Dissociable Identity- and Modality-Specific Neural Representations as Revealed by Cross-Modal Nonspatial Inhibition of Return

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Abstract: There are ongoing debates on whether object concepts are coded as supramodal identity-based or modality-specific representations in the human brain. In this fMRI study, we adopted a cross-modal “prime–neutral cue–target” semantic priming paradigm, in which the prime–target relationship was manipulated along both the identity and the modality dimensions. The prime and the target could refer to either the same or different semantic identities, and could be delivered via either the same or different sensory modalities. By calculating the main effects and interactions of this 2 (identity cue validity: “Identity_Cued” vs. “Identity_Uncued”) × 2 (modality cue validity: “Modality_Cued” vs. “Modality_Uncued”) factorial design, we aimed at dissociating three neural networks involved in creating novel identity-specific representations independent of sensory modality, in creating modality-specific representations independent of semantic identity, and in evaluating changes of an object along both the identity and the modality dimensions, respectively. Our results suggested that bilateral lateral occipital cortex was involved in creating a new supramodal semantic representation irrespective of the input modality, left dorsal premotor cortex, and left intraparietal sulcus were involved in creating a new modality-specific representation irrespective of its semantic identity, and bilateral superior temporal sulcus was involved in creating a representation when the identity and modality properties were both cued or both uncued. In addition, right inferior frontal gyrus showed enhanced neural activity only when both the identity and the modality of the target were new, indicating its functional role in novelty detection. *Hum Brain Mapp* 35:4002–4015, 2014. © 2014 Wiley Periodicals, Inc.

Key words: cross-modal priming paradigm; cue validity; identity-based; modality-based; fMRI

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INTRODUCTION

Both seeing a tiger and hearing its roars may give us a “run away” signal, which is crucial for survival. An unsolved issue, however, is that whether the visual image and the auditory roar of the tiger are coded in the brain as a supramodal representation, or as modality-specific representations based on the modality of sensory inputs. There have been ongoing debates on how object concepts are represented in the human brain [Martin, 2007]. Based on double dissociation in patients with either selective domain-specific knowledge disorders or selective sensory-motor-specific knowledge disorders, two major theories have been proposed: the domain-specific theory and the sensory-motor theory. The domain-specific theory proposes that object identities are coded in an amodal, unitary semantic system, depending on the semantic category to which the object concepts belong [Caramazza and Shelton, 1998]. From this perspective, semantic information of a specific domain is stored in its corresponding category system regardless of its sensory input modality, that is, a supramodal system. However, the sensory-motor theory suggests that semantic information about an object is represented in the neural substrates, which are involved in perceiving and/or interacting with that object. Different aspects of the meaning of a concept are stored in physically distal neural networks, depending on the sensory modality in which the information is acquired [Barsalou, 1999; Glenberg, 1997; Humphreys and Forde, 2001; Warington and McCarthy, 1987].

The human brain tends to avoid re-examinations of the previously attended (old) objects (including both spatial locations and nonspatial features of the objects), and bias the attention system toward novel objects [Klein, 2000; Posner and Cohen, 1984]. This phenomenon is termed as “inhibition of return (IOR)”, and it exists both in spatial and nonspatial domains, with spatial IOR biasing the attention system toward new spatial locations and nonspatial IOR biasing attention to new objects [Chen et al., 2010; Fox and de Fockert, 2001; Grison et al., 2005; Law et al., 1995; Riggio et al., 2004; Tipper et al., 2003; Zhou and Chen, 2008]. At the neural level, spatial and nonspatial IOR not only share neural correlates in bilateral premotor cortex and bilateral lateral occipital cortex (LOC), but also have specific neural substrates, indicating that despite the behavioral resemblances, spatial, and nonspatial IOR have their unique mechanisms [Zhou and Chen, 2008]. Several theories with regard to the mechanisms of spatial IOR have received substantial empirical supports, such as the reorienting hypothesis [Posner et al., 1985], the detection cost hypothesis [Lupianez, 2010], the inhibitory tagging hypothesis [Fuentes et al., 1999], and the habituation hypothesis [Dukewich, 2009] etc. Since spatial IOR specifically activated bilateral superior parietal cortex, it has been suggested to be associated with the attentional reorienting mechanisms [Zhou and Chen, 2008]. However, since nonspatial IOR specifically activated the left prefrontal

cortex, it has been suggested to be associated with the episodic memory retrieval process [Zhou and Chen, 2008]. For example, in the classical paradigm of nonspatial IOR, a prime, a neutral cue, and a target are consecutively presented at the same central location [e.g., Fuentes et al., 1999]. The appearance of the prime is coded in the brain as an episodic representation/an object file [Kahneman et al., 1992]. Upon the presentation of the neutral cue, a new representation is accordingly created and the old representation of the prime is tagged with inhibition [Grison et al., 2005; Tipper et al., 2003]. If the subsequent target shares properties with the prime, it will trigger the retrieval of the representation of the prime together with the inhibitory tag, and correspondingly result in IOR. On the contrary, if there is no match between the prime and the target, a new representation will be created for the new target.

In this event-related fMRI study, in order to dissociate neural correlates involved in creating novel identity-based and modality-based neural representations, respectively, and to explore the potential interaction between them, we adopted a cross-modal version of the “prime—neutral cue—target” paradigm of nonspatial IOR. Three consecutive objects (i.e., the prime, the neutral cue, and the target) were presented, with visual stimuli being presented at the center of the screen and auditory stimuli being delivered binaurally through headphones (Fig. 1A). Since both the identity and the sensory modality of the target were cued upon the presentation of the prime in this cross-modal paradigm, we manipulated the relationship between the prime and the target (i.e., cue validity) along both the identity dimension and the modality dimension. The prime and the target could refer to either the same or different object identities, and they could be from either the same or different modalities. Thus, the cue validity with regard to the object identity dimension and the cue validity with regard to the modality dimension were orthogonally crossed, resulting in a two (identity cue validity: Identity_Cued vs. Identity_Uncued) by two (modality cue validity: Modality_Cued vs. Modality_Uncued) factorial design. The neutral cue always referred to a different object identity from both the prime and the target. Moreover, since our previous behavioral data consistently suggested that the cross-modal identity-based IOR occurred only when the prime and the neutral cue shared sensory modality [Wang et al., 2012], we kept the modality of the prime and the neutral cue the same in the present fMRI study (Fig. 1A). By adopting the present design, we were both able to differentiate the effects induced by identity cueing and modality cueing, and to investigate the potential interaction between them.

For neural substrates specifically involved in creating a novel identity-based representation for the target irrespective of its sensory modality, they should be localized by the main effect of identity cue validity, “Identity_Uncued (Modality_Cued + Modality_Uncued) > Identity_Cued (Modality_Cued + Modality_Uncued)”. However, for neural substrates specifically involved in creating a new modality-based representation for the target irrespective of its identity, they should be

Figure 1.

A: Examples of experimental paradigm and the timing of stimuli in a single trial. In case that a visual picture of cat served as the prime, four examples in each of the four experimental conditions were given. **B:** Mean RTs, with standard errors from which the between-

subjects variability has been excluded [Cousineau, 2005; Morey, 2008], were shown as a function of all the experimental conditions. The asterisk indicates significant difference between conditions, $P < 0.05$ (new significance level after Bonferroni correction).

localized by the main effect of modality cue validity, “Modality_Uncued (Identity_Cued + Identity_Uncued) > Modality_Cued (Identity_Cued + Identity_Uncued)”. Furthermore, neural correlates, which are involved in evaluating changes of an object along both the identity and the modality dimensions, should be localized by the neural interaction between the identity and the modality cue validity, “Modality_Uncued (Identity_Uncued vs. Identity_Cued) vs. Modality_Cued (Identity_Uncued vs. Identity_Cued)”.

MATERIALS AND METHODS

Participants

Thirteen paid volunteers (seven females, mean age 23 years old) with no history of neurological or psychiatric disorders participated in this study. All of them have normal or corrected to normal vision and normal hearing. They were all right-handed and all of them gave their written informed consent before fMRI scanning. This study was performed in accordance with the Helsinki declaration and was approved by the Institutional Review Board of Beijing MRI Center for Brain Research.

Stimuli and Experimental Design

We chose the black and white outline-drawing pictures of a cat, a bird, and a dog from [Snodgrass and Vander-

wart, 1980] as visual stimuli (Fig. 1A). They were presented through a LCD projector onto a rear projection screen located behind the participants’ head. Participants viewed the screen through an angled mirror on the head-coil of the MRI set up. All the visual stimuli were presented in a box with a black frame which measured 4° (horizontally) $\times$ 4° (vertically) of visual angle at the center of the screen. The default visual display was a dark gray cross measured $1^\circ \times 1^\circ$ of visual angle inside this box, serving as the fixation point. Participants were instructed to fixate at the central fixation cross without moving their eyes throughout the experiment. Auditory stimuli were vocalizations of the three animals, which were standardized in amplitude and were edited to start from the beginning of the sound file. They were presented via MR-compatible head phones. For each participant, the applied output volume was adjusted individually to a comfortable level.

At the start of each trial, the prime (either the picture or the vocalization of a cat or a dog) was presented for 400 ms. The prime was uninformative with respect to either the identity or the modality of the target. After an interval of 200 ms, the neutral cue (a bird), the identity of which was different from both the prime and the target, appeared for 400 ms. Since our previous behavioral data consistently suggested that the cross-modal identity-based IOR occurred only when the neutral cue shared sensory modality with the prime [Wang et al., 2012], we kept the modality of the prime and the neutral cue the same. After another interval of 300 ms, the target was presented for

400 ms. The target was also either the picture or the vocalization of a cat or a dog, that is, it could refer to either the same or different animal from the prime and it could be delivered in either the same or different modality from the prime. Therefore, the identity of the target could be either cued or uncued, and the modality of the target could be either cued or uncued as well (Fig. 1A). Participants were asked to press one of the two buttons on the response pad to discriminate the identity of the target, one button for the cat and the other for the dog. The mapping between the two response buttons and the two target animals was counter-balanced across participants.

Therefore, the experiment was a 2 (identity cue validity: Identity_Cued vs. Identity_Uncued) $\times$ 2 (modality cue validity: Modality_Cued vs. Modality_Uncued) within-subject design, and the fMRI design was event-related. There were 4 experimental conditions (Fig. 1A): (1) the target both referred to the same identity and was from the same modality as the prime ("Identity_Cued & Modality_Cued"); (2) the target referred to a new identity but was from the same modality as the prime ("Identity_Uncued & Modality_Cued"); (3) the target referred to the same identity while was from a new modality compared with the prime ("Identity_Cued & Modality_Uncued"); and (4) the target both referred to a new identity and was from a new modality compared with the prime ("Identity_Uncued & Modality_Uncued"). Within each experimental condition, the possibilities of the target being visual/ auditory and being cat/ dog were equal. There were 96 trials in each of the four experimental conditions. The 384 (4×96) experimental trials and another 96 null trials in which only the central fixation default frame was presented were randomly mixed. The temporal order of trials was randomized for each participant individually in order to avoid potential problems of unbalanced transition probabilities. There was a 10-s rest after every 160 trials, during which only the fixation frame was presented. The inter-trial-intervals were jittered from 1100 to 2100 ms (1100, 1350, 1600, 1850, and 2100 ms). All participants completed a training session of 5 min outside the scanner prior to the formal experiment.

Data Acquisition and Preprocessing

Imaging was conducted using a 3T Siemens Trio system at Beijing MRI Center for Brain Research. Through one run of functional scanning, 802 T2*-weighted echo-planar image (EPI) volumes with blood oxygenation level-dependent contrast (matrix size: 64×64 , pixel size: $3.4 \times 3.4 \times 3.5$ mm³) were obtained. Thirty-seven transversal slices of 3.5 mm thickness that covered the whole brain were interleavedly acquired with a 0.4 mm gap (TR = 2.2 s, TE = 30 ms, FOV = 220 mm, flip angle = 90°). The first five volumes were discarded to allow for T1 equilibration effects.

Functional data were preprocessed using Statistical Parameter Mapping software SPM8 (Wellcome Department of Imaging Neuroscience, London, [http://www.fil.](http://www.fil.ion.ucl.ac.uk)

[ion.ucl.ac.uk](http://www.fil.ion.ucl.ac.uk)). Images were realigned to the first volume to correct for interscan head movements. Then the mean EPI image of each participant was computed and spatially normalized to the Montreal Neurological Institute (MNI) single subject template [Collins et al., 1994; Evans et al., 1994; Holmes et al., 1998], using the "unified segmentation" function in SPM8. This algorithm is based on a probabilistic framework that enables image registration, tissue classification, and bias correction to be combined within the same generative model. The resulting parameters of a discrete cosine transform, which define the deformation field necessary to move individual data into the space of the MNI tissue probability maps [Evans et al., 1994], were then combined with the deformation field transforming between the latter and the MNI single subject template. The ensuing deformation was subsequently applied to individual EPI volumes. All images were transformed into a standard MNI space and resampled to $2 \times 2 \times 2$ mm³ voxel size. The data were then smoothed with a Gaussian kernel of 8 mm full-width-half-maximum to accommodate inter-subject anatomical variability.

Statistical Analysis of Behavioral Data

For each of the four experimental conditions, omissions, incorrect responses and trials with RTs outside mean RT of all the trials $\pm$ 3SD for each condition were excluded from further analysis (2.2% of the overall data points were excluded as outliers in the whole experiment). Mean RTs of the remaining trials were then calculated for each experimental condition. Error rates in each experimental condition were calculated as the proportion between the sum of omissions and incorrect trials and the overall trial number. The mean RTs and error rates were submitted to a 2 (identity cue validity: Identity_Cued vs. Identity_Uncued) $\times$ 2 (modality cue validity: Modality_Cued vs. Modality_Uncued) repeated measures ANOVA, respectively. Significant effects were further examined by planned *t*-tests (with Bonferroni correction).

Statistical Analysis of Imaging Data

Data were highpass-filtered with a cutoff period of 128 s and corrected for serial correlation. We calculated a general linear model to construct a multiple regression design matrix, with the four experimental conditions being modeled as separate regressors (events). Since, we were most interested in the neural activity evoked by the appearance of the target and since neural processes underlying the presentations of the prime and the neutral cue were kept constant across experimental conditions, the four event types were time-locked to the onset of the target of each trial by a canonical synthetic hemodynamic response function and its time derivatives. In addition, since we did not jitter the time interval between the prime, the neutral cue and the target, we could not isolate neural activity related

to the prime and the neutral cue by the present fMRI design. Additionally, all the instructive trials and short rest periods were modeled as confounds, and the behaviorally missed and error trials were included as another regressor of no interest. The six head movement parameters derived from the realignment procedure were also included as confounds. Parameter estimates were subsequently calculated for each voxel using weighted least squares to provide maximum likelihood estimators based on the temporal auto-correlation of the data. No global scaling was applied.

For each participant, simple main effects for each of the four experimental conditions were computed by applying appropriate “1 0” baseline contrasts, that is, the experimental conditions vs. implicit baseline (null trials) contrasts. The four first-level individual contrast images were then fed to a 2×2 within-subject ANOVA at the second group level employing a random-effects model (i.e., the flexible factorial design in SPM8 including an additional factor modeling the subject means). In the modeling of variance components, we allowed for violations of sphericity by modeling non-independence across parameter estimates from the same participant and allowed for unequal variances between conditions and between participants using the standard implementation in SPM8. The significance criterion was set to $P < 0.005$, family wise error corrected for multiple comparisons at cluster level, with an underlying voxel level of $P < 0.001$, uncorrected [Poline et al., 1997].

Masking and Conjunction Procedures

Since the cortical network revealed by the main effect of modality cue validity (Fig. 3A, in red, Supporting Information Table S1a) partly overlapped with the network activated by the interaction between the identity and the modality cue validity (Fig. 3A, in blue, Supporting Information Table S1b), we exclusively masked the two contrasts with each other, to isolate the brain regions which were exclusively involved in the main effect of modality cue validity and the interaction, respectively. Moreover, to localize the brain regions, which were commonly activated by the two contrasts, we did a conjunction analysis between them.

RESULTS

Behavioral Data

A 2 (identity cue validity: Identity_Cued vs. Identity_Uncued) $\times 2$ (modality cue validity: Modality_Cued vs. Modality_Uncued) repeated measures ANOVA on mean RTs showed that the main effect of identity cue validity was significant, $F(1, 12) = 14.9$, $P < 0.005$, indicating that RTs in the Identity_Cued condition (708 ms) were significantly longer than RTs in the Identity_Uncued condition

(684 ms), that is, a significant identity-based repetition inhibition (Fig. 1B). The main effect of modality cue validity was not significant, $F < 1$. Moreover, the interaction was significant, $F(1, 12) = 4.97$, $P < 0.05$. Further planned t tests on simple effects showed that the size of the identity-based repetition inhibition effect was significantly larger when the target and the prime were from different modalities (Modality_Uncued, 33 ms) than when they were from the same modality (Modality_Cued, 14 ms), $t(12) = 2.23$, $P < 0.05$ (Fig. 1B). In addition, analysis of error rates (1.9, 1.7, 2.1, and 2.9% for “Identity_Cued & Modality_Cued”, “Identity_Uncued & Modality_Cued”, “Identity_Cued & Modality_Uncued” and “Identity_Uncued & Modality_Uncued” conditions, respectively) did not show any significant effects, all P values > 0.1 .

Imaging Data

Main effect of identity cue validity

Bilateral LOC extending to the inferior temporal gyrus were significantly activated in the neural contrast “Identity_Uncued (Modality_Cued + Modality_Uncued) $>$ Identity_Cued (Modality_Cued + Modality_Uncued),” by showing higher neural activity in the Identity_Uncued condition than in the Identity_Cued condition, irrespective of the sensory modality (Fig. 2A, in green and Table I). Mean parameter estimates in the four experimental conditions were extracted from the activated clusters, respectively, and were submitted to a 2 (identity cue validity: Identity_Cued vs. Identity_Uncued) $\times 2$ (modality cue validity: Modality_Cued vs. Modality_Uncued) repeated measures ANOVA (Fig. 2B). For the left LOC, the only significant effect was the main effect of identity cue validity, $F(1, 12) = 27.2$, $P < 0.001$, indicating that neural activity was significantly higher when the identity of the target was uncued (new) than cued (old) irrespective of whether the modality of the target was cued or not (Fig. 2B, left). Neither the main effect of modality cue validity nor the interaction was significant, both $P > 0.1$. Similarly for the right LOC, the main effect of identity cue validity was the only significant effect, $F(1, 12) = 20.9$, $P < 0.005$, indicating significantly higher neural activity when the identity of the target was uncued (new) than cued (old) irrespective of whether the modality of the target was old or new (Fig. 2B, right). Neither the main effect of modality cue validity nor the interaction was significant, both $P > 0.1$. There was no significant activation in the reverse contrast, that is, “Identity_Cued (Modality_Cued + Modality_Uncued) $>$ Identity_Uncued (Modality_Cued + Modality_Uncued)”.

Main effect of modality cue validity

The neural contrast “Modality_Uncued (Identity_Cued + Identity_Uncued) $>$ Modality_Cued (Identity_Cued + Identity_Uncued)” was calculated to localize the brain regions responsible for building up modality-based neural

Figure 2.

A: Three dissociated brain networks. Green: bilateral LOC was involved in the main effect of identity cue validity, that is, the contrast “Identity_Uncued (Modality_Cued + Modality_Uncued) > Identity_Cued (Modality_Cued + Modality_Uncued)”. Red: left dorsal premotor cortex and left IPS were specifically involved in the main effect of modality cue validity, that is, the main effect contrast “Modality_Uncued (Identity_Cued + Identity_Uncued) > Modality_Cued (Identity_Cued + Identity_Uncued)” exclusively masked by the interaction contrast “Modality_Uncued (Identity_Uncued > Identity_Cued) > Modality_Cued (Identity_Uncued > Identity_Cued)” at a liberal threshold of $P < 0.05$, uncorrected. Blue: bilateral superior temporal sulcus (STS) was specifically involved in the interaction between the identity and

the modality cue validity, that is, the interaction contrast “Modality_Uncued (Identity_Uncued > Identity_Cued) > Modality_Cued (Identity_Uncued > Identity_Cued)” exclusively masked by the main effect contrast “Modality_Uncued (Identity_Cued + Identity_Uncued) > Modality_Cued (Identity_Cued + Identity_Uncued)” at a liberal threshold of $P < 0.05$, uncorrected. Mean parameter estimates were extracted from the clusters of the identity-specific network (**B**), the modality-specific network (**C**), and the interaction-specific network (**D**), and are displayed as a function of the experimental conditions (IC: Identity_Cued; IU: Identity_Uncued), respectively. The asterisk indicates significant difference between conditions, $P < 0.05$ (new significance level after Bonferroni correction).

Figure 3.

A: Main effect of modality cue validity and interaction between the identity and modality cue validity without masking with each other. Red: the main effect of modality cue validity, that is, the contrast “Modality_Uncued (Identity_Cued + Identity_Uncued) > Modality_Cued (Identity_Cued + Identity_Uncued)”. Blue: the interaction between identity and modality cue validity, that is, the contrast “Modality_Uncued (Identity_Uncued > Identity_Cued) > Modality_Cued (Identity_Uncued > Identity_

Cued)”. **B:** Statistical conjunction between main effect of modality cue validity and interaction. Mean parameter estimates were extracted from the commonly activated cluster, and are displayed as a function of the experimental conditions (IC: Identity_Cued; IU: Identity_Uncued). The asterisk indicates significant difference between conditions, $P < 0.05$ (new significance level after Bonferroni correction).

representations for the target irrespective of whether its identity was cued or not. A neural network including bilateral precentral gyrus, bilateral intraparietal sulcus (IPS), bilateral middle temporal gyrus, anterior cingulate cortex (ACC), supplementary motor area, and cerebellum, was significantly activated (Fig. 3A, in red and Supporting Information Table S1). There was no significant activation

in the reverse contrast, that is, “Modality_Cued (Identity_Cued + Identity_Uncued) > Modality_Uncued (Identity_Cued + Identity_Uncued)”.

To further localize the brain regions, which were activated only by the main effect of modality cue validity but not by the interaction, we exclusively masked the main effect contrast “Modality_Uncued (Identity_Cued + Identity_

TABLE I. The three networks exclusively involved in the main effect of identity cue validity, the main effect of modality cue validity, and the interaction between identity and modality cue validity

Anatomical regions	Cluster peak	Z scores	No. of voxels
(a) Identity_Uncued > Identity_Cued (with Modality_Cued and Modality_Uncued combined)			
Left middle occipital gyrus	-38, -84, 6	5.46	3425
Right inferior occipital gyrus	26, -84, -4	5.03	927
(b) Modality_Uncued > Modality_Cued (with Identity_Cued and Identity_Uncued combined) masked by interaction			
Left premotor cortex	-38, 0, 62	5.68	987
Left IPS	-18, -54, 48	4.29	472
(c) Modality_Uncued (Identity_Uncued > Identity_Cued) > Modality_Cued (Identity_Uncued > Identity_Cued) masked by modality cue validity			
Right superior temporal sulcus	52, -4, -6	4.87	839
Left superior temporal sulcus	-50, -12, 0	4.79	302

Coordinates (x, y, z) correspond to MNI space.

Uncued) > Modality_Cued (Identity_Cued + Identity_Uncued)" with the interaction contrast "Modality_Uncued (Identity_Uncued > Identity_Cued) > Modality_Cued (Identity_Uncued > Identity_Cued)" at a liberal threshold of $P < 0.05$, uncorrected at the voxel level. In this way, those voxels that reached a level of significance at $P < 0.05$ (uncorrected) in the mask contrast (i.e., in the interaction contrast) were excluded from the analysis. Left dorsal premotor cortex and left IPS were significantly activated (Fig. 2A, in red and Table I). Mean parameter estimates in the four experimental conditions were further extracted from the activated clusters and submitted to a 2 (identity cue validity: Identity_Cued vs. Identity_Uncued) $\times$ 2 (modality cue validity: Modality_Cued vs. Modality_Uncued) repeated measures ANOVA, respectively (Fig. 2C). For the left precentral gyrus, the main effect of modality cue validity was the only significant effect, $F(1, 12) = 13.5$, $P < 0.005$, indicating that neural activity was significantly higher when the modality of the target was new (uncued) than old (cued) irrespective of whether the identity of the target was cued or not (Fig. 2C, left). Neither the main effect of identity cue validity nor the interaction was significant, both $ps > 0.1$. Similarly for the left IPS, the main effect of modality cue validity was the only significant effect, $F(1, 12) = 14.9$, $P < 0.005$, showing that neural activity was significantly higher in the Modality_Uncued condition than in the Modality_Cued condition irrespective of whether the identity of the target was cued or not (Fig. 2C, right).

Interaction between identity cue validity and modality cue validity

The interaction contrast "Modality_Uncued (Identity_Uncued > Identity_Cued) > Modality_Cued (Identity_Uncued > Identity_Cued)" revealed a neural network including bilateral middle frontal gyrus, left inferior frontal cortex, bilateral IPS, bilateral superior temporal sulcus (STS), and ACC (Fig. 3A, in blue and Supporting Information Table I). There was no significant activation in the reverse contrast,

that is, "Modality_Cued (Identity_Uncued > Identity_Cued) > Modality_Uncued (Identity_Uncued > Identity_Cued)".

To further localize the brain regions, which were activated only by the interaction but not by the main effect of modality cue validity, we exclusively masked the interaction contrast with the main effect of modality cue validity "Modality_Uncued (Identity_Cued + Identity_Uncued) > Modality_Cued (Identity_Cued + Identity_Uncued)" at a liberal threshold of $P < 0.05$, uncorrected at the voxel level. In this way, those voxels that reached a level of significance at $P < 0.05$ (uncorrected) in the mask contrast (i.e., in the main effect of modality cue validity) were excluded from the analysis. Bilateral STS were significantly activated (Fig. 2A, in blue and Table I). Mean parameter estimates extracted from the bilateral STS were entered into a 2 (identity cue validity: Identity_Cued vs. Identity_Uncued) $\times$ 2 (modality cue validity: Modality_Cued vs. Modality_Uncued) repeated measures ANOVA, respectively. For the right STS, the only significant effect was the interaction between identity cue validity and modality cue validity, $F(1, 12) = 54.4$, $P < 0.001$. Neither the main effect of identity cue validity nor the main effect of modality cue validity was significant, both $F < 1$. Planned t tests on simple effects showed that neural interaction in this area was caused by significantly higher neural activity in the "Identity_Cued and Modality_Cued" condition and the "Identity_Uncued and Modality_Uncued" condition than in the "Identity_Uncued and Modality_Cued" condition and the "Identity_Cued and Modality_Uncued" condition, all P values < 0.01 (Fig. 2D, left). The left STS showed a similar pattern of neural activity as the right STS (Fig. 2D, right).

Conjunction analysis between main effect of modality cue validity and interaction

To further localize the brain regions, which were commonly involved in the main effect of modality cue validity and the interaction, we performed a statistical conjunction analysis between the two contrasts (Friston et al., 2005).

Right inferior frontal gyrus extending to right superior frontal gyrus via right middle frontal cortex (MNI coordinates of peak voxel: $x = 48$, $y = 12$, $z = 38$, and $Z = 4.37$) was significantly activated (Fig. 3B, in violet and Supporting Information Table S1c). Mean parameter estimates were extracted from the activated region and submitted into a 2 (identity cue validity: “Identity_Cued” vs. “Identity_Uncued”) $\times$ 2 (modality cue validity: “Modality_Cued” vs. “Modality_Uncued”) repeated measures ANOVA. Both main effect of modality cue validity, $F(1, 12) = 13.1$, $P < 0.005$, and the interaction, $F(1, 12) = 19.3$, $P < 0.005$, were significant. The main effect of identity cue validity was not significant, $F(1, 12) = 1.96$, $P > 0.1$. With regard to the significant interaction, planned t tests on simple effects suggested that neural activity was significantly higher in the “Identity_Cued and Modality_Cued” condition than in the “Identity_Uncued and Modality_Cued” condition on the one hand, $t(12) = 3.94$, $P < 0.005$, and neural activity was significantly higher in the “Identity_Uncued and Modality_Uncued” condition than in the “Identity_Cued and Modality_Uncued” condition on the other hand, $t(12) = 3.31$, $P < 0.01$. More importantly, with regard to the significant main effect of modality cue validity, it was driven by the significantly enhanced neural activity in the “Identity_Uncued and Modality_Uncued” condition: neural activity in the “Identity_Uncued and Modality_Uncued” condition was significantly higher than neural activity in all the other three conditions, i.e., all the planned t -test comparisons were significant both before and after Bonferroni correction, P values < 0.05 (new significance level after Bonferroni correction; Fig. 3B). This pattern of neural activity differed from both the brain regions which were exclusively involved in the main effect of modality cue validity (Fig. 2C) and the brain regions, which were exclusively involved in the interaction (Fig. 2D).

DISCUSSION

By adopting a novel cross-modal semantic priming paradigm in this fMRI study, we aimed at dissociating the three neural networks involved in creating novel identity-based representations irrespective of input modality, in creating novel modality-based representations irrespective of object identity, and in evaluating the identity and modality dimensions of an object in an interactive way, respectively.

Theoretical Implications on the Cognitive Models of Nonspatial IOR

At the behavioural level, the identity-based inhibition was significant both when the modality of the target was cued and uncued. The modality-based inhibition, however, was not significant. Since the prime and the neutral cue were always from the same sensory modality in this study, there was no need to create a new modality representation

upon the appearance of the neutral cue. It was thus not necessary to tag inhibition to the modality representation of the prime, and accordingly no modality-based inhibition was observed in this study.

More importantly, the identity-based inhibition was significantly larger when the modality was uncued than cued (Fig. 1B). This pattern of interaction was consistent with previous behavioral evidence which showed that IOR based on the task-relevant dimension was larger when the task-irrelevant dimension was uncued than cued [Chen et al., 2007, 2010]. To explain the cognitive mechanisms that IOR emerges at longer SOAs in discrimination tasks than in simple detection tasks and the finding that the more difficult the discrimination task, the longer the SOA at which IOR emerges, Lupiáñez et al. [1997, 2001] proposed that the process of integrating current perceptual information with memory representations of prior experience determines when and how IOR emerges. Kahneman et al. [1992] suggested that the onset of a visual target initiates the retrieval of memory representation of similar prior events, which they called “object files.” The spatiotemporal information of the current target is then compared with that of the prior event. If this process reveals a spatiotemporal match, the memory representation of a prior event is updated with information from the current target; if there is no spatiotemporal match with an existing memory representation, a new representation is created for target. Borrowing this framework, Milliken et al. [2000] and Lupiáñez et al. [1997, 2001] proposed further that whether an existing memory representation is updated or a new representation is created is determined not only by the physical spatiotemporal correspondence between the present and past events, but also by the attentional set that participants adopt in a particular task context. For example in the identity discrimination task of this study, when the prime and the target differed on the task-relevant identity dimension, participants might adopt an attentional set of creating a new representation for the target because integrating the distinctively different (on the task-relevant identity dimension) prime and target representations would incur costs to the task performance. In this context, having different task-irrelevant modality between the prime and the target would make easier the creation of a new representation for the target while having the same task-irrelevant modality would make the creation of the new object representation more difficult (Fig. 1B, the two triangle data points). The two cognitive processes together resulted in larger identity-based IOR when the modality was uncued than cued.

Since we used a limited number of visual (one dog picture and one cat picture) and auditory (one dog sound and one cat sound) stimuli as the prime and the target, one may argue that the repetition-induced inhibition in this study might be simply based on basic sensory features, rather than object identity per se. For example, the repetition-induced inhibition could be simply based on visual shapes when the prime and the target were both

the dog picture or both the cat picture, or simply based on auditory frequency or timbre when the prime and the target were both the dog sound or both the cat sound. Please note, however, the repetition-induced inhibition was observed not only when the prime and the target shared sensory modality, but also when they differed in input modalities (Fig. 2B). In the latter case, since the prime and the target differed in the initial sensory processing stages, the repetition-induced inhibition must be based on object identities per se rather than basic sensory input properties. Furthermore, the limited set of stimuli could neither limit the generalization of our results nor be simply attributed to adaptation. First, in the study, in which the phenomenon of nonspatial (color-based) IOR was first observed, only two colors (red and blue) were used for the prime and the target as well [Law et al., 1995]. Later studies, however, consistently suggested that this phenomenon of nonspatial IOR can be generalized to many other nonspatial object features, such as shape, line length, face etc. [Fox and de Fockert, 2001; Francis and Milliken, 2003; Grison et al., 2005; Riggio et al., 2004; Tipper et al., 2003]. Second, in the classical adaptation paradigm, two identical stimuli are consecutively presented with a short interstimulus interval [Grill-Spector et al., 2001, 2006]. In the “prime- neutral cue- target” paradigm of our study, however, a different stimulus (neutral cue) was presented between the prime and the target, and the SOA between the prime and the target was relatively long (1300 ms). Therefore, there should be no adaptation to the target.

The Domain-Specific Theory vs. the Sensory-Motor Theory

At the neural level, we found neural evidence supporting the domain-specific theory and the sensory-motor theory, respectively. In the multisensory environment around us, upon the appearance of a new object, its identity-specific representation and modality-specific representation are coded in physically distal neural networks. Furthermore, we found neural correlates underlying the interaction between the sensory modality and the semantic identity of an object. Specifically speaking, three distinct networks were exclusively involved in the two main effects and the interaction of the present experiment: bilateral LOC showed significantly higher neural activity when the identity of the target was uncued (new) than cued (old), irrespective of whether the modality of the target was cued or uncued, which thus supported the domain-specific theory; left dorsal premotor cortex and left IPS showed significantly higher neural activity when the modality of the target was uncued (new) than cued (old), irrespective of whether the identity of the target was cued or uncued, which thus supported the sensory-motor theory; and bilateral STS were significantly activated when the modality and the identity of the target were both cued or both uncued (Fig. 2), which thus indicated the func-

tional role of STS in evaluating changes of an object along both the modality and the identity dimensions.

First, the domain-specific theory proposes that object identities are coded in a supramodal semantic system, depending on the semantic category to which the object concepts belong [Caramazza and Shelton, 1998]. Our results suggested that bilateral LOC was involved in creating such supramodal representations by showing higher neural activity to new objects irrespective of whether the modality of the objects was new or old (Fig. 2B). LOC has been suggested to be a multimodal brain region for processing objects [Amedi et al., 2001; Lacey et al., 2009]. For example, LOC was activated not only when participants were viewing pictures of objects [Grill-Spector, 2003; Grill-Spector et al., 2001; Malach et al., 1995], but also when recognizing objects through touch [Amedi et al., 2001, 2002]. The functional role of LOC in responding to identity-specific representations was also revealed in the object priming paradigm in which two object pictures were consecutively presented, that is, the prime and the target [Grill-Spector et al., 2001; Simons et al., 2003]. When the identity of the target was the same as that of the prime, there was a facilitatory (fastened) behavioral effect for repeated targets while neural activity in LOC was lower for the repeated targets as compared to new targets [Grill-Spector et al., 2001, 2006; Martin, 2007; Simons et al., 2003]. This reduced neural activation to repeated targets is termed as repetition suppression (RS), which indicates neural adaptation to old object identities and sensitivity to new identities [Grill-Spector et al., 2006]. The RS effect in LOC thus suggests that LOC plays an important role in coding object representations. Moreover, the RS effect in LOC was also observed in a cross-modal priming paradigm in which an object picture was presented prior to tactile exploration of the same or a different object [Tal and Amedi, 2009]. Neural activity in LOC was reduced by repeated target identities irrespective of the input sensory modality, that is, a supramodal RS effect, suggesting that coding a new object representation in LOC is supramodal. Therefore, together with previous evidence on the RS effect, our results suggest that LOC is involved in coding supramodal identity representations.

Previous studies on neural correlates underlying spatial IOR have consistently revealed the involvement of bilateral precentral gyrus (including frontal eye fields) and bilateral parietal cortex, by collapsing cued and uncued trials at long stimulus onset asynchronies (SOAs) between the prime and the target, and comparing them with those at short SOAs [Lepsien and Pollmann, 2002; Mayer et al., 2004a,b; Rosen, 1999]. In one of our previous studies, we directly compared the neural correlates underlying spatial and nonspatial IOR, and found both shared and specific neural mechanisms [Zhou and Chen, 2008]. By comparing long SOA trials with short SOA trials (cued and uncued trials combined), we found that spatial and nonspatial IOR commonly activated bilateral precentral gyrus and bilateral LOC, supporting the functional role of bilateral LOC in

coding both spatial and nonspatial representations. On the other hand, bilateral superior parietal cortex was specifically activated by spatial, rather than nonspatial, IOR in the “long SOA trials vs. short SOA trials” contrast, indicating the functional role of bilateral superior parietal cortex in specifically representing spatial locations. Furthermore, left prefrontal cortex showed significantly higher neural activity in cued trials than in uncued trials specifically during nonspatial, rather than spatial, IOR, implying that the episodic retrieval process in the prefrontal cortex may be implicated to inhibit old nonspatial representations during nonspatial IOR [Grison et al., 2005; Tipper et al., 2003]. In this study, we did not find any significant neural activations associated with the Identity_Cued condition as compared with the Identity_Uncued condition (i.e., in the main effect contrast “Identity_Cued > Identity_Uncued”). In the reverse contrast, however, we found that bilateral LOC was significantly activated by the Identity_Uncued condition compared to the Identity_Cued condition (i.e., in the main effect contrast “Identity_Uncued > Identity_Cued”; Fig. 2B), suggesting that bilateral LOC is involved in coding novel identity-based representations during nonspatial IOR. Nonspatial identity-based IOR is conjointly achieved by the two processes in the cued and uncued conditions: when the identity of the target is identical to that of the prime (cued), the episodic representation of the prime, which is tagged with inhibition, is retrieved, and inhibitory responses are accordingly induced; when the identity of the target is new (uncued), a new identity-based representation is accordingly created for the target. Our present results, together with previous evidence, suggest that the episodic retrieval process in the left prefrontal cortex is involved in inhibiting old identity representations [Zhou and Chen, 2008], and the bilateral LOC is involved in creating new identity representations during nonspatial IOR.

Second, the sensory-motor theory emphasizes the role of sensory properties in organizing object information [Barsalou, 1999; Goldberg et al., 2006; Humphreys and Forde, 2001; Warrington and McCarthy, 1987], and our results suggest that left dorsal premotor cortex and left IPS are involved in coding new modality-specific representations irrespective of object identity (Fig. 2C). The left frontal and parietal areas are part of the dorsal fronto-parietal network which is implicated in the control of both spatial and nonspatial attention [Corbetta and Shulman, 2002; Corbetta et al., 2000; Hopfinger et al., 2000; Liu et al., 2003; Serences et al., 2004; Yantis et al., 2002]. This fronto-parietal network was involved not only in guiding location-based and object-based attentional orienting, but also in voluntarily directing attention between sensory modalities. For example, Shomstein and Yantis [2004] found that left posterior parietal and right middle frontal cortices exhibited transient increased signal when attention was voluntarily shifted from audition to vision or vice versa [Shomstein and Yantis, 2004]. Similar evidence comes from a visual-tactile study in which brain activity in the left IPS was enhanced when participants transferred object information

between vision and touch [Grefkes et al., 2002]. Our results further showed that the left dorsal premotor cortex and the left IPS were involved in creating a new modality-specific representation, which was independent of whether the identity of the target was old or new.

In a recent study, Langner et al. [2011] presented a cue prior to the actual presentation of the targets, and the cue was highly predictive of the sensory modality (visual, auditory, or tactile) of the subsequent target [Langner et al., 2011]. A fronto-parietal network, including the dorsal premotor cortex and the IPS, was active when participants were expecting the modality of the target, in the absence of bottom-up stimulations, suggesting that the dorsal fronto-parietal network plays an important role in directing attention to stimulus modality regardless of the specific channels [Langner et al., 2011]. Please note, however, the fronto-parietal activations in the Langner et al. [2011] study were bilateral while were lateralized in the left hemisphere in this study. A key difference between the paradigms in Langner et al. [2011] and this study was that participants voluntarily directed attention to a certain sensory modality without any bottom-up stimuli during the cue period in the former study while participants actually created a new modality-specific representation based on the bottom-up input of a new target in the latter study. Therefore, our results, together with previous evidence, imply that bilateral premotor and parietal cortex might be involved in voluntarily allocating attention to a certain sensory modality without bottom-up inputs while left premotor and parietal cortex might be specifically involved in creating new modality-specific representations based on actual bottom-up inputs.

Third, besides the dissociated identity- and modality-specific neural networks, bilateral STS was involved in evaluating the identity dimension and the modality dimension of an object in an interactive way. Bilateral STS showed higher neural activity when the identity and the modality of the target were both old (cued) or both new (uncued) (Fig. 2D). Human STS is known as a binding site for different properties of a certain object [Beauchamp et al., 2003, 2004b; Calvert, 2001]. For example, STS responded to both the form and the moving direction of a visual stimulus [Oram and Perrett, 1996], and integrated different types of object information within a certain sensory modality [Beauchamp et al., 2003]. Moreover, the audio-visual convergence effects have consistently been found in the STS [Taylor et al., 2006; van Atteveldt et al., 2004, 2007]. For example, with regard to multisensory processing, neural response in STS was greater to audiovisual inputs than to auditory or visual inputs alone [Calvert et al., 2000; van Atteveldt et al., 2004], indicating that STS was involved in converging information from different modalities. In a high-resolution fMRI study, Beauchamp et al. [2004] proposed a functional architecture that auditory and visual inputs arrive at STS from separate paths and are then integrated in the intervening cortex [Beauchamp et al., 2004a]. In this study, when the identity and the modality of the target were both old, an old episodic

representation with integrated modality and identity information was retrieved; when the identity and the modality of the target were both new, a new episodic representation with integrated novel modality and identity features was created. In both conditions, STS might be involved in combining the sensory property and the semantic identity to a coherent episodic representation.

In addition to the above three distinct neural networks, we found that right prefrontal cortex was commonly activated by the main effect of modality cue validity and the interaction. The main effect and the interaction in this right prefrontal area were mainly driven by the significantly enhanced neural response when both the identity and the modality of the target were novel (uncued; Fig. 3B). This result is in good accordance with previous evidence suggesting that right prefrontal cortex is associated with novelty detection during episodic retrieval [Dobbins and Wagner, 2005; Opitz et al., 1999]. By contrast, when either the identity or the modality of the target was novel (uncued) while the other dimension was old (cued), that is, in the “Identity_Cued & Modality_Uncued” and the “Identity_Uncued & Modality_Cued” conditions, a so called “associative novelty” mechanism will be involved, which implicates hippocampus, rather than the right prefrontal cortex [Chen et al., 2010; Kumaran and Maguire, 2006, 2007]. Therefore, in this study, the right prefrontal cortex showed enhanced neural activity only when both dimensions of the target were novel, but neither when both dimensions were old nor when one dimension was novel while the other dimension was old.

CONCLUSIONS

To summarize, by orthogonally crossing the identity and the modality cue validity in a cross-modal nonspatial IOR paradigm, we found three dissociated neural networks, which were differentially involved in creating identity-specific representations independent of input modalities (bilateral LOC), creating modality-specific representations independent of object identities (left dorsal premotor cortex and left IPS), and creating object representations based on changes along both the identity and the modality dimensions (bilateral STS).

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