

Memory

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ABSTRACT

After learning semantically related words, some people are more likely than others to incorrectly recall unstudied but semantically related lures (i.e., Deese-Roediger-McDermott [DRM] false recall). Previous studies have suggested that neural activity in subcortical regions (e.g., the caudate) is involved in false memory, and that there may be sex differences in the neural basis of false memory. However, sex-specific associations between subcortical volumes and false memory are not well understood. This study investigated whether sex modulates the associations between subcortical volumes and DRM false recall in 400 healthy college students. Volumes of subcortical regions including the caudate, accumbens, amygdala, hippocampus, pallidum, putamen and thalamus were obtained from structural magnetic resonance images and measured using FreeSurfer. The results showed that males had lower true and false recall but larger subcortical volumes than females. Interestingly, higher false recall was associated with a larger caudate in males, but not in females. This association was significant after controlling for age and intracranial volume. This study provides new evidence on the neural basis of false recall. It suggests that the caudate plays a role in false recall in young men, and that future studies of the neural correlates of false memory should consider sex differences.

Memory varies greatly from person to person. After being exposed to a list of semantically related words (e.g., apple, melon, banana, grape, and pear), some people will accurately recall many of them (i.e., true recall), while they may also recall some semantically related but unstudied words such as fruit (i.e., false recall), but they will rarely recall unrelated and unstudied words such as paper (i.e., foil) (Robinson & Roediger, 1997; Roediger et al., 2001; Stadler et al., 1999). This is a widely used paradigm for false memory experiments, known as the Deese-Roediger-McDermott (DRM) paradigm (Roediger & McDermott, 1995). According to the activation-monitoring framework (Roediger et al., 2001), DRM false memories are caused by a combination of semantic activation and monitoring failure.

Sex differences in DRM false memories have been controversial (Gallo, 2006). It should be noted that some previous studies did not find sex differences in DRM false recall (Bauste & Ferraro, 2004; Seamon et al., 2002), which may be due to their limited sample size and the number and content of the word lists. However, several **ARTICLE HISTORY**

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False memory; DRM; individual differences; subcortical volumes; sex differences

recent studies have shown that females have higher rates of DRM false recall and recognition than males (Aguilar-Moreno, 2016; Dewhurst et al., 2012). This suggests that the production of DRM false memories in males and females may be caused by different cognitive processing and its underlying neural mechanisms.

Recently, there has been increasing evidence that there are sex differences in the functional activity and anatomy of subcortical regions that support true and false memories induced by different experimental paradigms. For example, using a perceptual-related paradigm, recent functional neuroimaging studies found that hippocampal activity was higher in males than in females, but putamen activity was higher in females than in males during the production of perceptual false recognition (Spets et al., 2021; Spets & Slotnick, 2019). There was also male-specific activity in the caudate and female-specific activity in the thalamus during the production of perceptual true recognition (Slotnick, 2021; Spets et al., 2019; Spets & Slotnick, 2021, 2022). Using the misinformation paradigm with

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121 female and 84 male participants, our previous structural neuroimaging study showed that the negative correlation between hippocampal volume and false recognition induced by the misinformation paradigm was primarily driven by female outcomes (Zhu et al., 2016). Specifically, participants with a larger hippocampus had less misinformation-induced false recognition on the immediate memory test, especially in female participants.

However, it remained unclear whether there would be sex differences in the neural mechanisms underlying DRM false memory, as the neural mechanisms of false memory may differ between paradigms. As shown in the meta-analysis study (Kurkela & Dennis, 2016), several brain regions showed paradigm-specific effects in false memory. For example, perceptual false memory appears to be more strongly associated with activity in visual/ spatial brain regions (Slotnick & Schacter, 2004), misinformation false memory is associated with prefrontal source monitoring (Okado & Stark, 2005; Shao et al., 2023), and DRM false memory is associated with semantically related brain regions (Chadwick et al., 2016; Zhu et al., 2019).

Previous studies with small samples have reported that grey and white matter in the brain are associated with individual differences in DRM false recall, but have ignored potential sex differences (Dennis et al., 2022). According to a study comparing 7 patients with brain lesions to 14 healthy comparison participants, DRM false recall is reduced by damage to the ventromedial prefrontal cortex (Warren et al., 2014). Furthermore, in a sample of 16 male and 32 female healthy young college students, DRM false recall was associated with the superior longitudinal fascicle connecting frontoparietal structures (Fuentemilla et al., 2009). These studies suggest that frontoparietal regions may contribute to individual differences in DRM false recall. However, the role of subcortical regions in DRM false recall and their potential sex differences have not been considered in these previous studies. False recall as measured by the DRM paradigm may be supported by different subcortical regions in males and females.

The caudate nucleus has been identified as the only subcortical region to show consistent activity during false memory retrieval based on a meta-analysis study (Kurkela & Dennis, 2016). They proposed that the caudate may be involved in cognitive control (i.e., making difficult memory decisions to lures in the DRM task). Contrary to the notion that "bigger is better", previous studies suggest that caudate volume inversely predicts cognitive control in male-dominated samples of chess players (Duan et al., 2012), adolescents with attention deficit hyperactivity disorder (Mataró et al., 1997), and children diagnosed with autism spectrum disorders (Voelbel et al., 2006). They suggest that males with larger caudate volumes may have a lower level of cognitive control and thus may be more likely to produce a higher number of false recall. However, to our knowledge, no studies have examined the relationship between caudate volume and DRM false memory in healthy young males and females.

The main aim of this study was to determine whether sex modulates the association between caudate volume and DRM false recall. We tested two hypotheses as follows. Based on the results of previous behavioural DRM studies (Aquilar-Moreno, 2016; Dewhurst et al., 2012), we predicted that females should have higher true and false recall than males. Given the critical role of the caudate nucleus in false memory (Kurkela & Dennis, 2016), we then examined whether caudate volume would predict false recall. Given that the caudate nucleus may play a more important role in cognitive function in males than in females (Duan et al., 2012; Mataró et al., 1997; Spets et al., 2019; Voelbel et al., 2006), we examined whether the association between caudate volume and false recall would be stronger in males than in females. To test these assumptions, we measured individual differences in DRM false recall in healthy young adults (i.e., 189 males and 211 females) and then obtained their structural imaging data to measure the volume of subcortical regions (e.g., caudate nucleus) segmented using the latest version of FreeSurfer. Given the exploratory nature of this analysis, we included all seven subcortical regions as in previous studies as regions of interest (ROIs) (Hibar et al., 2015; Wu et al., 2021).

Methods

Participants

This study recruited 416 Chinese college students (mean age: 21.33 ± 1.95 years [M ± SD]; 214 females and 202 males). Sex was self-reported by the participants. All participants had normal vision and hearing and no history of psychiatric or neurological diseases. Two exclusion criteria were used. Two male participants were excluded due to their abnormal brain structure, and eleven male and three female participants were further excluded because their false or foil recall exceeding three standard deviations from the mean. The final sample comprised 400 participants (mean age: 21.33 ± 1.97 years $[M \pm SD]$; 211 females and 189 males). Sample size was determined by power analysis using G*Power. To measure the neural-behavioural correlation between subcortical volume and false memory (Zhu et al., 2016), power analysis (correlation [bivariate normal model], minimum effect size $[r^2] = 0.04$, $\alpha = 0.05$, and power = 0.80) determined that the minimum required sample size was 193. This study was approved by the Institutional Review Board of the State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, China. Written informed consent was obtained from all participants.

Behavioural assessments

The DRM recall task was administered (Roediger & McDermott, 1995) (Figure 1). During encoding, participants studied 12 lists of 8 semantically related Chinese words. These 96 words were all two-character Chinese words. They were translated and adapted from DRM word lists used in previous studies (Roediger & McDermott, 1995; Stadler et al., 1999). The themes of these 12 lists were fruit, chair, sweet, lion, needle, sleep, cry, lie, anger, evil, thief and alone. For example, the fruit word list contains the following eight words: apple, veggies, lychee, melon, banana, grape, cherry and pear. These words were presented visually on the computer screen. The beginning of each word list was preceded by a 2-second visual cue (e.g., List 1). Each word was presented only once for 2 s. The order in which the 96 words presented was the same for all participants. During the presentation of these 96 words at encoding, participants were asked to remember as many words as possible. After a 10-minute filler task (i.e., an anti-saccade task), participants were asked to write down as many words as they could remember on a piece of paper within the next 10 min. All participants were debriefed at the end of the second session.

The raw scores for true, false, and foil recall were the number of recalled targets (studied words), lures (unstudied but semantically related words), and foils (unstudied and unrelated words). Instead of using only one critical lure for each word list in the traditional DRM task, we allowed multiple lures for each word list by counting the total number of both critical lures (e.g., fruit) and non-critical but semantically related lures (e.g., orange). In the traditional DRM task, there is only one critical lure per word list, and this critical lure has the strongest semantic associations with the studied words in the



Figure 1. Experimental design of the DRM recall task.

word list (Roediger & McDermott, 1995). It should be noted that, however, participants are likely to recall non-critical but semantically related lures (e.g., orange). Following the methodology of previous studies (Beato & Arndt, 2021; Cadavid & Beato, 2016), the current study allows for multiple lures per word list. This approach may be useful for examining individual differences in false recall, as participants may form idiosyncratic semantic associations based on their personal experiences (Chadwick et al., 2016). Each response in the recall test was scored independently by two raters and the interrater reliability (kappa) was 0.95.

MRI data acquisition and analysis

All participants' brain imaging scans were acquired on a 3.0 T Siemens Magnetom Trio scanner at the Beijing Normal University Brain Imaging Center. Structural MRI was acquired using a T1-weighted, 3D, gradient-echo pulse-sequence (MPRAGE). The following parameters were used for this sequence: matrix of 256×256 , FOV = 256×256 mm, T1/TR/TE/ θ = 1100 ms/2530 ms/3.39 ms/7°, and slice thickness = 1.33 mm. To obtain high-resolution structural images of the whole brain, 144 sagittal slices were acquired. For all participants, structural MRI data were collected approximately one year after completion of the DRM memory test.

FreeSurfer (version 7.1.1, http://surfer.nmr.mgh.harvard. edu) was used for subcortical segmentation (Dale et al., 1999; Fischl, 2012; Fischl et al., 2002) (Figure S1). Briefly, the process includes motion correction and intensity normalisation of T1-weighted images, removal of non-brain tissue, automated Talairach transformation, and segmentation of subcortical structures. The estimated total intracranial volume (ICV), which includes brain tissue and other biological materials such as meninges and cerebrospinal fluid, was obtained from the standard output of the FreeSurfer analysis. To obtain the volumes of the hippocampal subfields, we used the FreeSurfer segmentation software (version 7). The hippocampal subfields include the parasubiculum, presubiculum, subiculum, CA1, CA2/3, CA4, granule cells in the molecular layer of the dentate gyrus (GC-ML-DG), hippocampal-amygdaloid transitional area (HATA), fimbria, molecular layer of the hippocampus, hippocampal fissure, and hippocampal tail. Their volumes were derived using a refined probabilistic atlas. To ensure accurate segmentation and precise assignment of subcortical regions and hippocampal subfields, a thorough visual inspection was performed for each segmented image overlaid on the corresponding T1-weighted image. For each of the seven subcortical regions, their volumes were summed across the left and right hemispheres as reported in the main text, as we had no assumptions about lateralisation in any of the regions. Additional analysis and results regarding the left and right hemispheres are provided in the supplementary materials.

Data analysis

Repeated measures ANOVA and post-hoc t-tests were used to examine sex differences in memory performance (i.e., true, false and foil recall) and subcortical volumes (i.e., bilateral caudate, accumbens, amygdala, hippocampus, pallidum, putamen, and thalamus volumes). Linear regression models were then used to examine whether sex moderated the relationship between memory performance and subcortical volumes. In each regression model, we examined the main effects of subcortical volume (e.g., caudate volume) and sex (i.e., male = 1, female = -1) and their interaction term, with age and ICV as covariates. Finally, partial correlation analysis was used to calculate the relationship between subcortical volume and true or false recall after controlling for age and ICV in males and females separately. The Bonferroni method was used to control for multiple comparisons when calculating separate tests for seven subcortical regions (e.g., correcting for *p*-values of the interaction term between sex and subcortical volume).

Results

Sex differences in memory

Figure 2 and Table S1 show the distributions of true, false and foil recall for males and females. A 2×3 repeated measures ANOVA revealed significant main effects of sex $(F(1, 398) = 19.41, p < 0.001, partial <math>\eta^2 = 0.05)$ and memory type (*F*(2, 796) = 998.21, p < 0.001, partial η^2 = 0.72) as well as their interaction (F(2, 796) = 12.36, p < 12.360.001, partial $\eta^2 = 0.03$). In both males and females, true recall was higher than false recall (ps < 0.001, Cohen's d > 1.37), while false recall was higher than foil recall (ps < 0.001, d > 1.09). Compared to females, males had lower true recall (t(398) = -4.10, p < 0.001, d = -0.41) and false recall (t(398) = -2.14, p = 0.033, d = -0.21), but similar amounts of foil recall (t(398) = 0.08, p = 0.937, d = 0.01). Next, a 2×2 repeated measures ANOVA also revealed a significant interaction between sex and memory type (true vs. false) (F(2, 796) = 11.62, p < 0.001, partial η^2 = 0.03), indicating that the magnitude of the sex difference was greater for true recall than for false recall. In addition, similar results were found in the original sample before exclusion of ineligible participants (Figure S2).

Sex differences in subcortical volumes

Figure 3 and Table S2 show the distributions of subcortical volumes for males and females. Repeated measures ANOVA revealed significant main effects of sex (*F*(1, 398) = 144.78, p < 0.001, partial $\eta^2 = 0.27$) and subcortical type (*F*(6, 2388) = 27363.64, p < 0.001, partial $\eta^2 = 0.99$) as well as their interaction (*F*(6, 2388) = 37.69, p < 0.001, partial $\eta^2 = 0.09$). Compared to females, males had larger volumes of the caudate, accumbens, amygdala, hippocampus, pallidum, putamen and thalamus (ps < 0.001, d

> 0.48). Of these seven subcortical regions, the smallest sex differences were found in the volume of the accumbens, while the largest sex differences were found in the volumes of the putamen and thalamus (Table S2). In addition, we found that the proportion of subcortical volume relative to total intracranial volume was greater in females than in males (Figure S3 and Table S3). As part of the exploratory analyses, we also examined sex differences in subcortical volume in the left and right hemispheres. The results showed similar findings in subcortical regions on both sides of the brain (see Supplementary Table S4 for details).

Sex moderates association between false recall and caudate volume

We investigated predictors of individual differences in false recall. Among seven subcortical regions, we found that sex moderated the relationship between false recall and subcortical volumes of the caudate, after controlling for age and intracranial volume (ICV) (Figure 4 and Tables S5-6). Age and ICV served as covariates since they were correlated with memory performance and subcortical volumes (Tables S7-8).

In the caudate, only the interaction term between sex and volume reached significance ($\beta = 0.15$, t = 2.88, p =0.004), and the overall model predicting false recall was significant (F(5, 394) = 3.13, p = 0.009, $R^2 = 0.04$). Specifically, after controlling for age and ICV, there was a positive correlation between false recall and caudate volume in males (r(185) = 0.21, p = 0.005), but not in females (r(207))= -0.08, p = 0.243). Furthermore, we examined the difference between two independent correlation coefficients for males and females (Preacher, 2002). Results showed a significant difference for the caudate (p = 0.004), indicating the robustness of this effect. Similarly, in the accumbens, only the interaction term between sex and volume reached significance ($\beta = 0.13$, t = 2.52, p = 0.012), and the overall model predicting false recall was significant (F(5,394) = 2.48, p = 0.031, $R^2 = 0.03$). Specifically, after controlling for age and ICV, there was a positive correlation between false recall and accumbens volume in males (r (185) = 0.15, p = 0.039, but not in females (r(207) = -0.10), p = 0.161). The two independent correlation coefficients for males and females showed a significant difference for the accumbens (p = 0.014). After correcting for multiple comparisons, only in the caudate, its interaction term and the partial correlation in males remained significant. Except for the caudate, the interaction between sex and volume was not significant for false recall in other subcortical regions. It should be noted that the correlation between caudate volume and false recall was significant in males both before and after controlling for age and ICV (Tables S5-6). Furthermore, we found that sex moderated the relationship between false recall and caudate volume in both the left and right hemispheres (see Supplementary Tables S9-10 for details).



Figure 2. Memory performance in males (*n* = 189) and females (*n* = 211). The dashed line represents the mean. Compared to females, males had lower true recall and lower false recall, but similar amounts of foil recall.

Finally, individual differences in true recall were not associated with any of these seven subcortical volumes, and sex did not moderate their neural-behavioural relationships (Tables S5-10 and Figure S4). Given the important role of the hippocampus in memory, we also examined the relationship between hippocampal subfield volume and true and false recall in males and females. However, hippocampal subfield volumes did not correlate significantly with either true or false recall in either males or females after correcting for multiple comparisons (Table S11).

Discussion

This study provides new evidence that the caudate nucleus plays a different role in false memory in males and females in healthy young adults. Compared to females, males had lower true and false recall but larger subcortical volumes. Caudate volumes were positively associated with false recall in males but not in females. To our knowledge, this is the first study to show that individual differences in DRM false recall are associated with caudate volume in males but not in females, suggesting a sex-specific neural basis for false memory. They confirmed and extended previous functional neuroimaging studies supporting the critical role of the caudate in false memory by linking neural structural correlates to DRM false memory in healthy young men.

Extending previous behavioural studies showing that females have higher true and false recall than males (Aguilar-Moreno, 2016; Dewhurst et al., 2012), we observed a significant interaction between memory type and sex, indicating that the sex differences in true recall are larger than those in false recall. According to the activation monitoring framework, this may be due to a combination of better semantic associative memory in females and more impulsivity in memory decisions in males (Asperholm et al., 2020; Chang & Moscovitch, 2022; Weinstein & Dannon, 2015). However, this interaction between sex and memory type found in the present study suggests that semantic association is not the only cause and that monitoring processes also contribute to sex differences in false recall(Gaillard et al., 2020). It suggests that there are sex differences in the monitoring processes during the production of DRM false memory.

In this study, we used the raw number of recalled target or lure, rather than the proportion of targets or lures to the total number of recalled items by each participant. We argue that the raw number of recalled items reflects recall ability, whereas the proportion of recalled targets or lures to the total number of recalled items reflects memory response tendency. For example, one participant recalled 10 targets, 3 lures, and 0 foil (i.e., a total of 13), whereas another participant recalled 10 targets, 7 lures, and 10 foils (i.e., a total of 27). Although both participants recalled the same number of targets (i.e., 10), they recalled different proportions of targets (i.e., approximately 77% and 37%, respectively). As another example, one participant recalled 34 targets, 5 lures, and 0 foil (i.e., a total of 39), whereas another participant recalled 5 targets, 5 lures, and 9 foils (i.e., a total of 19 in). Although both participants recalled the same number of lures (i.e., 5), they recalled different proportions of lures (i.e., approximately 13% and 26%, respectively).

Extending previous fMRI studies showing caudate activity in false memory (Kurkela & Dennis, 2016), we found that sex moderated the correlation between caudate structure and false memory. It is important to note that the neural-behavioural correlations were



Figure 3. Subcortical volumes for males (n = 189) and females (n = 211). (A) Seven subcortical regions are shown in the sagittal, coronal, ventral and dorsal views (from left to right). (B) Males had larger subcortical volumes than females. The error bar indicates the standard error of the mean. M = male, F = female, Cau = caudate, Acc = accumbens, Amy = amygdala, Hip = hippocampus, Pal = pallidum, Put = putamen, Tha = thalamus. The unit of volume is 10^3 mm^3 .

adjusted for both total intracranial volume and age. Specifically, larger caudate volume was associated with higher false memory in young men but not in women. This may be due to sex-specific functions in the caudate nucleus. Previous studies have also suggested that both the caudate nucleus and the frontal cortex play a key role in cognitive control (Grahn et al., 2008). Extending previous studies highlighting the role of the frontal cortex in DRM false recall (Fuentemilla et al., 2009; Warren et al., 2014), our study suggests that subcortical structures such as the caudate nucleus also contribute to DRM false recall at least in young men. As shown in previous studies (Duan et al., 2012; Mataró et al., 1997; Voelbel et al., 2006), larger caudate volume may be associated with poorer cognitive control in males. Notably, previous meta-analyses indicate sex differences in cognitive control (Gaillard et al., 2020). Evidence suggests that individual differences in cognitive control influence DRM



Figure 4. Scatter plots with normalised residuals showing relationships between subcortical volumes and false recall in males (blue lines with triangles) and females (orange lines with dots) after controlling for age and intracranial volume. Individual differences in false recall were associated with caudate volume in males. Vol = volume.

false memory (Watson et al., 2005). Males with larger caudate volumes may have poorer cognitive control, resulting in greater difficulty suppressing semantically related lures (i.e., higher false recall). Taken together, the current study provides evidence for a sex-specific role of the caudate nucleus in false memory.

This study has several limitations, which provide directions for future research. Although we found a positive correlation between caudate volume and DRM false recall in males, there was no such significant correlation in females in the current sample. Previous research suggests that false memories in females may rely on other regions, such as the language processing cortex (Slotnick, 2021; Spets & Slotnick, 2019). Since the current study used structural rather than functional brain data, it is impossible to directly confirm the idea. Future studies employing functional MRI should investigate whether the relationship between DRM false recall and neural activity in cortical and subcortical regions is moderated by sex. Unexpectedly, the volume of the hippocampus and its subfields did not correlate with true or false memory in either males or females. Due to the functional heterogeneity of the hippocampus (Chadwick et al., 2014; Derix et al., 2014; Suthana et al., 2015), future studies using high-resolution MRI (e.g., 7 T) would help to elucidate the function of hippocampal subfields in true and false memory in males and females. The current findings are based on a sample of healthy young adults. However, several previous studies have suggested age differences in the neural basis of false memories (Bowman et al., 2019; Dennis et al., 2007; Dennis et al., 2008; Dennis et al., 2014). Future studies could further investigate sex differences in the neural correlates of false memory in older adults.

In conclusion, the current study suggests that sex modulates the relationship between caudate volumes and DRM false recall, suggesting that males and females produce false recall in different ways. Specifically, caudate volume was positively associated with false recall in males but not in females. This association was significant both before and after controlling for age and intracranial volume. The current study highlights the importance of including sex as a moderator when investigating the neural correlates of human memory.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

Data are available from the corresponding author on reasonable request.

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