in gambling disorder [Potenza, 2014]. In the current study, we designed a recollection task that addresses some of these aspects and allows separation of correctly and incorrectly recollected items. Based on the above descriptions, we hypothesized that the caudate should be implicated in correct versus incorrect recollection processes.

METHODS

Participants

One hundred participants who were university students were recruited through advertisements, with 78 (male, 43; female, 35; age: 21.2 ± 2.2) providing data meeting selection criteria for analyses (see information on selection criteria in “Conditions” section). All participants provided written informed consent and underwent structured psychiatric interviews (using the Mini-International Neuropsychiatric Interview [MINI]) [Lecrubier et al., 1997] performed by an experienced psychiatrist. All subjects were right-handed and recruited through advertisements at the East China Normal University. All participants were free of psychiatric disorders (including major depression, anxiety disorders, schizophrenia, and substance dependence disorders) as assessed by the MINI. The experiment conformed to The Code of Ethics of the World Medical Association (Declaration of Helsinki). The Human Investigations Committee of Zhejiang Normal University approved this research.

We designed a task which permits accurate separation of the two types of events. By comparing these two conditions, brain activations responsible for correct recollection could be identified. Behavioral and brain responses were measured and compared between these two types of events (correct vs. incorrect recollections).

Figure 1.

The timeline of one trial in the fMRI task. In each trial, a fixation was presented first for 500 ms. A recall period followed, lasting for 4,000 ms at most. During this period, one question was presented, participants were asked to read and recall the items and select “remember” or “forget” with relevant key presses. The stimulus turned black after the key pressing and lasted for (4,000-RT) ms. A black screen jittered from 500 to 2,500 ms was presented. The recognition stage (same question as during

the recall stage) followed; at this point, participants were asked to choose one answer from the listed possibilities. This stage lasted for 2,000 ms or until a button press, with a black screen following the button press to complete the 2,000 ms duration. A jitter ranging from 1,500 to 3,500 ms followed. In this study, we focused on brain activations in the recall stage (the window in blue frame) during presentation of novel stimuli.

Experiment Procedures

Before initiating scanning, participants were asked to remember answers to 40 questions within less than an hour prior to scanning (in a separate room). The duration of time was set based on a pilot study and was sufficient for subjects to perform the task. When subjects said they remembered all items, they could ask to stop the remembering process and prepare for the recollection task in the scanner. In order to avoid participants’ recitation during the waiting period after the remember process (about 10 minutes for preparing the following scan), participants were asked to perform a 5-minute distraction task (continuously subtract 4 from 99) and complete several questionnaires (taking at least 5 minutes).

To minimize potential influences of participants’ prior knowledge, the questions selected related to uncommon topics (e.g., asking what is the biggest church in the world). In addition, participants were asked to identify questions to which they already knew the answers during the learning period. These items were excluded from further analysis and on average were few (mean $\pm$ SD = 1.20 $\pm$ 0.32).

The answers in the recognition stage were generated with the goal of having them be confusing in order to detect if participants accurately recollected and recognized the correct answers. For example, the possible answers to the “biggest church” question included: A, St Peters Basilica; B, St Peters Baselica; C, St Peters Basalica; D, St Peters Basolica. For Chinese subjects who understand English, these differences are difficult to distinguish. Only subjects who remembered the answers exactly were given credit for giving correct answers.

Recollection Task

During fMRI, participants were asked to perform a “recollection and recognition” task (Fig. 1). Stimuli were presented and behavioral data were collected using

E-prime software (Psychology Software Tools, Inc.). In each trial, a fixation was presented first for 500 ms and then a recollection period followed, lasting up to 4,000 ms. In this period, one question was presented and participants were asked to read and recollect the information and select “remember” or “forget” via button press. The stimulus turned black after button-pressing and lasted for (4,000-RT) ms. A black screen was presented for a duration of 500–2,500 ms, with the duration jittered. A recognition stage followed (using the same question as in the recall stage) in which participants were asked to choose one answer from the answers listed. This stage lasted up to 2,000 ms (awaiting a button press), which was followed by a black screen with a jittered interval ranging from 1,500 to 3,500 ms (Fig. 1). We focused analyses on the recall stage in the current study.

Conditions

Participants were told that they would be paid a guaranteed 50 Chinese Yuan ($\approx$ 8 US\$) for participation and, to encourage their motivation to response accurately, were told they would be rewarded with an additional 0–40 Yuan based on their task performance. Specifically, if they responded “remember” in the “recall” stage and chose the correct answer in the “recognition” stage (correctly recollected), they would gain an extra 1 Yuan for each trial. If they responded “remember” in the “recall” stage and chose the incorrect answer in the “recognition” stage (incorrectly recollected), they would lose 1 Yuan. The other responses were not rewarded or punished. These strategies were implemented to help ensure that participants would perform the task in a motivated fashion to generate optimal performance. This study sought to compare brain activities in correctly recollected trials to incorrectly recollected trials. To maintain statistical power, only subjects who had more than six trials (the recollection stage in each trial lasting for 4,000 ms, two volumes) in each

condition were included in analysis. The trial numbers (mean $\pm$ SD) in the 78 participants meeting these criteria were 20.78 ± 2.06 correctly recollected trials and 10.02 ± 1.97 incorrectly recollected trials. The trials in which participants answered that they forgot in the recollection stage were 8 ± 1.22 .

fMRI Data Collection

Structural images were collected using a T1-weighted three-dimensional spoiled gradient-recalled sequence covering the whole brain (176 slices, repetition time = 1,700 ms, echo time TE = 3.93 ms, slice thickness = 1.0 mm, skip = 0 mm, flip angle = 15, inversion time = 1,100 ms, field of view = 240 * 240 mm, in-plane resolution = 256 * 256). Functional MRI was performed on a 3T scanner (Siemens Trio) with a gradient-echo EPI T2* weighted sensitive pulse sequence in 33 slices (interleaved sequence, 3 mm thickness, TR = 2,000 ms, TE = 30 ms, flip angle 90°, field of view 220 × 220 mm², matrix 64 × 64) [Dong et al., 2013]. Stimuli were presented using an Invivo synchronous system (Invivo Company, www.invivocorp.com) through a screen in the head coil, enabling participants to view the stimuli. The whole experiment lasted for 20 minutes.

Data Pre-Processing

The functional data were analyzed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>) and Neuroelf (<http://neuroelf.net>) as described previously [DeVito et al., 2012; Krishnan-Sarin et al., 2013]. Images were slice-timed, reoriented, and realigned to the first volume, with T1-co-registered volumes used to correct for head movements. Images were then normalized to MNI space and spatially smoothed using a 6 mm FWHM Gaussian kernel. A general linear model (GLM) was applied to identify BOLD activation in relation to brain activities in different conditions. All types of trials were included as separate conditions (correctly recollected; incorrectly recollected; forgotten; missed); however, only incorrectly recollected and correctly recollected trials were selected for analysis and reporting. Different types of trials were separately convolved with a canonical hemodynamic response function to form task regressors that involved correctly recollected, incorrectly recollected, forgotten, and missed trials. The duration of the recollection stage in each trial was 4,000 ms. The GLMs included a constant term per run. Six head-movement parameters derived from the realignment stage were included to exclude motion-related variances. Participants were excluded from further analysis if they exceeded movement criteria of 2 mm or 2 degrees between TRs. A GLM approach was used to identify voxels that were significantly activated for the each event that was modeled.

Condition Comparisons

We tested for voxels that showed higher or lower activities in the contrasts of correctly recollected and incorrectly recollected trials. Family-wise error (FWE) thresholds were determined using AlphaSim. Significant clusters (FWE-corrected, $P < 0.001$) were thresholded at $P < 0.001$, two-tailed, uncorrected, with an extent of at least 25 voxels, based on the unresliced voxel size (3 * 3 * 3). All of these steps were performed using Neuroelf. The smoothing kernel used during simulating false-positive (noise) maps using AlphaSim was 6 mm, and was estimated from the residual fields of the contrast maps being entered into the one-sample *t*-test. The formula used to compute the smoothness is that used in FSL (see <http://www.fmrib.ox.ac.uk/analysis/techrep/tr00df1/tr00df1/node6.html> for more information).

Correlation Analyses Between Behavioral Performance and Brain Responses

We first compared the brain activations between different conditions and then took the surviving clusters as ROIs in further analyses. For each ROI, a representative BOLD beta value was obtained by averaging the signal of all the voxels within the ROI. We performed the correlations between brain activations in the caudate and the response times (RTs) during correctly and incorrectly recollected trials, separately.

RESULTS

Behavioral Performance

No difference was found in RTs between correctly recollected trials ($1,462.97 \pm 279.34$ ms) and incorrectly recollected trials ($1,425.69 \pm 330.83$ ms) ($t(1, 77) = 0.70$, $P > 0.05$, $\text{partial } \eta^2 = 0.16$) (Table I).

TABLE I. Regional brain activity changes in recollection when comparing correct remembered to pseudo-remembered trials

	x, y, z^a	x, y, z^a	Cluster size ^b	Region ^c
1	30, -9, 3	10.63	205	R Caudate
2	-27, -6, -3	7.26	96	L Caudate

^aPeak MNI Coordinates.

^bNumber of voxels. We first identified clusters of contiguously significant voxels at an uncorrected threshold $P < 0.001$, as also used for display purposes in the figures. We then tested these clusters for cluster-level FWE correction $P < 0.001$ and the AlphaSim estimation indicated that clusters with 25 contiguous voxels would achieve an effective FWE threshold $P < 0.001$. Voxel size = 3 * 3 * 3.

^cThe brain regions were referenced to the software Xjview (<http://www.alivelearn.net/xjview8>) and verified through comparisons with a brain atlas.

Figure 2.

Brain areas showing different activations when comparing the correctly recollected to incorrectly recollected trials. (a) Brain activations in transverse view; (b, c) Beta-weight values from the bilateral caudate during correctly and incorrectly recollected trials. [Color figure can be viewed at wileyonlinelibrary.com]

Imaging Results

Brain activities showed many similarities in the two conditions (see Supporting Information Fig. 1). The recollection process engaged bilateral caudate, bilateral middle temporal gyri and bilateral frontal gyri, among other regions (see Supporting Information Table 1).

As compared with incorrectly recollected trials, the correctly recollected trials showed more brain activation in the caudate bilaterally (see Fig. 2a). These differences were related to more brain activation in the correctly recollected trials (Fig. 2b, c). No correlation was found between caudate activations and RTs in correctly or incorrectly recollected

trials (Right caudate: $r = -0.09$, $P > 0.05$; Left caudate: $r = -0.15$, $P > 0.05$) (Supporting Information Fig. 2).

DISCUSSION

Both of the correct recollection and incorrect recollection processes engaged bilateral caudate, bilateral middle temporal gyri and bilateral frontal gyri, among other regions (see Supporting Information Table 1). The findings suggest that these two conditions activate similar brain responses during recollection. Taken together, while both processes involve activation of similar brain regions, the correct

recollection trials are associated with greater brain activations than incorrect recollections.

When compared with incorrectly recollected trials, the correctly recollected trials were associated with more robust caudate activation bilaterally. The caudate nucleus is one of the three basic structures that comprise the basal ganglia (along with the putamen and globus pallidus). Multiple studies have implicated the caudate in controlling body movements, value processing, spatial memory, and decision-making [Postle and D'Esposito, 1999]. The caudate is also included in reward circuitry, contributing to the encoding of reward values [Kim and Hikosaka, 2015]. The current task involved a reward/punishment component, which was included to increase participants' motivation during task performance. Thus, this aspect may activate brain regions implicated in processing rewards and punishments, including the caudate [Knutson et al., 2001]. While several aspects of task design (e.g., not showing win/lose effects on a trial-by-trial basis) and analytic approach (comparing correctly recollected trials to incorrectly recollected trials) may have mitigated such influences, they cannot be excluded. Further research is needed to examine the extent to which the current findings may generalize to non-rewarded/non-punished recollection processes.

Imaging studies in humans have also found the caudate contributing to learning and memory processes [Arsalidou et al., 2013; Cropley et al., 2006; Seger and Cincotta, 2005; Spellman et al., 2015]. Seger and Cincotta used a task that asked subjects to learn to categorize visual stimuli by classifying images and receiving feedback on their responses. Bilateral activation of the body and tail of the caudate was associated with successful classification learning (correct categorization), and the head of the caudate was associated with processing feedback (the result of incorrect categorization) [Seger and Cincotta, 2005].

In the current study, the correctly recollected trials engaged more caudate activity than did incorrectly recollected trials. This difference was related to enhanced brain activation during correctly recollected trials; in contrast, the caudate did not activate significantly during incorrectly recollected trials. Together, these results suggest that involvement of the caudate is important in correct recollection. The current results provide additional support to a literature on a role for the caudate in correct recollection [Kim, 2013; Scimeca and Badre, 2012; Spaniol et al., 2009]. Kim's review suggests that the caudate is involved in recollection and associated with old/new effects during recollection [Kim, 2013]. The meta-analysis by Spaniol and colleagues suggests that caudate activation is important for both objective recollection and objective > subjective recollection [Spaniol et al., 2009]. Although these studies used different paradigms (including ones differing from our approach), the results provide converging support for a role for the caudate in correct recollection during retrieval processes. In addition, the current results provide experimental evidence for the hypothesis regarding a role

for the caudate in declarative memory retrieval [Scimeca and Badre, 2012]. Taken together, the current study employed a new task that provides additional support for the relevance of caudate activation in correct recollection.

Behaviorally, no difference was found in RTs between the correct and incorrect recollection conditions, suggesting that the time participants spent during correct and incorrect recollections was similar. In addition, no significant correlation was found between RTs and caudate activation. Together, these results suggest that subjects endeavored similarly during the correct and incorrect recollections.

A question arises regarding the precise role that the caudate plays during correct recollection. One possible explanation relates to learning processes as studies have shown greater neural pattern similarities between encoding (learning) and decoding (recalling) in remembered than in forgotten items [Jenkins and Ranganath, 2010; Karpicke and Blunt, 2011; Xue et al., 2010]. The activity in the caudate increased across trials as learning occurred, which is in line with other research involving non-human primates [Brown et al., 1995; Fernandez-Ruiz et al., 2001] and humans [Mattfeld and Stark, 2015; Seger and Cincotta, 2005]. In classified learning, the caudate has been found to be consistently active on trials in which subjects correctly classified stimuli regardless of positive or negative feedback [Seger and Cincotta, 2005]. In addition, participants who recruited the caudate learned better than those who did not [Seger and Cincotta, 2005]. Thus, the activation in the caudate in correct recollection might relate to caudate functioning in learning processes.

Limitations should be noted. In current study, we did not record brain activations during learning. Thus, a direct comparison of the brain processes involved in remembering versus recollection processes was not possible. Future studies should design tasks to investigate these processes. The current task design may not be able to disentangle features of goal consistency or perceived value in correctly recollected responses. Additionally, the extent to which these findings extend to other languages or other types of recollection processes (e.g., those not involving seemingly close choices) should be examined directly.

Taken together, the current study showed that caudate activation is important for correct recollection. The results extend our knowledge about the role of caudate in recollection processes.

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