**Title:** Neural mechanisms underlying the semantic recollections including lexical identity

**Abbreviated Titles**: Brain function for familiarity and specific-naming

**Author Names and affiliations:** Zhansheng Xu[1], Bo Shen[1,8], Wael Taji[1, 9], Pei Sun[6,7], Yuji Naya[1,2,3,4,5]

[1] School of Psychological and Cognitive Sciences, Peking University, Beijing 100871, China

[2] Center for Life Sciences, Peking University, Beijing 100871, China

[3] IDG/McGovern Institute for Brain Research at Peking University, Beijing 100871, China

[4] Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing 100871, China

[5] Interdisciplinary Institute of Neuroscience and Technology, Zhejiang University, Hangzhou 310027, China

[6] Department of Psychology, School of Social Sciences, Tsinghua University, Beijing 100084, China

[7] Tsinghua Laboratory for Brain and Intelligence, Tsinghua University, Beijing 100084, China

[8] Department of Psychology, Zhejiang Normal University, Jinhua 321004, China

[9] Yenching Academy, Peking University, Beijing 100871

**Corresponding Author**: Yuji Naya

Address: School of Psychological and Cognitive Sciences, Peking University, No. 52, Haidian Road, Wang Kezhen Building, Room 1707, Haidian District, Beijing 100871, China

E-mail: yujin@pku.edu.cn

Number of figures: 7

Number of tables: 4

Number of pages: 46

Number of words: 249 words for abstract, 597 words for introduction, 1469 words for discussion

**Conflict of Interest**: The authors declare no competing financial interests.

**Acknowledgments:** We thank K. Jimura for helpful comments. Funding: The present study was funded National Natural Science Foundation of China Grant 31421003 (to Y.N.).

## Abstract

Identifying individual persons or objects is accompanied by retrieval of object names as well as semantic recognition. A separation of this lexical retrieval from the semantic recognition has been supported by neuropsychological studies examining responsible brain regions for familiarity judgements and lexical retrieval. However, neuroimaging studies on this hypothesis have arrived at inconsistent findings. To address this problem, we investigated neural activations during lexical retrieval explained by either retrieval of specific-naming for an animal (i.e. 'pigeon,' as opposed to 'bird') or familiarity-indexing to the animal reflecting participants' feeling of knowing. By removing a confounding effect embedded in the stimuli, we separated the brain regions related with specific-naming (e.g., left TP) from those with familiarity-indexing (e.g., bilateral medial-PFC). In the left IFG, the posterior-dorsal and the anterior-ventral parts were related with the familiarity index and with the specific naming, respectively. Psychophysiological interaction analyses showed that posterior-dorsal IFG connected left TP and STG for specific-naming or with the right TP and hippocampus for high-familiarity, while anterior-ventral IFG connected only the brain regions related with specific-naming. Using separate memory retrieval tasks, we further examined the task-selective connectivity patterns and found that both parts of left IFG changed its targeting brain areas according to the memory contents such as animals' habitat and body color. These results suggest an involvement of the left IFG in controlling the semantic retrieval including the specific names, and furthermore a pivotal role of posterior-dorsal IFG as a hub, which in addition accesses the inherent information in familiar objects.

## Significance statement

We tend to remember specific names of objects (e.g., ‘beetle’ as opposed to ‘insect’) that induce feelings of familiarity. By removing the confounding effect between lexical retrieval and familiarity, we demonstrated separate functional modules selective for the specific naming and those inherent in familiar objects. We found two distinct sites in the left IFG of ventrolateral prefrontal cortex, both of which changed their connectivity patterns according to the modalities of to-be-retrieved memory contents, including animal name, body color, and habitat. However, only the posterior-dorsal but not anterior-ventral part accessed the module for familiar objects in addition to those for the semantic recollection, indicating a graded (anterior-ventral to posterior-dorsal) functional specialization in the left IFG during semantic recognition including lexical retrieval.

## Introduction

The identification of individual persons or objects is a composite cognitive function reported to contain three stages: (1) the pre-semantic stage, where an item is perceived; (2) the semantic stage, where the item is recognized, and its semantic information is retrieved; (3) the lexical retrieval stage, where the item's specific name is recalled (Bruce & Young, 1986; Gorno-Tempini and Price, 2001). Evidence from neuropsychological studies suggests that the recognition (stage 2) and specific-naming (stage 3) processes are distinguishable at the cognitive and neural level (Damasio et al., 1996, 2004; Bi et al., 2011; Drane et al., 2013). Specifically, several studies on patients with lesions in the left anterior temporal lobe (left ATL) found that patients showed intact object recognition, yet suffered from name retrieval deficits (Damasio et al., 1996; Bi et al., 2011). Furthermore, another study found that right temporal lobe epilepsy (TLE) patients exhibited deficits in famous face recognition without any problems in naming (Drane et al., 2013). However, in contrast to the suggested dissociation of the responsible brain regions for the two stages identified within this literature, neuroimaging studies using cognitively normal participants have not separate the capacity of recognition from naming (Damasio et al., 1996, 2004; Tranel et al., 1997; Gorno-Tempini and Price, 2001; Nakamura et al., 2001; Olson et al., 2013; Abel et al., 2015).

A possible explanation for the controversy is that previous neuroimaging studies targeted only one component of these functions (i.e. either naming or recognition; Damasio et al., 1996, 2004; Grabowski et al., 1998; Gorno-Tempini and Price, 2001; Nakamura et al., 2001; Abel et al., 2015). Accordingly, there might be an internal covariance between naming level and familiarity level of the items used in previous experiments because participants may tend

to retrieve specific names for familiar items. In addition, another confounding factor within previous experiments may be encountered when comparing the semantic stage with the lexical retrieval stage. In most of the naming tasks (Damasio et al., 1996, 2004; Abel et al., 2015), participants retrieved item names voluntarily, whereas in the recognition paradigm they simply monitor their feeling of knowing for the items, which is reflexively called to mind (Gorno-Tempini and Price, 2001; Nakamura et al., 2001; Leveroni et al., 2000). Thus, the activation areas in the naming tasks may contain the memory control areas which may mediate a general retrieval process not only for the naming, but also for other types of semantic memory.

In the present study, we addressed the two types of confounding factors inherent to the item stimuli and task conditions to investigate brain mechanisms involved in the voluntary recall of semantic memory, including specific-naming and its relationship with the familiarity effect. We measured blood-oxygenation-level-depend (BOLD) fMRI signal during three types of memory recall tasks (specific-naming, color retrieval and context retrieval) using same object stimuli as cues, followed by a post-scan test scoring how strongly participants felt they knew the objects presented as cue stimuli (Fig.1) (Kikyo et al., 2002; Belfi & Tranel, 2014). In imaging analyses, naming-level and familiarity-level were adjusted to examine the familiarity effect and naming effect separately. In addition, we compared functional connectivity patterns between the memory control areas [e.g., left inferior frontal gyrus (IFG)] and the representational areas [e.g., posterior superior temporal gyrus (pSTG), parahippocampal gyrus] using psychophysiological interaction analyses (Friston, 1994; Jackson et al., 2016) among the three task conditions. The results suggest that distributed

brain networks for semantic recognition and lexical retrieval are activated in a task-specific manner and that the networks, including those for processing of familiar objects, are linked at the posterior-dorsal part of the left IFG.

## Materials and Methods

### Participants

The present study recruited 38 student participants from Peking University (17 females, 21 males, mean age 22.7 ± 2.47 years). All 38 participants finished the naming task. Of these, 21 participants (10 males, 11 females; mean age 23.2 ± 2.3 years) participated in the color retrieval task. Two out of the 21 participants were excluded from subsequent data analyses for color-retrieval task due to performance problems (one for excessive head motion, and another didn't complete the task). Sixteen participants (11 males, 5 females; mean age 22.0 ± 2.4 years) participated in the animal-context retrieval task. Three among them (one for excessive head motion, and two for misunderstanding the instruction) were excluded from subsequent data analyses for context-retrieval task. All participants were native Chinese speakers and right-handed. For all participants, vision was normal or corrected to normal. No participants suffered from psychiatric or neurological disorders, had previously suffered head injuries, or were on any psychoactive medications. All participants completed a written informed consent form approved by the institutional review board of the School of Psychological and Cognitive Sciences of Peking University.

### Stimuli

The stimulus set consisted of 120 black-and-white photographs of animals, which were originally downloaded as colored photographs from the ImageNet website (Stanford Vision Lab, Stanford University). The original photographs were subsequently resized to 350 × 350 pixels, and removed color and all background features to leave only the animal present. The

visual stimuli were presented by using the Psychtoolbox 3 package (Brainard, 1997) in MATLAB (MathWorks, Natick, Massachusetts MathWorks).

**Task design and procedure**

*Naming experiment.* Participants were instructed to overtly (in speech) name the animals presented on the screen at specific (subordinate) level (e.g., pigeon; Fig. 1A). When unable to recall specific animal name, they were required to name the animals at a basic level (e.g., bird). During the naming task, fMRI BOLD signals from the participants were measured and their vocal responses were recorded using an antimagnetic microphone system, which is equipped with a real-time noise cancelling function (FOMRI III, Optoacoustics Ltd).

In this naming task, each trial began with the appearance of a fixation point ("+") on the center of the screen for 4-10s (4s, 6s, 8s, or 10s), which was then replaced by a target animal picture lasting 2s (Fig. 1B), participants were instructed to name the animal overtly during the interval. The naming task was conducted in two runs, each run consisting of 80 trials. The total time of each run was 12 minutes. The object presentation order for each run was pseudo-randomized for each participant, with no consecutive trials presenting the same category (e.g., bird) of pictures. In order to reduce head motion of participants during vocalizing, a short induction briefing was given prior to initialize fMRI scanning.

*Feature retrieval experiment.* Participants were instructed to retrieve modal-specific (i.e. color, context) contents of every animal vividly in the feature retrieval task. We used the same animal photographs as in the naming task. Each trial of the feature retrieval task began with the appearance of a fixation point ("+") on the center of the screen for 4-10s (4s, 6s, 8s, or 10s), which was then replaced by a target animal picture lasting 2s (Fig. 1C). During the

presence of an animal picture, the participants needed to retrieve modal-specific contents of every animal, and then to press the left button if they retrieved successfully, or pressed right button if they could not retrieve. In addition to the main condition requiring the recollection, the task also includes a low-level control condition, under which a scrambled picture was shown for 2s, and participants needed only to press the left button. The whole task included two runs, both consisting also of 80 trials. The total time of every run was 12 minutes.

*Post-scanning test.* After the fMRI scanning, we asked the participants to conduct a familiarity rating task. In this task, the participants were asked to evaluate the familiarity of the animal in each photograph by a scale of 1-7 (1 indicating extreme unfamiliarity, 7 indicating extreme familiarity), based on their sense of knowing rather than judging whether they feel that they watched the photo during the scan.

**Data acquisition and analysis**

*fMRI data acquisition.* MRI data were collected on a 3T Siemens Prisma scanner at the Peking University MRI center. High-resolution 3D structural images were acquired with a 3D-MPRAGE sequence (TR, 2530 ms; TE, 2.98 ms; flip angle, 7 degree; matrix size, 448×512; voxel size 0.5×0.5×1 $mm^3$). BOLD signal was acquired using a multi-band echo-planar imaging (EPI) sequence (TR, 2000 ms; TE, 30 ms; flip angle, 90 degrees; matrix size, 112×112; voxel size, 2×2×2 $mm^3$, 64 slices with gap of 0.1mm).

*fMRI data preprocessing.* The fMRI data was preprocessed and analyzed using SPM12 (Wellcome Trust Centre for Neuroimaging, London, UK) and MATLAB software (MathWorks, Natick, Massachusetts). Preprocessing of the functional MRI data included slice timing, realignment (head motion correction), co-registration, segmentation, normalization,

smoothing and high-pass filtering. Slice timing (sinc interpolation) was used to correct differences in image acquisition time between slices within a TR. Subsequently, realignment (3D rigid-body transformation) was conducted to correct head motion. To normalize functional images, each participant's structural brain image was co-registered to the mean functional image, and was subsequently segmented. The parameters obtained in segmentation were used to normalize each participant's functional image onto the Montreal Neurological Institute (MNI) space (resampling voxel size was $2\times2\times2$ $mm^3$). All volumes were spatially smoothed with an isotropic 6 mm full-width at half-maximum (FWHM) Gaussian kernel. In addition, a high pass filtering was used to remove low-frequency drifts.

*General Linear Model (GLM) Analyses.* For the naming task, in order to detect the brain regions related to specific-naming and recognition processing for familiar objects, two types of categorical GLM analyses of the functional MRI data were performed. Firstly, we examine the two effects separately without controlling for confounding factors present within the stimuli were examined. As to the naming-level difference, the analysis included 4 main regressors: the effect of specific-naming trials, the effect of basic-naming trials, the effect of baseline condition trials (i.e. scrambled-picture trials), and the effect of other no-interest trials (i.e. the error trials). In addition, the six motion regressors were also included as nuisance regressors. As to the familiarity-level difference, the analysis included 3 main regressors: the effect of high familiarity trials, the effect of low familiarity trials, and the effect of baseline condition trials in addition the six motion regressors.

Secondly, the effects of naming-level and familiarity-level via a single categorical GLM analysis were examined. Based on the participants' naming responses and familiarity ratings,

naming task trials were divided into three conditions: the high-familiarity & specific-naming (*HS*) trials, the high-familiarity & basic-naming (*Hb*) trials, and low-familiarity & basic-naming (*lb*) trials. The 'HS' trials were the specific-naming trials of which familiarity ratings were above the mean value of individual participants. The 'Hb' trials were the basic-naming trials for which familiarity ratings were above the mean value of individual participants. Then, we chose the 'lb' trials from the basic-naming trials with the lowest familiarity rating (i.e.1) until the number of the 'lb' trials neared that of the 'Hb' trials were chosen. Taken together, this GLM analysis included 5 main regressors: the effect of high familiarity & specific-naming (*HS*) trials, the effect of high familiarity & basic-naming (*Hb*) trials, the effect of low familiarity & basic-naming trials (*lb*), the effect of baseline condition trials, and the effect of other trials. Furthermore, the six motion regressors were also included as nuisance regressors. For group level analysis, we entered the contrast images (e.g., 'Hb > lb' contrast) that were generated by the subject-level GLM analyses into a second-level one-sample t-test. In addition to the categorical GLM analysis, the familiarity effect was also examined using a parametric modulation analysis based on the familiarity rating (7 levels) within the basic naming trials. In the parametric analysis, the polynominal function up to the second order were used. This analysis included 5 main regressors: the effect of specific-naming trials, the effect of basic-naming trials, the effects of the first and second order of familiarity ratings, and the effect of other trials (included the error trials). In addition, the six motion regressors were also included as nuisance regressors. Subject-level analyses were run to generate SPM contrast images, and these contrast images were entered into a group-level random-effects GLM.

For the feature retrieval task, one GLM analysis was made for each retrieval condition (i.e., color-retrieval; context-retrieval). Each GLM analysis included 4 main regressors: the effect of successful-retrieval ('Yes') trials, the effect of unsuccessful-retrieval ('No') trials, the effect of baseline condition trials (i.e. scrambled-picture trials), and the effect of other no-interest trials (i.e. the error trials). In addition, the six motion regressors were also included as nuisance regressors. In group level analysis, we entered the contrast images (i.e., 'Yes > No' contrast) that were generated by the subject-level GLM analyses into a second-level one-sample t-test.

*Psychophysiological interaction (PPI) analyses.* In order to assess functional connectivity patterns contributing to a particular cognitive function, PPI analyses were conducted by performing a separate GLM analysis involving three main regressors: (i) the "physiological" regressor; (ii) the "psychological" regressor; and (iii) the "PPI interaction" regressor (Friston, 1994; Jackson et al., 2016). In addition, the six motion regressors were also included as nuisance regressors for each session. As the physiological regressor, activities of a particular spherical brain region with six millimeters radii (i.e. seeds) were used. In left IFG, we totally defined six seeds. The first four seeds determined as peaks in the whole-brain results of GLM analyses (i.e., specific naming, high familiarity, color retrieval and context retrieval), one more seed was chosen according to previous literature (Badre et al, 2005; Whitney et al., 2011). The sixth seed was constructed from the coordinate of peak overlap in the anterior-ventral part of left IFG between color-retrieval condition and context-retrieval condition using low threshold ($p < 0.005$, uncorrected in voxel level). In order to compared with the lateral PFC seeds (left IFG), we also defined a seed in medial PFC, which was chose based on high

familiarity contrast ('Hb > lb'). As the psychological regressor, trial types related with a particular functional effect were used. A total of four contrasts between trial types were examined for each brain seed: the specific-naming (contrast: HS > Hb), the recognition of familiar objects (contrast: Hb > lb), and the two object-feature retrievals (contrast: successful retrieval > unsuccessful retrieval). The interaction regressor was used to identify voxels in which functional activity covaried in a task-dependent manner with the seed region. Subject-level PPI analyses were run to generate SPM contrast images similar to a subject-level GLM model, and these contrast images were entered into a group-level random-effects GLM (Friston, 1994; Jackson et al., 2016; Wang et al., 2017).

*ROI analysis of PPI effects.* In order to examine specificity of the connectivity patterns among the modalities of memory contents for their retrieval, ROIs analyses were performed on the whole-brain PPI analyses. Firstly, ROIs (6mm, cubical) were constructed around the peak coordinates from the whole-brain PPI results in key brain regions identified from previous literature, including the SMA, pSTG, TP, hippocampus, FG, and parahippocampal gyrus (Leveroni etl al., 2000; Davachi, 2006; Rogers et al., 2006; Simmons et al., 2007; Hickok, 2009; Olson et al., 2013; Hertrich et al., 2016). Secondly, beta values of interaction regressor were calculated and averaged for every ROIs for each seed under the four contrasts (name, familiarity, color and context). Thirdly, we did group-level one-sample t-test (Bonferroni corrected).

# Results

## Behavioral results

During the naming task, participants pronounced correct specific name and basic name for 31.2±9.0% and 59.1±10.4% of the total trials, and made error for 9.7±4.8% (mean ± s.d., n = 120). After the fMRI scanning, we examined how strongly the participants felt they knew the animals of the sample pictures presented in the naming task. In the post-scan familiarity test, we found a significant difference in familiarity ratings among the animals with different naming levels ($F$ (2, 74) = 214.3, $p < 0.0001$, repeated measures ANOVA). Post hoc tests using the Bonferroni correction revealed that subjects rated a significantly higher familiarity for the specific-named items than basic-named items ($p < 0.0001$, two tails) (Fig. 2 B). This pattern was consistent across all participants (Fig. 2A). Behavioral results demonstrated that familiarity covaried with naming performance, i.e., the specific-naming items usually had higher familiarity scores than the basic-naming items. In order to tease apart the effect of naming from familiarity, we divided trials of the naming task based on the participants' naming performances and familiarity ratings into three conditions: 1). high-familiarity & specific-naming (HS) trials, 2). high familiarity & basic-naming (Hb) trials, and 3). low familiarity & basic-naming (lb) trials (see Methods). As a result, familiarity level was adjusted between the 'HS' trials (mean familiarity = 5.50 ± 0.37) and the 'Hb' trials (mean familiarity = 5.44 ± 0.39; $p = 0.123$), and their familiarity levels were substantially larger than that of the 'lb' trials (mean familiarity = 1.53 ± 0.57, $p < 0.0001$ for both, Bonferroni corrected).

In the feature retrieval task, as the relationship between the naming levels and the familiarity ratings in the naming task, there was a significant difference in familiarity ratings between the successful and unsuccessful retrieval trials in both the color-retrieval task [$F$ (1, 18) = *171.1*, $p < 0.0001$, repeated measures ANOVA] and the context-retrieval task ($F$ (1, 12) = *174*, $p < 0.0001$, repeated measures ANOVA). We found that percentage of high familiarity rating trials (scores: 5, 6, 7) in unsuccessful retrieval were significantly smaller in both of the two feature-retrieval tasks (color:17%, n = 170; context:10.5%, n =63) compared with its percentage in basic-naming (28%, n =751) of the naming task (color vs. basic-naming: $\chi^2 = 61.1, p<0.0001;$ context vs. basic-naming: $\chi^2 = 90.5, p<0.0001$). This tendency was stronger in the context-retrieval task than the color retrieval task ($\chi^2 = 17.3, p<0.0001$). Because of the small number of high familiarity rating trials in unsuccessful retrieval, we could not balance them with the high-familiarity rating trials in successful retrieval trials for the feature retrieval tasks.

**Brain regions showing naming effect and familiarity effect**

Using these three trial-conditions as regressors, we successfully differentiated the brain regions that responded to specific-naming (i.e. 'HS > Hb' contrast) from brain regions responded to high familiarity (i.e. 'Hb > lb' contrast) (Table 1, Fig. 3), which contrasts with large overlapping between the brain regions associated with the two effects demonstrated by GLM analyses that did not remove the confounding effect (Fig. 4). The brain regions responsible for specific-naming included left temporal pole (TP, BA38), bilateral superior temporal gyrus (STG, BA41), bilateral supramarginal gyrus (BA40), and left posterior middle temporal gyrus (pMTG, BA21) ($p < 0.05$, FDR corrected in voxel level, Fig. 3, Table 1).

Meanwhile, the brain regions associated with familiarity indexing included the bilateral medial PFC (medial parts of BA9/10), bilateral OFC (BA11), and bilateral occipital cortex (BA18/19) ($p < 0.05$, FDR corrected in voxel level, Fig. 3, Table 1). The results of familiarity effect from categorical GLM contrast ('Hb > lb') was confirmed by a parametric modulation analysis with familiarity ratings (1 - 7) as the modulation parameter. While the two analyses showed similar patterns of brain activation, familiarity effect in the right TP (BA38), right hippocampus, and bilateral calcarine (BA30) reached a statistical significance only in the parametric modulation analysis (Table 2), presumably because of its statistical advantage compared with the categorical contrast. In contrast, results from analyses similar to previous studies, which neglected the covariance between naming and familiarity, showed large overlapping between the brain regions responding to specific-naming and familiarity (Fig. 4).

In addition to the specific brain regions responsible for the specific naming or familiarity effect, we found the left IFG (BA45) to be a commonly activated brain region although the activation sites within this brain region differed between the two effects (Fig. 3). Our results suggested that specific-naming and familiarity during object identification are supported by distinct brain networks, which may possess linkage in the left frontal lobe.

**Connectivity patterns for specific naming and high familiarity**

In order to examine the functional networks related with the naming and the familiarity effects, we conducted PPI analysis using two different seeds in the left IFG, which were determined as the peak positions for the contrasts of 'HS > Hb' and 'Hb > lb' (Fig. 5A).

Figure 5B shows the whole-brain results of the PPI analysis of the naming seed (-52, 44, -2) and familiarity seed (-52 26 14). The naming seed showed increased connectivity in the

'HS' condition, compared with the 'Hb' condition, with the left TP (BA38), left pMTG (BA21), bilateral STG (BA42), bilateral precentral gyrus (BA6), the left supramarginal gyrus (BA40), and bilateral SMA (BA6) ($P < 0.05$, FDR corrected in voxel level, Table 3), which are known to be involved in word generation and speech (Indefrey and Levelt, 2004; Hertrich et al., 2016). On the other hand, the familiarity seed showed stronger connectivity with the right TP and the right hippocampus in 'Hb' than 'Lb' condition (Table 3), which have been reported to support recognition of famous objects (e.g. famous faces, landmarks) and familiarity feeling (Leveroni etl al., 2000; Nakamura et al., 2001; Gainotti 2007; Damasio et al., 2004). Interestingly, under the specific-naming contrast ('HS > Hb'), we found familiarity seed (-52 26 14) connected with similar brain regions as results of the naming seed (-52, 44, -2) (Table 3). In contrast, the naming seed didn't show connectivity with the right TP or hippocampus under high-familiarity contrast ('Hb > lb') (Table 3). These results suggest that posterior-dorsal part of the IFG (i.e. familiarity seed) may be involved in the processes related with both the specific naming and the high familiarity effects, while anterior-ventral part of the IFG (i.e. naming seed) supports only specific naming process. One potential question here is whether or not the differential connectivity patterns in anterior-ventral part of the IFG are observed when the participants retrieve other memory contents of the cue stimuli. For example, is the anterior-ventral part of the IFG recruited only during specific-naming retrieval and not for other modalities of memory content such as color or context? Such a case might entail support by other parts of the IFG for these modalities instead.

## Connectivity patterns for color and context retrievals

We next investigated how the left IFG changed its functional connectivity pattern according to retrieval demands in domains outside of specific-naming. For this purpose, we measured BOLD signals during participants were performing the color-retrieval task and the context-retrieval task, in which the same animal pictures were used as those in the naming task (Fig. 1C). We examined activations to the contrasts of 'successful retrieval > unsuccessful retrieval' ('Yes > No') in the color-retrieval task and the context-retrieval task separately, and found that the left IFG showed significant retrieval effects in both tasks (Fig. 6A). The activation peaks [(-58, 24, 16) for color-retrieval; (-52 28 16) for context-retrieval] were close to the familiarity seed defined by the naming task (-52, 26, 14) as well as the seed reported in the previous literature ["Badre's seed" (-54, 20, 12), (Badre et al., 2005; Badre & Wagner, 2007; Whitney et al., 2011)] suggesting its pivotal role in cognitive control of semantic memory (Fig. 6A). We conducted PPI analyses using Badre's seed as well as the two seeds determined by the activation peaks for color retrieval and context retrieval, and found that the results using the Badre's seed were consistent with those using the other two seeds (Table 4). We note that the Badre's seed (-54, 20, 12) also showed similar results as the familiarity seed in the PPI analyses testing either the specific-naming contrast or the high-familiarity contrast. Hereafter, we showed the results of PPI analyses using the Badre's seed as the present findings can be directly compared with those of the preceding studies.

Figure 6B shows the whole-brain results of the PPI analysis during feature retrieval tasks. The seed showed increased connectivity with the bilateral fusiform gyrus (FG), the bilateral SMA, the right lingual gyrus (LG) during the color-retrieval ($p < 0.001$ uncorrected in voxel level and $p < 0.05$, FDR corrected in cluster level, Table 4). Among these regions, the

fusiform gyrus and lingual gyrus have been implicated in color perception and object color knowledge retrieval (Miceli et al., 2001; Simmons et al., 2007; Hsu et al., 2012; Wang et al., 2013). On the other hand, the same seed showed significantly stronger connectivity with the right parahippocampal gyrus (PHC) ($p < 0.001$, uncorrected in voxel level and $p < 0.05$, FDR corrected in cluster level, Table 4), and the left SMA, and the bilateral occipital lobe ($p < 0.0005$, uncorrected in voxel level, Table 4) during the context-retrieval. The parahippocampal cortex has been reported to support contextual information encoding and retrieving (Davachi, 2006; Diana et al., 2007, 2010; Staresina et al., 2011; Ranganath and Ritchey, 2012). These results indicate that a region within the left IFG connected with different brain regions during the feature retrieval depending on the modalities of to-be-retrieved semantic attributes (i.e. color or context).

## Connectivity patterns across multiple semantic attributes of an object

In order to examine specificity of the connectivity patterns among the modalities of memory contents for their retrieval, we conducted the PPI analyses using the same seeds and the same ROIs in different contrast conditions. In addition to the anterior-ventral naming seed and the posterior-dorsal seed (i.e., Badre's seed) in the left IFG, we used mPFC familiarity seed (-14, 60, 18) as a control, which showed a significant familiarity ('Hb > lb' contrast) effect out of the IFG (Fig. 3). In the present study, totally, eight ROIs were determined (see Methods): the left SMA, left TP, and left pSTG were selected from the specific naming; the right TP, and the right hippocampus were from the familiarity; the bilateral FG were related to color retrieval; the right parahippocampal gyrus was related to context retrieval (Fig. 5 and Fig. 6).

We calculated the beta values of the ROIs in the PPI analyses testing the four contrasts (name, familiarity, color and context).

Figure 7 shows the results of ROI analysis. The bilateral FG and the left SMA showed a significant connectivity increase with the naming seed (anterior-ventral part of IFG) and the Badre's seed (posterior-dorsal part of IFG) for all the retrieval contrasts including name, color and context but not for the familiarity contrast. In addition to these common brain regions, left TP, left pSTG and right PHC increased their connectivity with the two seeds of the left IFG for the specific naming and/or the context retrieval. The patterns of connectivity between the naming seed among the ROIs were similar to those found with Badre's seed for the all three retrieval-dependent contrasts. In contrast to the two seeds in the left IFG, exhibiting a substantial connectivity increase in all three retrieval contrasts, the mPFC familiarity seed showed only a small but significant connectivity increase with the left FG and the left SMA in the context retrieval. The connectivity between mPFC familiarity seed and the left FG was also observed for the high familiarity contrast. The recruitment of the FG across the seeds as well as the contrast types may depend on the attributes of the present stimulus set (i.e. visual objects) (Bi et al., 2016). Interestingly, the Bardre's seed increased connectivity with right TP and HP rather than the left FG under the high familiarity condition.

In addition to the naming seed (-52, 44, -2), we also tested the brain region (-46, 44, -2) determined by the contrast analysis in the feature retrieval tasks (color-retrieval & context-retrieval, see Methods) as a seed for the anterior-ventral part of left IFG. The results in the ROI-based PPI analyses were consistent with those using the naming seed, indicating the robust

involvements of anterior-ventral part of the left IFG in the semantic recollection including the specific naming.

## Discussion

The present study utilized a new object-naming paradigm to unequivocally distinguish the brain mechanisms associated with specific-naming and familiarity indexing. In doing so, strong evidence has been provided for previous suggestions that the lexical retrieval and familiarity assessment stages within visual object identification are differentially processed at the neural level. Additional verification is provided by the connectivity patterns shown in the PPI analyses. These showed significant connectivity of the posterior-dorsal part of left IFG to regions involved in word generation under the specific-naming condition, but significant connectivity with the right TP and right hippocampus under familiarity evaluation for familiar objects. Compared with the posterior-dorsal part of left IFG (e.g., familiarity seed, Badre's seed), the anterior-ventral part of left IFG (e.g., naming seed) only showed the specific-naming effect, which could indicate a graded functional specialization in the left IFG. Furthermore, we detected feature-dependent connectivity patterns that changed in accordance with the target modality of semantic retrieval during feature retrieval tasks.

The first major finding from the present study is that specific naming and recognition of familiar objects operate via different brain networks. The brain areas showing activations under specific-naming condition ('HS > Hb') are highly consistent with results from previous speech and word production studies. The word production network mainly includes the IFG, the posterior STG, the premotor cortex, the SMA, and the parietal–temporal junction (Grabowski et al., 1998; Indefrey and Levelt, 2004; Hickok and Poeppel, 2007; Hickok, 2009; Indefrey, 2011; Hertrich et al., 2016). In addition, the anterior-ventral part of left IFG showed significant connectivity with these word production regions (e.g., SMA, pSTG, etc) under

specific naming. Compared with specific-naming, different brain regions have been detected under high familiarity condition (‘Hb > lb’). In which, the posterior-dorsal part of left IFG connected with the right TP and right hippocampus which have been reported to support recognition and familiarity feeling of familiar objects (Leveroni etl al., 2000; Nakamura et al., 2001; Gainotti 2007; Damasio et al., 2004). Overall, a strong contrast is noted between familiarity and specific-naming retrieval, instantiated at the level of functional connectivity and activation, supporting a great role for the IFG in lexical retrieval and semantic recognition.

Notable results were also detected from the ATL. GLM contrast analyses showed that specific-naming cues activated the left TP. Additional PPI analyses also showed significant connectivity of the left IFG (which has semantic control hub functionality) to the left TP under the specific-naming condition. Compared to the specific-naming condition, the left IFG showed more significant connectivity with the right TP under the high-familiarity objects recognition. These results are of particular interest when compared with the extant literature on the functionality of the ATL in human cognition, for which a number of accounts have been proposed. One view holds that the ATL provides the basis for knowledge of unique entities (e.g. famous people and landmarks). This account also suggests at laterality differences between the left and right ATL (Damasio et al., 1996, 2004; Tranel et al., 1997; Tranel, 2006; Abel et al., 2015), wherein the function of lexical associativity (i.e. naming) for unique entities is domain-specific to the left ATL, and recognition of these items is associated instead with the right ATL. Yet alternative explanations compete for acceptance. For instance, another account claims that the ATL is a domain-general semantic hub (Patterson et al., 2007;

Wong and Gallate, 2012; Ralph et al., 2017). Supporting evidence for this claim is derived mainly from neuropsychological studies of semantic dementia (SD) patients with neural atrophy centering on the anterior temporal regions, bilaterally (Ralph et al., 2001; Jefferies and Ralph, 2006; Rogers et al., 2006; Patterson et al., 2007). These preceding studies have detected object naming deficits in patients that are observed for all categories (e.g. people, animal, tool) and occur secondary to degeneration of conceptual knowledge.

Our results are consistent with the functional lateralization hypothesis laid out within the first account: the left ATL underlies the naming function, and the right ATL supports familiar object recognition and feeling of familiarity. However, an important qualification to these findings is that the present study used images of animals as experimental stimuli. The claim above holds that the ATL only underlies knowledge of unique items (e.g. famous people, landmarks), which would thus exclude generic entities such as animals or tools. On this basis our results would provide partial support for the 'semantic hub' theory; the ATL may indeed serve broader categories of object knowledge. A synthesis of these two positions may be merited in future studies, based on our results and those of the works referenced.

The second major finding was that the semantic control hub of the left IFG possesses a task-dependent connectivity pattern, connecting it with different representational brain regions under corresponding semantic retrieval processes. While the semantic control hub functionality of the left IFG itself is well attested within the literature, this pattern of task-dependent connectivity within the left IFG is a novel discovery. Previous neuropsychological studies have shown that semantic aphasia (SA) patients with brain lesions in the left IFG display object naming deficits. Yet unlike SD patients, the SA patients' naming performance

improved considerably when supplied with phonemic cues, suggesting that the left IFG may not be the storage site for semantic representations but rather the facilitator of top-down control for the retrieval of semantic information (Badre and Wagner, 2007; Whitney et al., 2011; Krieger-Redwood & Jefferies, 2014; Ralph et al., 2017). Distinct from semantic control, semantic representations are assumed to be distributed in or near cortical areas involved in processing corresponding sensory or motor features (Barsalou, 1999; Barsalou et al., 2003; Hauk et al., 2004; Simmons et al., 2007; Kiefer et al., 2008; Binder and Desai, 2011; Hsu et al., 2012). For instance, previous human neuroimaging studies showed that color-knowledge retrieval activates the color-processing system, which includes the fusiform gyrus and lingual gyrus (Hsu et al., 2012; Wang et al., 2013).

While numerous studies have emphasized the role of the left IFG and the representational areas (e.g. sensory, language areas) in semantic processing, comparatively few studies have probed the connectivity patterns between the semantic control area and the semantic representational areas during feature-retrieval task. PPI analyses in the present study showed significant connectivity of the left IFG to word production regions under specific-naming condition; to the FG and LG during the color-retrieval; to the left TP, and right parahippocampal gyrus during the context-retrieval. From the previous studies, we know that the FG and LG have previously been implicated in color knowledge retrieval; the parahippocampal gyrus contributes to context information encoding and storage. This means that the IFG may in fact control different modality-specific representational areas, under correspondingly different semantic retrieval demands. Several previous studies have suggested that there is a graded functional specialization within the left IFG (Badre &

Wagner, 2007; Ralph et al., 2017). Commonly, they distinguished two functional subregions in left IFG. The anterior-ventral part of left IFG top-down controls retrieval process that activates goal relevant knowledge (e.g., object color). The posterior-dorsal part underlies postretrieval selection between simultaneously active semantic representations (irrespective of automatically or controlled retrieved). In the present study, our results showed that the anterior-ventral part of left IFG supports specific naming, color retrieval, and context retrieval, while the posterior-dorsal part of left IFG also supports familiarity. Compared with retrieving names, colors, and contexts of items voluntarily, familiarity comes in our mind more automatically. It means that anterior-ventral part of left IFG correlates with the semantic recollection of task-relevant knowledge, while posterior-dorsal part of left IFG correlates with executive demands across multiple domains, for example, postretrieval selection for automatically activated information.

Unlike the left IFG, the left medial PFC showed no such connectivity pattern. Thought the medial PFC showed high activation under familiar objects recognition ('Hb > Lb' contrast), the brain region didn't connect with domain-specific representational brain regions under semantic memory retrieval task (i.e. name, color, and context retrieval) as the lateral PFC area.

In summary, our results provide strong evidence that specific-naming and familiarity indexing are embedded within different brain networks. In addition, retrieval of specific-name is controlled by the same region in left IFG associated with other attributes retrieval (e.g., color). The specific naming network includes the classical areas related to word production: the left SMA, left pSTG, etc. By contrast, the familiarity network includes the right TP, right

hippocampus. Perhaps foremost importance is our indication that the semantic control hub functionality of the left IFG may be task-dependent; that is to say, it may connect with different domain-specific representational brain regions under the corresponding semantic memory retrieval task (i.e. name, color, and context). It would be future studies to explore the semantic control hub potentiality of the IFG further in relation to its capacity to handle item knowledge of more broad categories, as opposed to strictly unique categories of item (e.g., animals).

## References

Abel TJ, Rhone AE, Nourski KV, Kawasaki H, Oya H, Griffiths TD, Howard III MA, Tranel D (2015) Direct physiologic evidence of a heteromodal convergence region for proper naming in human left anterior temporal lobe. J Neurosci 35:1513–1520.

Badre D, Poldrack RA, Paré-Blagoev EJ, Insler RZ, Wagner AD (2005) Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. Neuron 47:907–918.

Badre D, Wagner AD (2007) Left ventrolateral prefrontal cortex and the cognitive control of memory. Neuropsychologia 45:2883–2901.

Barsalou LW (1999) Perceptual symbol systems. Behav Brain Sci 22:577–660.

Barsalou LW, Simmons WK, Barbey AK, Wilson CD (2003) Grounding conceptual knowledge in modality-specific systems. Trends Cogn Sci 7:84–91.

Belfi AM, Tranel D (2014) Impaired naming of famous musical melodies is associated with left temporal polar damage. Neuropsychology 28(3):429–435.

Bi Y, Wang X, Caramazza A (2016) Object domain and modality in the ventral visual pathway. Trends Cogn Sci 20:282–290.

Bi Y, Wei T, Wu C, Han Z, Jiang T, Caramazza A (2011) The role of the left anterior temporal lobe in language processing revisited: Evidence from an individual with ATL resection. Cortex 47:575–587.

Binder JR, Desai RH (2011) The neurobiology of semantic memory. Trends Cogn Sci 15:527–536.

Bruce V, Young A (1986) Understanding face recognition. Br J Psychol 77:305–327.

Damasio H, Grabowski TJ, Tranel D, Hichwa RD, Damasio AR (1996) A neural basis for lexical retrieval. Nature 380:499–505.

Damasio H, Tranel D, Grabowski TJ, Adolphs R, Damasio AR (2004) Neural systems behind word and concept retrieval. Cognition 92:179–229.

Davachi L (2006) Item, context and relational episodic encoding in humans. Curr Opin Neurobiol 16:693–700.

Deng J, Dong W, Socher R, Li L, Li K, Fei-Fei L (2009) ImageNet: A large-scale hierarchical image database. IEEE computer vision and pattern recognition (CVPR).

Diana RA, Yonelinas AP, Ranganath C (2007) Imaging recollection and familiarity in the medial temporal lobe: a three-component model. Trends Cogn Sci 11:379–386.

Diana RA, Yonelinas AP, Ranganath C (2009) Medial temporal lobe activity during source retrieval reflects information type, not memory strength. J Cogn Neurosci 22:1808–1818.

Drane DL, Ojemann JG, Phatak V, Loring DW, Gross RE, Hebb AO, Silbergeld DL, Miller JW, Voets NL, Saindane AM, Barsalou L, Meador KJ, Ojemann GA, Tranel D (2013) Famous face identification in temporal lobe epilepsy: Support for a multimodal integration model of semantic memory. Cortex 49:1648 –1667.

Friston KJ (1994) Functional and effective connectivity in neuroimaging: a synthesis. Hum Brain Mapp 2:56–78.

Gainotti G (2007) Face familiarity feelings, the right temporal lobe and the possible underlying neural mechanisms. Brain Res Rev 56:214–235.

Gorno-Tempini ML, Price CJ (2001) Identification of famous faces and buildings A functional neuroimaging study of semantically unique items. Brain 124:2087–2097.

Grabowski TJ, Damasio H, Damasio AR (1998) Premotor and prefrontal correlates of category-related lexical retrieval. Neuroimage 7:232–243.

Hauk O, Johnsrude I, Pulvermuller F (2004) Somatotopic representation of action words in human motor and premotor cortex. Neuron 41:301–307.

Hertrich I, Dietrich S, Ackermann H (2016) The role of the supplementary motor area for speech and language processing. Neurosci Biobehav Rev 68: 602–610.

Hickok G (2009) The functional neuroanatomy of language. Phys Life Rev 6: 121–143.

Hickok G, Poeppel D (2007) The cortical organization of speech processing. Nat Rev Neurosci 8:393–402.

Hsu NS, Frankland SM, Thompson-Schill SL (2012) Chromaticity of color perception and object color knowledge. Neuropsychologia 50:327–333.

Indefrey P (2011) The spatial and temporal signatures of word production components: a critical update. Front psychol 2:1–16.

Indefrey P, Levelt WJ (2004) The spatial and temporal signatures of word production components. Cognition 92:101–144.

Jackson RL, Hoffman P, Pobric G, Ralph MA (2016) The semantic network at work and rest: differential connectivity of anterior temporal lobe subregions. J Neurosci 36:1490 –1501.

Jefferies E, Ralph MA (2006) Semantic impairment in stroke aphasia versus semantic dementia: a case-series comparison. Brain 129:2132–2147.

Kiefer M, Sim E, Herrnberger B, Grothe J, Hoenig K (2008) The sound of concepts: Four markers for a link between auditory and conceptual brain systems. J Neurosci 28:12224–12230.

Kikyo H, Ohki K, Miyashita Y (2002) Neural correlates for feeling-of-knowing: an fMRI parametric analysis. Neuron 36:177–186.

Krieger-Redwood K, Jefferies E (2014) TMS interferes with lexical-semantic retrieval in left inferior frontal gyrus and posterior middle temporal gyrus: Evidence from cyclical picture naming. Neuropsychologia 64:24–32.

Leveroni CL, Seidenberg M, Mayer AR, Mead LA, Binder JR, Rao SM (2000) Neural systems underlying the recognition of familiar and newly learned faces. J Neurosci 20:878–886.

Miceli G, Fouch E, Capasso R, Shelton JR, Tomaiuolo F, Caramazza A (2001) The dissociation of color from form and function knowledge. Nat Neurosci 4:662–667.

Nakamura K, Kawashima R, Sugiura M, Kato T, Nakamura A, Hatano K, Nagumo S, Kubota K, Fukuda H, Ito K, Kojima S (2001) Neural substrates for recognition of familiar voices: a PET study. Neuropsychologia 39:1047–1054.

Olson IR, McCoy D, Klobusicky E, Ross LA (2013) Social cognition and the anterior temporal lobes: a review and theoretical framework. SCAN 8:123–133.

Patterson K, Nestor PJ, Rogers TT (2007) Where do you know what you know? The representation of semantic knowledge in the human brain. Nat Rev Neurosci 8:976–987.

Ralph MA, Jefferies E, Patterson K, Rogers TT (2017) The neural and computational bases of semantic cognition. Nat Rev Neurosci 18:42–55.

Ralph MA, McClelland JL, Patterson K, Galton CJ, Hodges JR (2001) No right to speak? The relationship between object naming and semantic impairment: neuropsychological evidence and a computational model. J Cogn Neurosci 13:341–356.

Ranganath C, Ritchey M (2012) Two cortical systems for memory-guided behavior. Nar Rev Neurosci 13:713–726.

Rogers TT, Hocking J, Noppeney U, Mechelli A, Gorno-Tempini ML, Patterson K, Price CJ (2006) Anterior temporal cortex and semantic memory: Reconciling findings from neuropsychology and functional imaging. Cogn Affect Behav Neurosci 6:201–213.

Simmons WK, Ramjee V, Beauchamp MS, McRae K, Martin A, Barsalou LW (2007) A common neural substrate for perceiving and knowing about color. Neuropsychologia 45:2802–2810.

Staresina BP, Duncan KD, Davachi L (2011) Perirhinal and parahippocampal cortices differentially contribute to later recollection of object- and scene-related event details. J Neurosci 31:8739–8747.

Tranel D (2006) Impaired naming of unique landmarks is associated with left temporal polar damage. Neuropsychology 20:1–10.

Tranel D, Damasio H, Damasio AR (1997) A neural basis for the retrieval of conceptual knowledge. Neuropsychologia 35:1319–1327.

Wang Y, Collins JA, Koski J, Nugiel T, Metoki A, Olson IR (2017) Dynamic neural architecture for social knowledge retrieval. Proc Natl Acad Sci U S A 114:3305–3314.

Wang X, Han Z, He Y, Caramazza A, Song L, Bi Y (2013) Where color rests: Spontaneous brain activity of bilateral fusiform and lingual regions predicts object color knowledge performance. NeuroImage 76:252–263.

Whitney C, Kirk M, O'Sullivan J, Ralph MA, Jefferies E (2011) The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior

middle temporal gyrus. Cereb Cortex 21:1066–1075.

Wong C, Gallate J (2012) The function of the anterior temporal lobe: A review of the empirical evidence. Bain Res 1449:94–116.

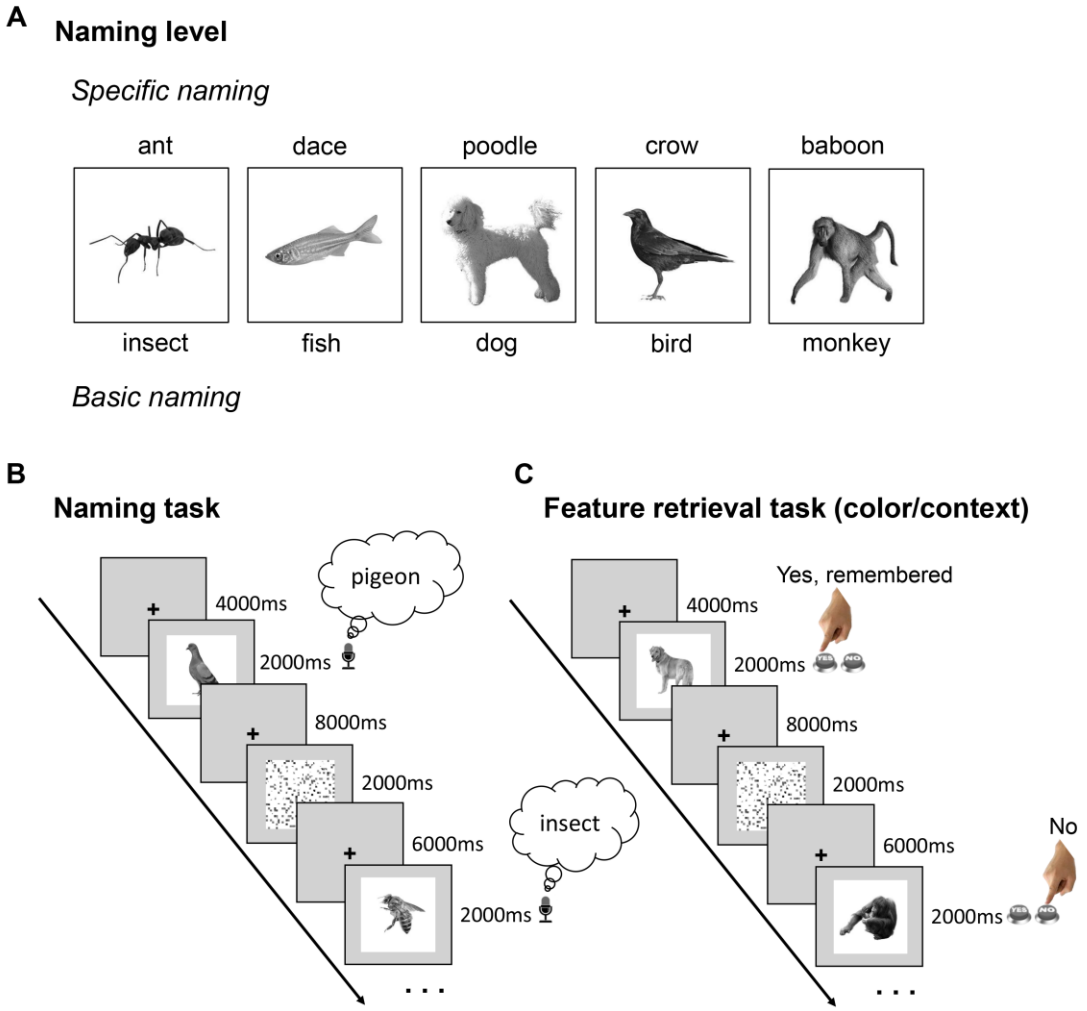


**Figure 1.** Overview of the behavioral paradigm. ***A,*** Examples of stimuli used in both naming and feature-retrieval tasks. Stimulus set consists of five animal categories: bird, fish, insect, dog, and monkey. Each animal has two levels of naming: specific and basic. ***B,*** Schematic depiction of naming task. Participants tried to name the animals overtly at specific level (e.g., pigeon). When they could not remember the specific names of the animals, they named the animals at basic level (e.g., bird). ***C,*** Schematic depiction of feature retrieving task. Participants reported silently whether or not they retrieved modal-specific contents of the animals by pressing one of two buttons (left/'yes', right/'no').

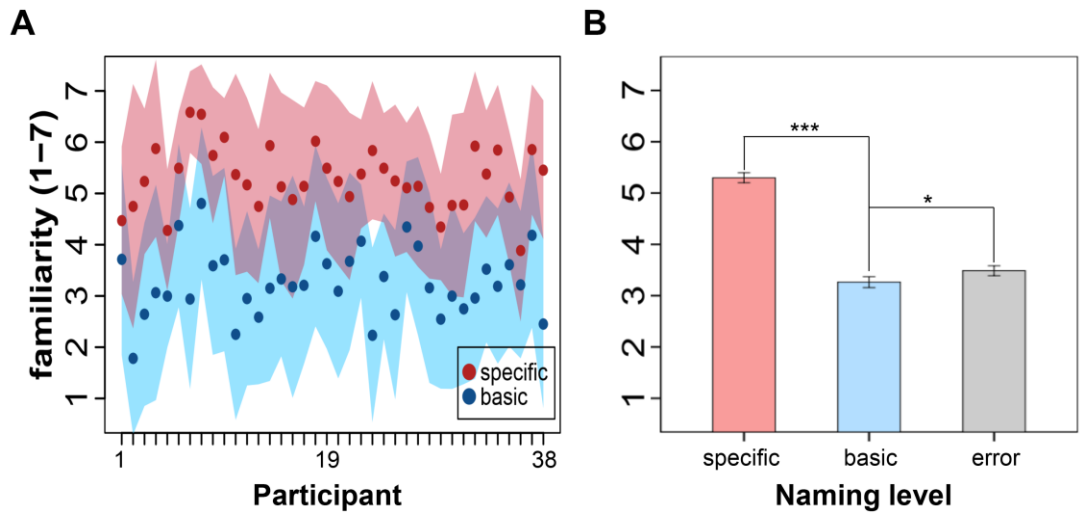


**Figure 2.** Familiarity ratings of specific and basic specific naming trials. ***A***, Single subject's familiarity rating. Each dot indicates an average of familiarity rating of each subject across trials of each naming type (blue: basic; red: specific). SD shown as shading around the mean (pink, specific naming; cyan, basic naming; dark part, overlap between them). ***B***, Mean group familiarity rating of the specific, basic, and error naming trials. Post hoc tests (Bonferroni correction) of the repeated measures ANOVA revealed that the mean familiarity rating of the specific naming trials was significantly higher than the basic naming trials ($p < 0.001$), and the familiarity rating of the error trials was also significantly higher than the basic trials ($p = 0.035$). Error bars indic*at*e SEM. ***:** $p < 0.05$, *******: $p < 0.001$.

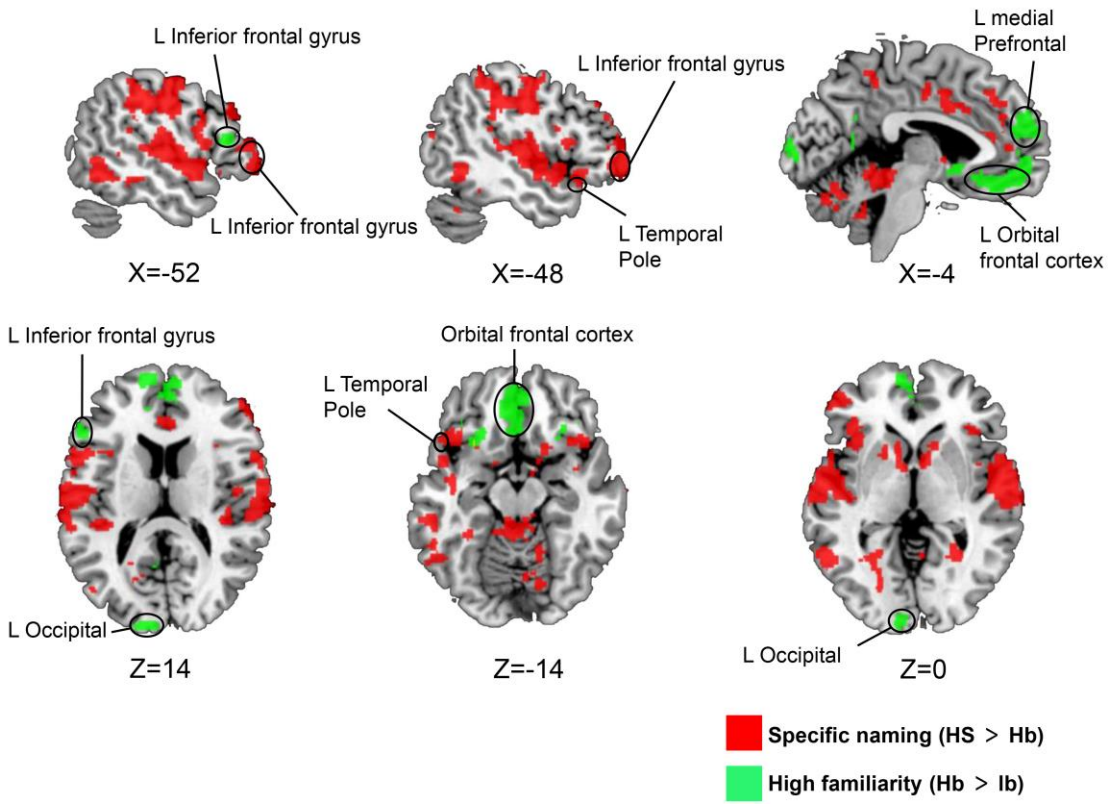


**Figure 3.** Brain regions associated with specific naming or high familiarity. Brain regions related to specific naming were showed in red ($p<0.05$, FDR corrected in voxel level; cluster size $\geqslant$ 10), while those related to high familiarity were showed in green ($p<0.001$, uncorrected at the voxel level; cluster size $\geqslant$ 10). HS, high familiarity under the specific-naming level; Hb, high familiarity under the basic-naming level; lb, low familiarity under the basic-naming level.

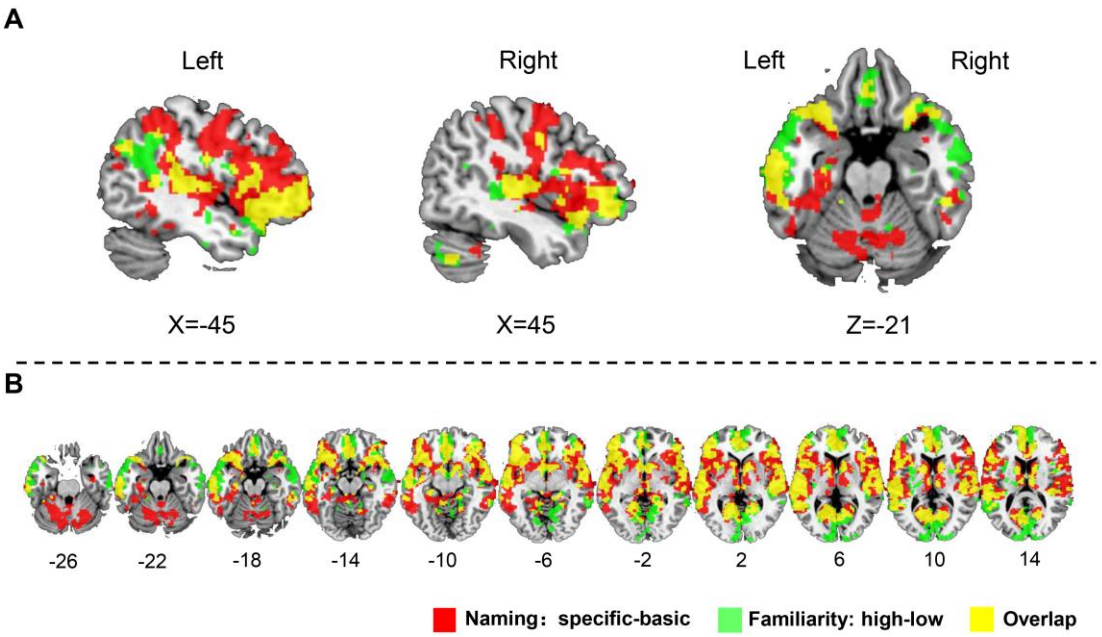


**Figure 4.** Brain regions associated with specific naming or high familiarity without controlling confounding factors. ***A,*** Two symmetric sagittal slices and one horizontal slice showed high overlapping activations (yellow part) between naming level contrast (red part) and familiarity level contrast (green, $p<0.01$, FDR corrected at voxel level; cluster size $\geqslant$ 10). ***B,*** Horizontal slices covering the TP and IFG areas.

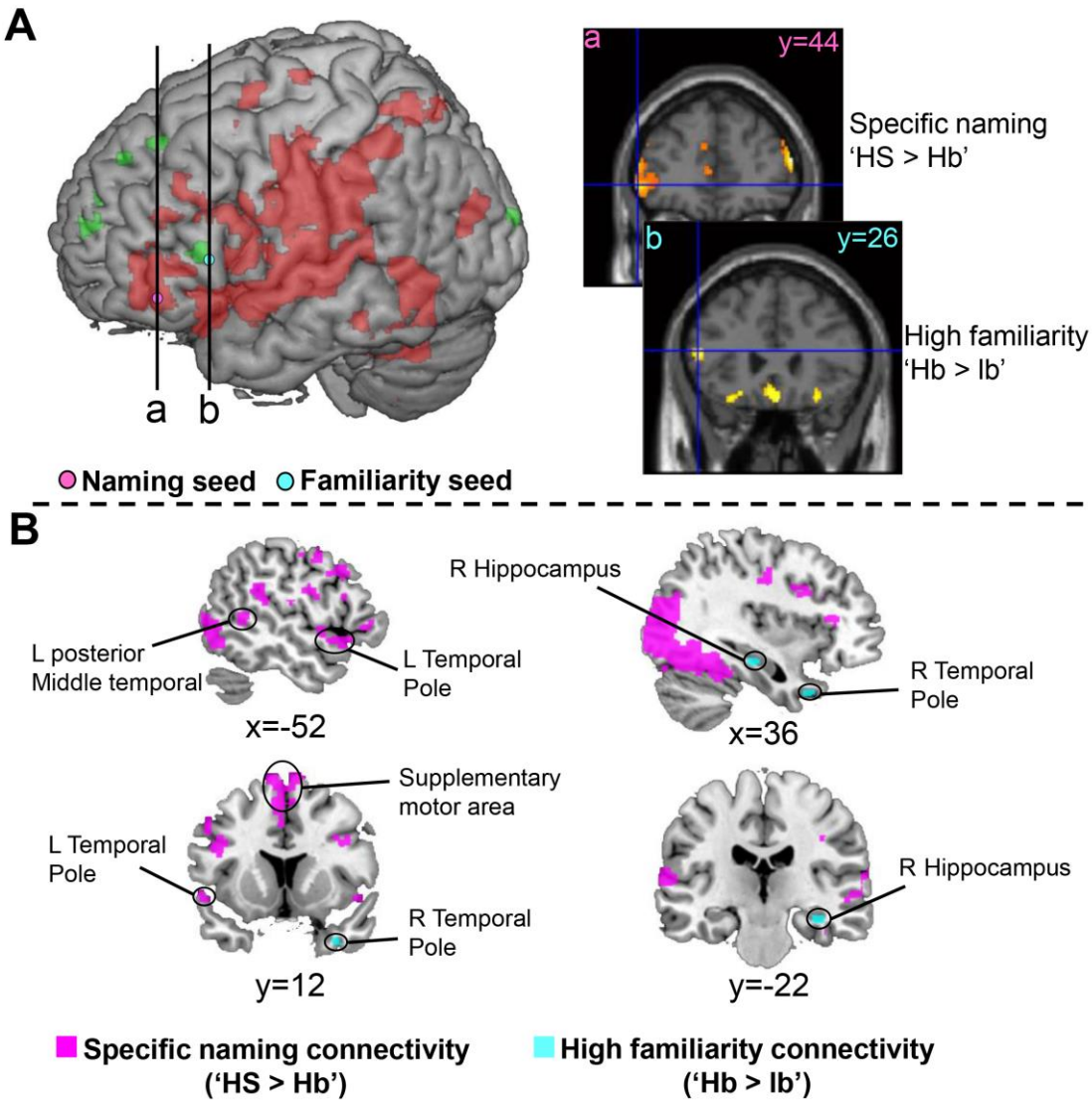


**Figure 5.** PPI analyses of IFG seed areas in contrast: HS＞Hb, and contrast: Hb＞lb. ***A,*** Seed positions of the naming task PPI analyses. The left part shows the positions of the naming seed (pink) and familiarity seed (cyan) on a 3D brain template. The right part shows the same seeds using coronal slices (a, naming seed; b, familiarity seed) to clearly demarcate the anatomical boundaries. ***B,*** Results of the PPI analyses for the two contrasts. Voxels that have significantly stronger connectivity with the naming seed (IFG) during the 'HS' than the 'Hb' condition are shown in pink; voxels that have stronger connectivity with the familiarity seed (IFG) in the 'Hb' than the 'lb' condition are shown in cyan ($p$＜0.001, uncorrected at the voxel level; cluster size ≥ 10).

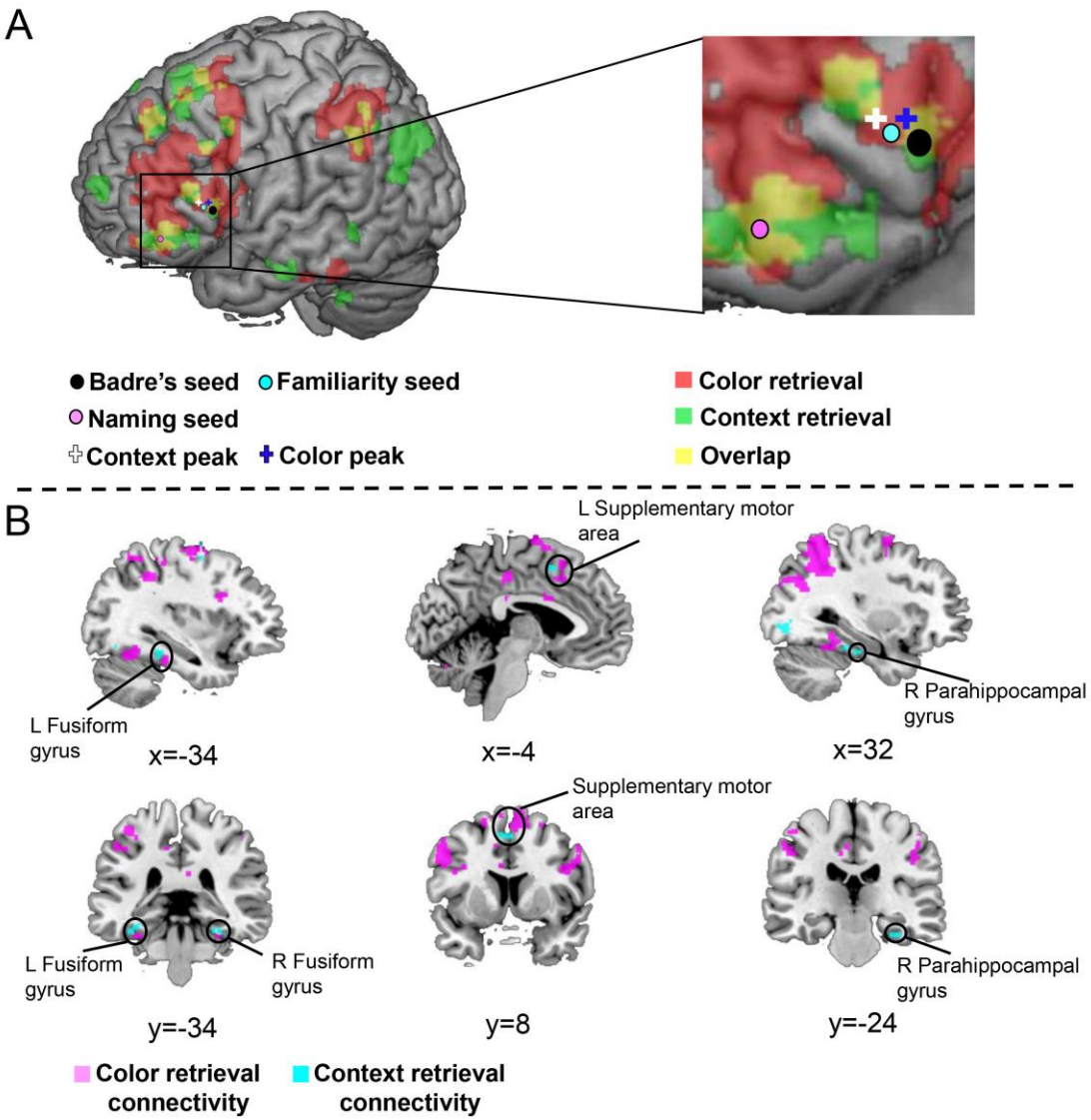


**Figure 6.** PPI analyses of IFG seed areas during context retrieval and color retrieval. ***A,*** Seed positions of the feature retrieval task PPI analyses. The left part shows the positions of the Badre's seed (black), familiarity seed (cyan), naming seed (pink), and the context peak (white cross), color peak (blue cross) on a 3D brain template. The right part shows their positions on an amplified figure of the left IFG area. ***B,*** Results of the PPI analyses of Badre's seed. Voxels that have stronger connectivity with this seed during the retrieval of animal-color information are shown in pink; voxels that have significantly stronger connectivity with this seed during the retrieval of animal-context information are shown in cyan ($p < 0.001$, uncorrected at the voxel level).

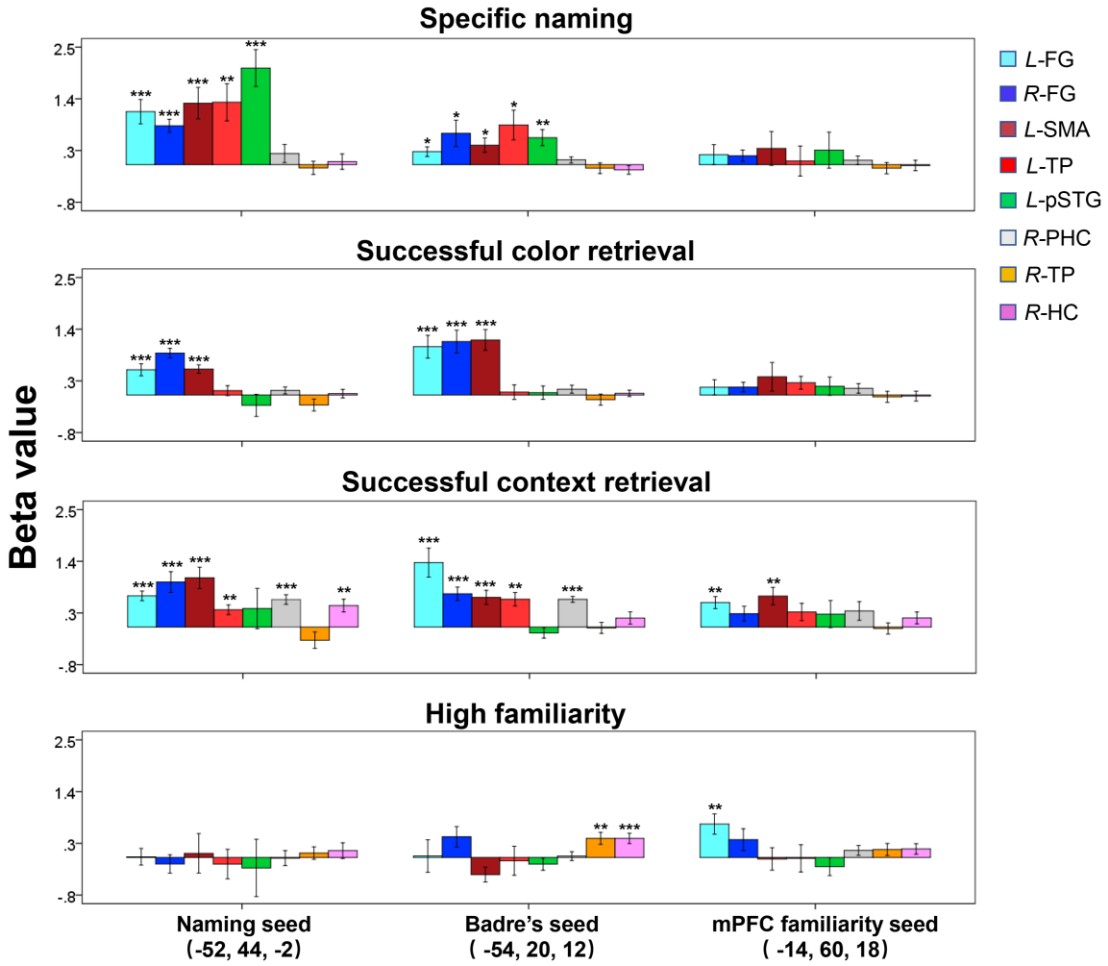


**Figure 7.** ROI analyses of the PPI effects under different retrieval processes. The bilateral FG and the left SMA showed a significant connectivity with the naming seed (IFG, -52, 44, -2) and the Badre's seed (IFG, -54, 20, 12) for all the retrieval conditions including specific name, color and context but not for the familiarity contrast. In addition, the two left IFG seeds showed significant connectivity with the left TP, and left pSTG under the specific naming; with the left TP, and right PHC under context retrieval. Compared with the naming seed, the Bardre's seed also increased connectivity with right TP and HP under the high familiarity condition. In contrast to the two left IFG seeds, the mPFC familiarity seed (medial PFC, -14, 60, 18) didn't show substantial connectivity under specific naming, and color retrieval. It showed only a small but significant connectivity with the left FG and the left SMA in the

context retrieval. The connectivity between mPFC familiarity seed and the left FG was also observed for the high familiarity contrast. Error bars indicate SEM. ***:** $p < 0.05$ (uncorrected t-test); ****:** $p < 0.05$, *****:** $p < 0.01$ (Bonferroni corrected t-test).

*FG, fusiform gyrus; SMA, supplementary motor area; TP, temporal lobe; pSTG, posterior superior temporal gyrus; PHC, parahippocampal gyrus; HC, hippocampus.*

**Table 1. Brain regions associated with specific naming, or high familiarity after controlling the confounding factors**

| Brain Regions | Left/Right | Cluster Size (Voxels) | *t* Value | MNI coordinates | | |
|---|---|---|---|---|---|---|
| | | | | *X* | *Y* | *Z* |
| **Specific Naming (HS＞Hb)** | | | | | | |
| Temporal pole | L | 44 | 3.88 | -48 | 20 | -14 |
| Temporal Sup | L | 1150 | 7.28 | -56 | -18 | 12 |
| | R | 1157 | 7.06 | 52 | -2 | -4 |
| Frontal Inf Tri | L | 169 | 5.72 | -52 | 44 | -2 |
| Frontal Inf Orb | L | 312 | 4.62 | -42 | 18 | -6 |
| Frontal Sup Medial | L | 12 | 3.17 | -4 | 32 | 40 |
| Temporal Mid | L | 83 | 3.78 | -58 | -34 | -16 |
| Temporal Inf | L | 217 | 4.39 | -52 | -56 | -10 |
| Frontal Inf Oper | L | 229 | 4.16 | -52 | 12 | 10 |
| Cingulum Ant | L/R | 123 | 4.76 | 4 | 32 | 16 |
| Cingulum Mid | L/R | 229 | 4.79 | 6 | 8 | 34 |
| Parietal Inf | L | 719 | 5.85 | -54 | -24 | 38 |
| SupraMarginal | L | 402 | 4.80 | -46 | -36 | 28 |
| | R | 60 | 4.91 | 48 | -32 | 46 |
| Precentral | L | 82 | 3.82 | -18 | -24 | 62 |
| Supp Motor Area | R | 22 | 3.84 | 8 | -2 | 60 |
| **High Familiarity (Hb＞Ib)** | | | | | | |
| Frontal Inf Tri | L | 27 | 4.89 | -52 | 26 | 14 |
| Frontal Inf Orb | L | 66 | 5.15 | -22 | 24 | -14 |
| Rectus | L | 126 | 5.89 | -4 | 36 | -16 |
| Frontal Med Orb | L/R | 312 | 5.52 | -4 | 50 | -10 |
| Frontal Sup Medial | L/R | 257 | 5.23 | -14 | 60 | 18 |
| Cingulum Ant | L | 48 | 4.31 | 0 | 50 | 6 |
| Precuneus | L | 10 | 4.23 | -8 | -56 | 28 |
| Occipital Sup | L | 170 | 5.53 | -10 | -98 | 6 |

L/R, the clusters covered bilateral hemispheres. Only clusters with a significant activity of voxel-level threshold $p_{FDR\text{-}corr}＜0.05$ are reported. The *t* values are at the peak voxels in each cluster.

**Table 2. Brain regions parametrically modulated by the familiarity rating**

| Brain Regions | Left/Right | Cluster Size (Voxels) | *t* Value | MNI coordinates | | |
|---|---|---|---|---|---|---|
| | | | | *X* | *Y* | *Z* |
| Temporal pole | L | 53 | 5.17 | -34 | 18 | -26 |
| | R | 10 | 3.74 | 56 | 14 | -10 |
| Hippocampus | R | 24 | 4.69 | 20 | -6 | -14 |
| Rectus | L/R | 187 | 5.16 | -2 | 36 | -18 |
| Frontal Med Orb | L/R | 334 | 5.24 | -2 | 48 | -12 |
| Frontal Sup Medial | L/R | 804 | 5.38 | 0 | 56 | 18 |
| | R | 65 | 4.00 | 62 | -4 | -18 |
| Insula | L | 163 | 6.19 | -30 | 20 | -18 |
| Frontal Inf Tri | L | 396 | 5.62 | -48 | 36 | 0 |
| Frontal Inf Orb | L | 380 | 4.90 | -40 | 28 | -12 |
| | R | 278 | 4.81 | 42 | 32 | -10 |
| Frontal Mid | L | 72 | 4.04 | -34 | 52 | 16 |
| | R | 21 | 4.40 | 48 | 22 | 48 |
| Cingulum Ant | L | 22 | 5.09 | -2 | 48 | 10 |
| Supp Motor Area | L | 91 | 4.66 | -8 | 22 | 56 |
| Precuneus | L | 93 | 4.12 | -2 | -56 | 24 |
| Lingual | L | 58 | 4.46 | -16 | -48 | -2 |
| | R | 48 | 4.73 | 18 | -44 | 0 |
| Calcarine | L | 82 | 5.15 | -16 | -54 | 4 |
| | R | 62 | 4.25 | 10 | -72 | 4 |
| Occipital Sup | L | 180 | 5.21 | -12 | -96 | 6 |

L/R, the clusters covered bilateral hemispheres. Only clusters with a significant activity of voxel-level threshold $p_{FDR\text{-}corr} < 0.05$ are reported. The *t* values are at the peak voxels in each cluster.

**Table 3. Brain regions connected with the lFG seeds in specific naming, or high familiarity condition**

| Brain Regions | Left/Right | Cluster Size (Voxels) | *t* Value | MNI coordinates | | |
|---|---|---|---|---|---|---|
| | | | | *X* | *Y* | Z |
| **Specific Naming (HS＞Hb)** | | | | | | |
| | | *Naming Seed (-52, 44, -2)* | | | | |
| Temporal Pole | L | 61 | 3.63* | -52 | 12 | -8 |
| Temporal Sup | L | 168 | 5.43* | -62 | -22 | 10 |
| | R | 347 | 5.31* | 64 | -30 | 16 |
| Frontal Inf Tri | L | 253 | 5.49* | -44 | 32 | 0 |
| Frontal Inf Orb | R | 27 | 3.23* | 56 | 20 | -6 |
| Temporal Mid | L | 93 | 5.32* | -54 | -48 | 6 |
| SupraMarginal | L | 90 | 5.99* | -46 | -36 | 26 |
| Supp Motor Area | L/R | 903 | 4.17* | -10 | 6 | 70 |
| Precentral | L | 490 | 3.86* | -44 | -6 | 48 |
| | R | 1112 | 5.08* | 42 | -16 | 38 |
| Parietal Sup | L | 56 | 4.12* | -28 | -62 | 54 |
| Fusiform | L | 858 | 4.65* | -40 | -44 | -24 |
| | R | 845 | 6.20* | 32 | -46 | -14 |
| Occipital Mid | L | 1743 | 6.60* | -36 | -88 | 20 |
| | R | 1156 | 5.80* | 46 | -84 | 4 |
| | | *Familiarity Seed (-52, 26, 14)* | | | | |
| Temporal Sup | L | 7 | 3.21 | -52 | -38 | 10 |
| | R | 119 | 4.57 | 48 | -30 | 16 |
| Supp Motor Area | L | 5 | 3.09 | -6 | -12 | 64 |
| | R | 10 | 4.37 | 12 | 4 | 52 |
| Frontal Inf Tri | L | 14 | 3.68 | -44 | 34 | 2 |
| SupraMarginal | L | 28 | 3.67 | -48 | -38 | 28 |
| Precentral | L | 68 | 4.35 | -38 | -6 | 64 |
| | R | 188 | 4.08 | 44 | -10 | 48 |
| Fusiform | L | 28 | 3.37 | -34 | -48 | -14 |
| **High Familarity (Hb＞lb)** | | | | | | |
| | | *Naming Seed (-52, 44, -2)* | | | | |
| Temporal Inf | L | 12 | 4.19 | -48 | -24 | -18 |
| | | *Familiarity Seed (-52, 26, 14)* | | | | |
| Temporal Pole | R | 29 | 4.68* | 34 | 12 | -36 |
| Hippocampus | R | 20 | 4.15* | 36 | -24 | -16 |

L/R, the clusters covered bilateral hemispheres. The asterisks (*) indicates the clusters with a significant activity of voxel-level threshold $p_{FDR\text{-}corr}<0.05$; without asterisks *t* values indicate the clusters with a activity of voxel-level threshold $p_{uncorr}<0.005$. The *t* values are at the peak voxels in each cluster.

**Table 4. Brain regions connected with the Badre's IFG seed in color retrieval, or context retrieval task**

| Brain Regions | Left/Right | Cluster Size (Voxels) | *t* Value | MNI coordinates | | |
|---|---|---|---|---|---|---|
| | | | | *X* | *Y* | *Z* |
| **Color Retrieval (Y＞N)** | | | | | | |
| Fusiform | L | 70 | 4.44* | -32 | -60 | -18 |
| | R | 183 | 5.57* | 30 | -42 | -16 |
| Lingual | R | 256 | 5.92* | 26 | -54 | 2 |
| Frontal Inf Tri | L | 91 | 4.92* | -34 | 10 | 26 |
| | R | 119 | 5.86* | 46 | 32 | 24 |
| Supp Motor Area | L | 205 | 5.50* | -8 | -4 | 74 |
| | R | 230 | 5.06* | 8 | 10 | 60 |
| Precentral | L | 221 | 5.63* | -34 | -4 | 62 |
| | R | 139 | 4.87* | 30 | -2 | 62 |
| Parietal Sup | L | 311 | 5.42* | -22 | -66 | 40 |
| | R | 556 | 7.24* | 34 | -52 | 60 |
| Parietal Inf | L | 349 | 5.14* | -48 | -28 | 42 |
| **Context Retrieval (Y＞N)** | | | | | | |
| ParaHippocampal | R | 87 | 8.71* | 30 | -24 | -24 |
| Supp Motor Area | L | 14 | 4.67 | -8 | 12 | 54 |
| Precentral | L | 22 | 6.25 | -32 | -4 | 60 |
| Occipital Inf | R | 22 | 6.94 | 38 | -64 | -10 |
| | R | 23 | 7.07 | 32 | -80 | -6 |

The asterisks (*) indicates the clusters with a significant activity of voxel-level $p_{uncorr}$＜0.001 and cluster-level $p_{FDR\text{-}corr}$＜0.05. Without asterisks *t* values indicate the clusters with a activity of $p$＜ 0.0005, uncorrected at the voxel level. The *t* values are at the peak voxels in each cluster.