



Stimulus-dependent modulation of working memory for identity monitoring: A functional MRI study



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ABSTRACT

While the neural correlates of identity monitoring working memory (WM) have been well characterised in literature, the WM subsystems for different types of stimuli have not been established. The aim of our study was to examine the neural network subtending WM for identity monitoring of both verbal and visual stimuli. We used functional magnetic resonance imaging (fMRI) with words, objects, and faces as stimuli in an *n*-back WM task to delineate the similarities and differences in brain activation during presentation of verbal and visual stimuli. The results revealed a predominantly left lateralized core fronto-parieto-cerebellar identity WM network comprising bilateral insula, left inferior frontal gyrus, inferior parietal gyrus, and cerebellum that is common to all stimuli. In addition, our results showed stimulus-specific recruitment of brain regions, with exclusive activations in left inferior frontal gyrus and inferior temporal gyrus for identity WM for verbal stimuli, and left middle occipital gyrus and cerebellum for identity WM for visual stimuli. The present study reveals the existence of a central identity WM network for both verbal and visual information, along with activation of distinct verbal and visual representational regions that are sensitive to respective stimuli.

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1. Introduction

Working memory (WM) is a fundamental feature of human cognition that subtends several higher cognitive functions such as planning, decision-making, and problem solving. Extensive earlier research has attempted to elucidate the underlying neural substrates for WM (D'Esposito et al., 1995; Paulesu, Frith, & Frackowiak, 1993; Peterson, 1966; Pribram & Tubbs, 1967; Smith & Jonides, 1997), and the key brain areas activated during WM are well defined. Various WM studies have revealed the role of a fronto-parieto-cerebellar network comprising the prefrontal cortex (Barde & Thompson-Schill, 2002; Braver et al., 1997, 2001; Glahn et al., 2002; Manoach et al., 1997; Nystrom et al., 2000), the inferior parietal lobe (IPL) (Alain, He, & Grady, 2008; Ravizza, Delgado, Chein, Becker, & Fiez, 2004), and cerebellar regions (Durisko & Fiez, 2010; Hautzel, Mottaghy, Specht, Muller, & Krause, 2009; Owen, McMillan, Laird, & Bullmore, 2005).

WM networks can be modulated by the type of sensory modality of the presented stimuli (e.g., visual, auditory or olfactory), the type of monitoring (e.g., location of the stimuli or identity of the stimuli) and the type of stimuli incorporated (e.g., verbal or visual) (Rottschy et al., 2012). Of the several proposed models reflecting the diverse organisation of human WM network (Barnard, 1985; Cowan, 1999; Daneman & Merikle, 1996; Engle & Kane, 2004; Jonides et al., 2008), one of the frequently referred to model suggests the presence of a central executive system that monitors two modality-dependent subsystems: the phonological loop, responsible for WM involving verbal information, and a visuospatial sketchpad responsible for WM involving visual material, its features, and location information (Baddeley, 2003, 2012). In support of this model, various neuroimaging studies have reported significant distinctions in WM neural networks subtending stimuli with verbal and spatial information (Gruber & von Cramon, 2003; Lycke, Specht, Ersland, & Hugdahl, 2008; Zurowski et al., 2002), with preferential activation in the left inferior frontal gyrus (IFG) and the supramarginal gyrus (SMG) ascribed to WM for verbal information, and activation in right occipito-parietal and occipito-temporal junctions ascribed to WM for visuospatial information. Accumulating neuroimaging data evidences that distinct brain regions are activated during WM for identity monitoring, i.e. WM

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required for monitoring the 'identity' of stimuli, and location monitoring, i.e. WM required for monitoring the 'location' of stimuli, (Rottschy et al., 2012; Smith et al., 1995). A distinction between these two types of WM networks is also supported by studies that used interference tasks (Darling, Della Sala, & Logie, 2007; Klauer & Zhao, 2004), which reveal separate cognitive subsystems for identity and location information.

However, within the realm of identity monitoring-based WM (henceforth referred to as identity WM), there is scant knowledge of the neural networks subserving different stimulus types. It remains unclear whether the same or distinct neural networks underpin WM for identity of verbal stimuli such as words and visual stimuli such as faces. Some studies have observed a common activation for identity WM irrespective of stimulus type (Hautzel et al., 2002, 2009; Nystrom et al., 2000). In contrast, other studies have reported stimulus-specific effects in identity WM networks, with increased activation in left superior temporal and mid-fusiform areas during presentation of verbal word stimuli, and in right hippocampal and fusiform face processing areas during presentation of visual face stimuli (Majerus et al., 2010).

Furthermore, much uncertainty remains regarding functional lateralization of identity WM for verbal and visual stimuli. An assessment of WM for letters, shapes, and locations failed to find any hemispheric dissociation (Nystrom et al., 2000). Further, no laterality effects were observed in the cerebellum for WM for verbal and abstract visual stimuli (Hautzel et al., 2009). In contrast, some studies that used both words and faces as stimuli for *n*-back WM have inferred left sided activation for words and right sided activation for faces (Braver et al., 2001; Haut & Barch, 2006). The interpretability of these lateralization studies is further obscured by use of visual inspection at arbitrary thresholds for assessing lateralization.

These prevailing ambiguities and inconsistencies in the literature pertaining to the neural correlates of identity WM and its modulation by stimulus types offered the impetus for the present

fMRI study. The main goals of this study were thus to (i) delineate the core stimulus-independent identity WM network, (ii) investigate the stimulus-specific regions underpinning identity WM for verbal and visual stimuli, and (iii) assess functional lateralization of identity WM for verbal and visual stimuli. To this end, we have assessed the neural correlates of identity WM for the following stimuli – verbal i.e. words, nonverbal-visual i.e. unfamiliar faces and verbal-visual i.e. nameable objects in an *n*-back WM paradigm. These different stimulus types have been chosen to maximize differences in the processing strategies adopted by subjects.

Our rationale was that in addition to a core representational mechanism underlying identity WM for all stimuli, specific brain regions pertaining to perception networks would be recruited during identity WM for respective stimuli. We thus conjectured that identity WM for words would specifically activate regions involved in verbal and semantic processing such as the anterior–ventral IFG, whilst identity WM for faces would preferentially recruit posterior cortical visual areas involved in visual processing and recognition. In contrast, identity WM for objects would be associated with activation of both verbal and visual perception centres.

2. Methods

2.1. Subject recruitment

Fifty healthy young adults (22 females and 28 males, aged 23.62 ± 3.17 years, average education 15.98 ± 1.55 years) were recruited via advertising from National Capital Region and New Delhi, India. All participants were right handed and reported normal or corrected-to-normal vision. Subjects with history or presence of any medical, neurological, or psychiatric disorders were excluded from the study. The study protocol was approved by the ethics committee at National Brain Research Centre, India. Informed consent was obtained from all subjects prior to their participation.

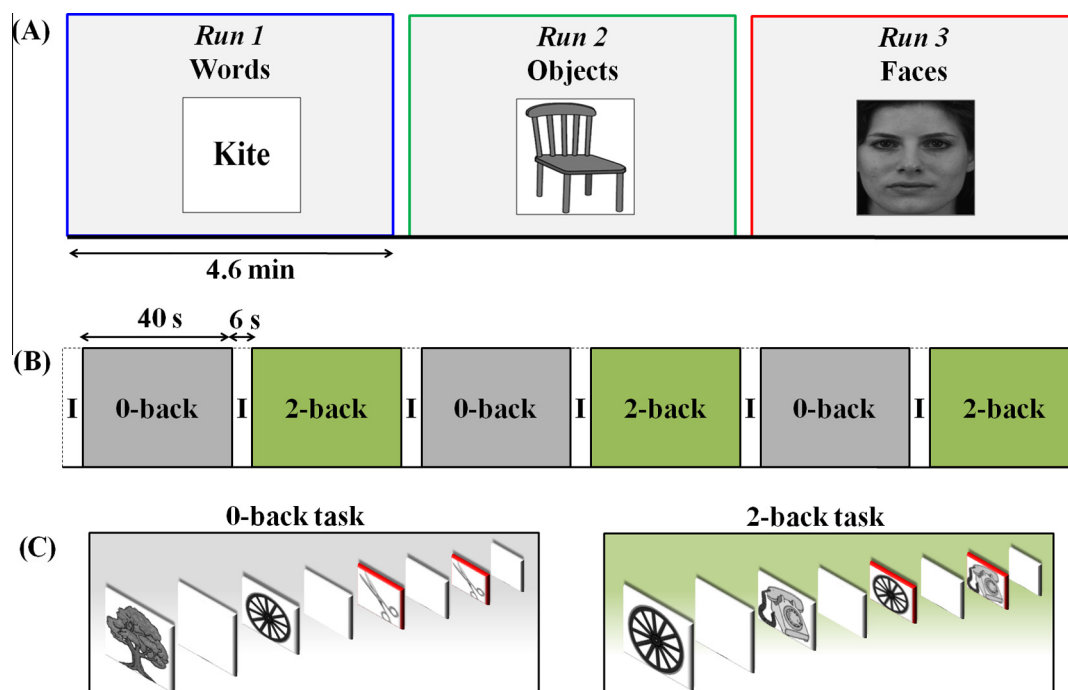


Fig. 1. Schematic representation of experimental design. (A) fMRI WM paradigm comprising of three runs involving word, object and face stimuli. (B) Time course of one exemplary run with alternating two-back and zero-back task blocks. Each block contains 20 stimuli and starts with a 6 s long instruction which is denoted by the letter 'I' in the figure (C) detailed representation of two-back and zero-back tasks wherein target stimuli are marked with red border. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Experimental paradigm

2.2.1. Procedure

The fMRI paradigm consisted of three runs involving words, objects, and faces stimuli as depicted in Fig. 1. For each run, we employed the “two-back” version of “*n*-back” WM paradigm (Braver et al., 1997), with the two-back condition as the active task and the zero-back condition as the high level baseline task. In the two-back task the target was the stimulus that matched the one presented two trials back, while in the zero-back task the target was a predetermined stimulus. The zero-back baseline condition was designed to control for stimulus perception, identification processes, motor responses, and for decision-making processes. Targets occurred with 33% frequency, and non-target repeated stimuli (one-back and three-back repeats) occurred occasionally as foils.

The paradigm was presented in a block design comprising six blocks per run, with each block spanning 40 s and divided into 20 trials. Each trial comprised a stimulus that was displayed for 1000 ms followed by 1000 ms of inter-stimulus interval. Instructions were displayed before each block for 6 s. All the runs of this block design paradigm were designed and presented using E-Prime v1.1 software (Psychology Software Tools, Pittsburgh, PA, USA). Stimulus images were displayed on a screen mounted on the MRI head coil (Invivo Eloquence fMRI System). A headband was used to minimize head movement in subjects. Subjects' responses were given on an fMRI-compatible response keypad by pressing the key under their right index finger. All subjects were made to practice the task prior to the main experiment till they achieved at least 75% accuracy.

2.2.2. Stimuli

For both words and objects stimuli, images were taken from Snodgrass and Vanderwart database (Snodgrass & Vanderwart, 1980). For faces stimuli, images of neutral faces were taken from ‘The Karolinska Directed Emotional Faces’ database (<http://www.emotionlab.se/resources/kdef>) (Lundqvist, Flykt, & Åhman, 1998). All stimuli were shown in gray scale with standard portrait dimensions of 480 × 640 pixels.

2.3. fMRI data acquisition

Anatomical and functional data were collected using a 3T Philips scanner (Phillips Achieva, Netherlands) with an eight channel head coil. A standard, high resolution, T1-weighted volumetric anatomical MRI (field of view = 22 cm × 22 cm × 15 cm, resolution = 1 × 1 × 1 mm³, number of slices = 150, acquisition matrix = 256 × 256 × 124, repetition time (TR) = 8.399 ms, echo time (TE) = 6 ms, flip angle = 8°) was acquired for each subject. It was succeeded by functional scans during which subjects performed the two-back WM task. For functional imaging, T2*-weighted images were acquired using spin echo-planar imaging sequence with the following parameters: TR = 2000 ms, TE = 70 ms, flip angle = 90°, number of slices = 21, slice thickness = 6 mm, slice gap = 0 mm. Images were acquired in ascending order in transverse orientation.

2.4. Data analysis

2.4.1. Behavioural analysis

Subject responses during the fMRI task and their respective reaction times (RTs) were registered using E-prime software and analysed using Statistical Package for Social Sciences (SPSS, version 18.0, Chicago, IL, USA). Performance accuracy and mean RT during the two-back task were calculated as % true hits and mean time taken to respond to targets, respectively.

2.4.2. Image analysis

Functional images were preprocessed and statistically analysed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK; see <http://www.fil.ion.ucl.ac.uk/spm>) installed on MATLAB R2011a (The MathWorks, Inc., Natick, Massachusetts, USA). Individual functional images were slice time corrected followed by realignment to the mean functional image using 6 parameter rigid body transformation to correct for head movements. Data from four subjects were excluded from the analysis due to within-run head motion of >1 mm and/or 1°. The anatomical T1-weighted MR image was co-registered with functional images and then segmented. The normalization parameters thus obtained were used to normalize the functional images to Montreal Neurological Institute space. Finally, the normalized functional images were spatially smoothed using a Gaussian kernel with 4 mm full-width at half maximum.

At subject level, general linear model analysis was performed to obtain whole brain activation maps. The design matrix consisted of three sessions corresponding to each run. In each run, two regressors corresponding to active and baseline conditions were defined. In addition, six motion regressors derived from the rigid body realignment were included to model linear residual movement effects.

At group level, the contrast images from each subject were transferred to random effects analysis. One way within-subjects ANOVA was performed and activations corresponding to the following contrasts were assessed: two-back words > zero-back words, two-back objects > zero-back objects, two-back faces > zero-back faces. Final activations are reported at peak $T \geq 4$ and $p < 0.001$, and with a cluster extent of 35 contiguous voxels (equivalent to a volume of 280 mm³). Monte Carlo simulation of the brain volume with 1000 iterations demonstrated that this cluster extent threshold gave activations with individual voxel significance of FDR (q) < 0.05 whole brain corrected (Slotnick, Moo, Segal, & Hart, 2003).

2.4.2.1. Conjunction analysis. To identify the stimulus-independent core identity WM network, a conjunction analysis (Friston, Penny, & Glaser, 2005) was performed on [two-back words \cap two-back faces] as well as [two-back faces \cap two-back objects \cap two-back words].

2.4.2.2. Stimulus-specific activations. To further delineate the exclusive regions responsible for verbal and visual identity WM, respective words and faces contrasts were exclusively masked, i.e. exclusive words: [(two-back words > zero-back words) exclusively masked by (two-back faces > zero-back faces)] and vice versa. To include activations solely associated with respective stimuli, all masks were generated at a generous uncorrected $p < 0.05$. Stimulus-dependent identity WM for objects was also assessed by exclusively masking (two-back objects > zero-back objects) by (two-back words > zero-back words) and (two-back faces > zero-back faces).

2.4.2.3. Laterality indices. Functional hemispheric laterality for verbal and visual identity WM was calculated with the laterality index (LI) toolbox (Wilke & Lidzba, 2007) using a combined bootstrap procedure involving histogram analysis approach (Wilke & Schmithorst, 2006). LIs were calculated for whole brain as well as for the major brain lobes, i.e. frontal, parietal, occipital, temporal, and cerebellar. LI > +0.2 was considered as left lateralized whereas LI < −0.2 was considered as right lateralized (Jansen et al., 2006).

2.4.2.4. Effect size calculation. In addition to whole-brain statistics, we also report effect sizes for stimulus-specific functional regions

Table 1

Mean reaction time in milliseconds and accuracy expressed as percentage of correct hits during two-back WM task.

Stimulus	RT (ms)	Accuracy (%)
Words	394.11 ± 30.85	79.77 ± 5.49
Objects	392.74 ± 33.02	79.15 ± 6.41
Faces	423.36 ± 36.05	71.65 ± 5.03

of interest (ROIs). ROIs were created as follows: First, search volumes were defined at group level for each stimulus type on the basis of the exclusive activation clusters obtained from random effects analysis. Next, subject-specific functional ROIs were defined within each search volume as 6 mm spheres drawn around subjects' respective peak MNI coordinates. The effect sizes for each ROI were calculated as contrast estimates (CE) using the "rfxplot" toolbox (Glascher, 2009).

3. Results

3.1. Behavioural data

Performance accuracies and RTs for the two-back WM task with different stimuli are provided in Table 1. Analysis of the task performance data with one way ANOVA revealed a significant difference between the mean percent accuracies of two-back task with words, objects, and faces as stimuli ($F(2, 126) = 12.626$, $p < 0.001$). Post hoc analysis showed that average accuracy for two-back faces was significantly lower than both for objects and for words ($p < 0.001$). The mean RTs were also found to be significantly different between the three stimuli type as revealed by one way ANOVA ($F(2, 126) = 10.611$, $p < 0.001$), with higher average RT for two-back faces than for objects and words ($p < 0.001$) (Fig. 2). There was no significant difference in the mean task accuracy or RT for objects and words.

3.2. Imaging data

3.2.1. Neural correlates of WM for words, objects, and faces: two-back versus zero-back task analysis

To identify the neural correlates of identity WM for each stimulus type, respective two-back task activations were cognitively subtracted from their zero-back baselines. Detailed results including the MNI coordinates and t statistics of the peak voxels are summarized in Table 2. Interestingly, we observed a striking similarity between the identity WM neural networks subtending words, objects, and faces stimuli. All three stimuli elicited activations in a similar fronto-parieto-cerebellar network encompassing the bilateral IFG/insula, the left IPL, the left precentral gyrus (PreCG), and bilateral cerebellar Crus 1/lobule 6 regions (Table 2).

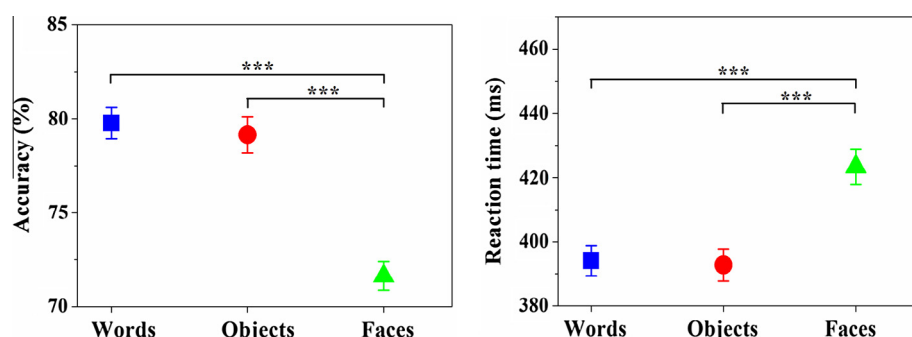


Fig. 2. Reaction time in milliseconds and accuracy expressed as percentage of correct hits during two-back WM task. Vertical bars indicate SEM *** $p < 0.001$.

3.2.2. Laterality

Whole brain lateralization analysis revealed left lateralization ($LI > +0.2$) in WM networks for all stimulus types, i.e., words, objects and faces. Region-wise lateralization analysis for the major brain lobes (frontal, parietal, occipital and cerebellum) also revealed a left lateralized identity WM network ($LI > +0.2$) for both words and faces. Identity WM for objects showed left laterality ($LI > +0.2$) in parietal, occipital, temporal, and cerebellar regions, and bilaterality ($-0.2 < LI < +0.2$) in the frontal lobe (Table 3).

3.2.3. Core identity WM network

We next aimed to identify the core stimulus-independent brain network responsible for execution of two-back WM. To this end, we performed a conjunction analysis to identify regions commonly activated for identity WM of words and faces. The analysis revealed common activations in the bilateral IFG/insula, left PreCG, left IPL, and left cerebellar lobule 6/Crus1 (Table 4, Fig. 3). A conjunction analysis between all three stimuli (words, objects, and faces) also showed activation in the same network (data not shown).

3.2.4. Stimulus-specific regions in identity WM network

Having identified a common fronto-parieto-cerebellar identity WM network subtending both verbal and visual stimuli, we also assessed whether stimulus perception-related brain regions were specifically activated during WM for these stimuli. To carry this out, we exclusively masked the activations obtained for words stimuli with the activations obtained for faces stimuli, and vice versa. Stimulus-specific activations are reported in Table 4. WM for words led to exclusive activation in the left IFG pars opercularis and pars triangularis, right IFG/insula, and the left inferior temporal gyrus (ITG) (Table 4, Fig. 4). In contrast, WM for faces led to exclusive activation in the left middle occipital lobe and cerebellum Crus 1 (Table 4, Fig. 4). These findings suggest that in addition to a central core network for identity WM, distinct stimulus-specific regions are exclusively activated for verbal and visual stimuli.

To determine whether any brain regions were exclusively recruited for identity WM for objects, activations were exclusively masked by the other two stimulus contrasts. Our analysis revealed no exclusive regions for objects WM. No activations were observed even at a lenient uncorrected threshold of $p < 0.001$, indicating that our failure to identify any object-selective regions was not due to overly stringent criteria.

4. Discussion

The present fMRI study has examined the neural underpinnings of identity WM and investigated whether identity WM for different stimuli requires recruitment of specific neural resources. Our

Table 2

Brain activations during two-back WM with words, objects and faces as stimuli, contrasted with their respective zero-back baseline task.

Brain region	Hemisphere	Peak MNI coordinate			Voxel level		Cluster size
		x (mm)	y (mm)	z (mm)	FDR (q)	T score	K (voxels)
(a) Two-back words > zero-back words							
Insula	Right	32	24	2	0.000	7.22	299
Cerebellum (Lobule VI)	Left	−30	−58	−34	0.001	6.13	672
Cerebellum (Crus1)	Left	−42	−70	−20	0.026	4.81	
Cerebellum (Crus1)	Left	−46	−48	−28	0.041	4.62	
Inferior parietal	Left	−36	−50	44	0.001	5.99	1672
Inferior parietal	Left	−36	−44	38	0.001	5.93	
Inferior parietal	Left	−36	−44	38	0.001	5.68	
Precentral	Left	−44	2	28	0.001	5.81	695
Inferior frontal tri	Left	−48	22	26	0.014	5.00	
Inferior frontal tri	Left	−38	20	26	0.045	4.57	
Insula	Left	−30	24	−2	0.006	5.31	347
Inferior frontal tri	Left	−44	16	4	0.014	5.00	
Inferior frontal oper	Left	−54	12	2	0.014	4.97	
Cerebellum (Crus 2)	Left	−10	−76	−32	0.040	4.65	52
Supplementary motor area	Left	−8	12	48	0.085	4.32	65
Middle frontal	Left	−26	4	50	0.108	4.23	98
Superior motor area	Right	8	16	46	0.120	4.19	113
Middle cingulum	Right	8	22	40	0.141	4.08	
Middle frontal	Right	38	48	12	0.158	4.03	43
(b) Two-back objects > zero-back objects							
Insula	Right	32	24	0	0.000	6.34	299
Inferior frontal oper	Right	46	16	4	0.003	5.72	
Cerebellum (Lobule VI)	Left	−30	−56	−34	0.007	5.33	839
Cerebellum (Crus1)	Left	−42	−50	−26	0.041	4.79	
Cerebellum (Crus1)	Left	−34	−72	−26	0.046	4.71	
Inferior parietal	Left	−34	−50	42	0.021	5.11	794
Inferior parietal	Left	−44	−48	46	0.029	4.94	
Middle occipital	Left	−30	−72	24	0.041	4.82	
Insula	Left	−32	20	4	0.022	5.04	149
Cerebellum (Crus 1)	Left	−12	−74	−32	0.053	4.57	50
Precentral	Left	−42	2	30	0.068	4.48	103
Inferior frontal tri	Left	−46	20	30	0.139	4.18	75
Middle frontal	Left	−44	30	36	0.187	4.05	
(c) Two-back faces > zero-back faces							
Precentral	Left	−44	6	30	0.006	5.56	242
Cerebellum (Crus1)	Left	−26	−64	−32	0.006	5.52	370
Cerebellum (Crus2)	Left	−10	−76	−32	0.021	4.99	
Cerebellum (Crus1)	Left	−14	−68	−32	0.155	4.18	
Inferior parietal	Left	−42	−48	54	0.006	5.52	995
Inferior parietal	Left	−36	−48	38	0.016	5.21	
Inferior parietal	Left	−52	−36	46	0.021	5.04	
Insula	Right	32	26	2	0.037	4.75	152
Inferior frontal tri	Right	42	20	8	0.18	4.08	
Insula	Left	−30	28	2	0.084	4.52	89
Vermis_8	Right	−2	−60	−30	0.091	4.44	71
Middle cingulum	Right	10	22	38	0.091	4.42	102
Middle occipital	Left	−30	−82	20	0.109	4.35	120
Cerebellum (Crus1)	Left	−40	−78	−18	0.155	4.17	208
Fusiform gyrus	Left	−40	−66	−14	0.154	4.16	

Note: Activations reported at $p < 0.001$, cluster FDR < 0.05 , Peak T value > 4 , cluster size > 35 voxels. Coordinates reported in MNI space.**Table 3**

Laterality indices of different brain regions during for 2-back WM for words, objects, and faces.

Brain regions	Word	Object	Face
Whole brain	0.37	0.26	0.28
Frontal	0.34	0.11	0.21
Parietal	0.48	0.29	0.28
Occipital	0.24	0.25	0.21
Cerebellum	0.31	0.32	0.22

results demonstrate the presence of a common core identity WM network. Our study further supports the idea of modulation of this core identity WM network by stimulus type, with exclusive recruitment of stimulus-specific regions.

4.1. Core network of identity WM

Our conjunction analysis revealed a common fronto-parieto-cerebellar identity WM network for all stimuli comprising of the bilateral IFG/insula, the left IPL/SMG, the left PreCG regions, and the left cerebellar Crus 1 region (Table 4), indicating that these regions may be considered the core regions of identity WM that serve a stimulus-independent central function. Our results are in line with the extant literature that indicates the involvement of a fronto-parietal network in WM, specifically n -back tasks (Owen et al., 2005; Rottschy et al., 2012).

We observed two clusters of activation in the IFG, one dorsal corresponding to PreCG [–44630] and the other lying in the insular cortex [–30282]. Both of these regions have been previously implicated in WM tasks with both verbal and visual stimuli (Braver et al., 1997; Cohen et al., 1997; Druzgal & D'Esposito,

Table 4
Common and stimulus-specific activations during two-back WM with words and faces as stimuli.

Brain region	Hemisphere	Peak MNI coordinate			Voxel level		Cluster size <i>K</i> (voxels)
		<i>x</i> (mm)	<i>y</i> (mm)	<i>z</i> (mm)	FDR (<i>q</i>)	<i>T</i> score	
<i>(a) Common activations (two-back faces ∩ two-back words)</i>							
Cerebellum (Crus 1)	Left	−26	−64	−32	0.013	5.27	117
Inferior parietal	Left	−36	−48	38	0.013	5.22	671
Supramarginal	Left	−50	−40	42	0.046	4.70	
Angular	Left	−34	−62	38	0.141	4.27	
Precentral	Left	−44	6	30	0.013	5.21	187
Insula	Right	32	26	2	0.044	4.75	105
Insula	Left	−30	28	2	0.121	4.31	58
<i>(b) Two-back words masked by two-back faces</i>							
Inferior frontal/insula	Right	32	20	−6	0.006	5.60	63
	Right	32	18	4	0.006	5.55	
Inferior frontal oper	Left	−54	12	2	0.014	4.97	58
Inferior temporal	Left	−46	−48	−28	0.041	4.62	57
Inferior frontal tri	Left	−38	20	26	0.045	4.57	70
Middle frontal	Right	38	48	12	0.158	4.03	43
<i>(c) Two-back faces masked by two-back words</i>							
Middle occipital	Left	−30	−82	20	0.105	4.35	79
Cerebellum (Crus 1, Lobule 6)	Left	−12	−70	−30	0.268	4.05	79

Note: Activations reported at $p < 0.001$, cluster FDR < 0.05 , Peak T value > 4 , cluster size > 35 voxels. Coordinates reported in MNI space.

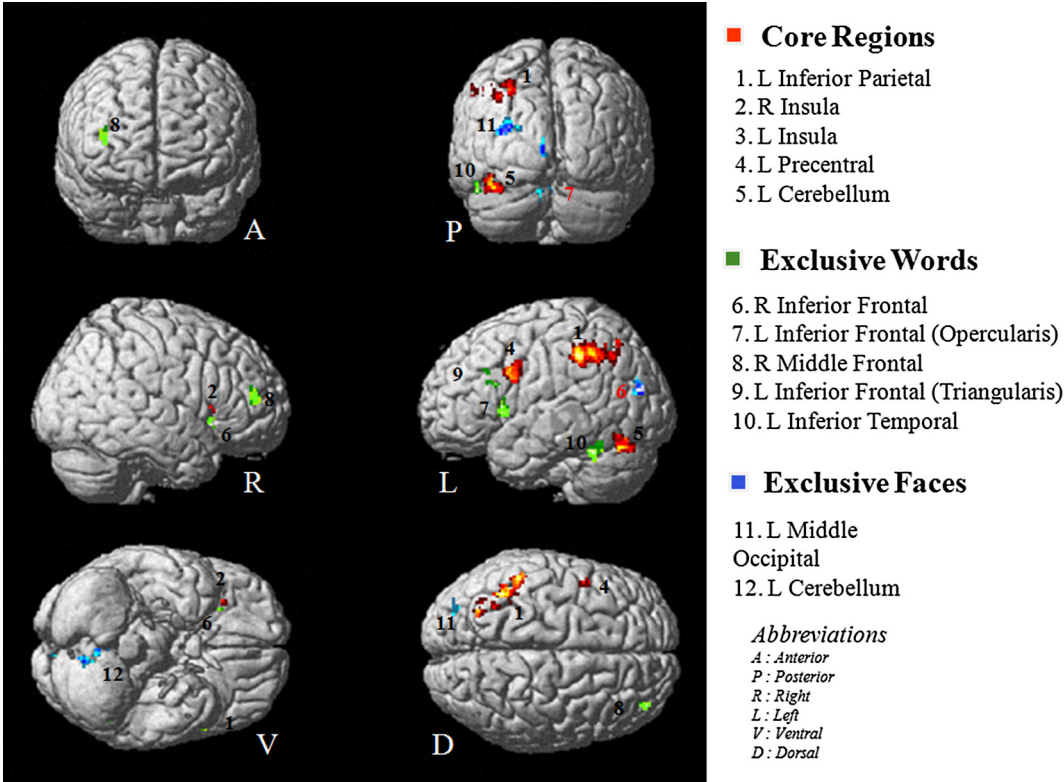


Fig. 3. Brain regions commonly and specifically activated during two-back WM for words and faces at $p < 0.001$ and cluster size of 10 voxels.

2001; Jonides et al., 1997; Spinks, Zhang, Fox, Gao, & Hai Tan, 2004). While dorsal IFG/PreCG has shown to be involved in updating of maintained information (Wager & Smith, 2003), the insula is a key part of the ‘fronto-parietal control network’ and is reported to be engaged in tasks requiring controlled processing of information (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). Apart from the frontal cortex, our conjunction analysis revealed significant activation in the IPL [−36 −48 38]. Studies have shown that activity in IPL is important for maintenance of verbal as well as visual stimuli (Cabeza & Nyberg, 2000; Collette, Hogge, Salmon, & Van der Linden, 2006; Owen et al., 2005). In an empirical

study, a cluster in IPL [−32 −51 36] was reported to be activated for a variety of identity WM tasks e.g. letters, words, faces, etc. (D’Esposito et al., 1998). This closely matches the local maxima [−36 −48 38] observed in the present study, thus corroborating the involvement of IPL in stimulus-independent identity WM. In addition to the fronto-parietal network, various fMRI meta-analyses have established a significant role of cerebellum in WM (Keren-Happuch, Chen, Ho, & Desmond, 2012; Stoodley & Schmahmann, 2009). Bilateral Crus I is one of the key cerebellar locations identified for WM (Keren-Happuch et al., 2012). Studies that have compared cerebellar activations in verbal and abstract

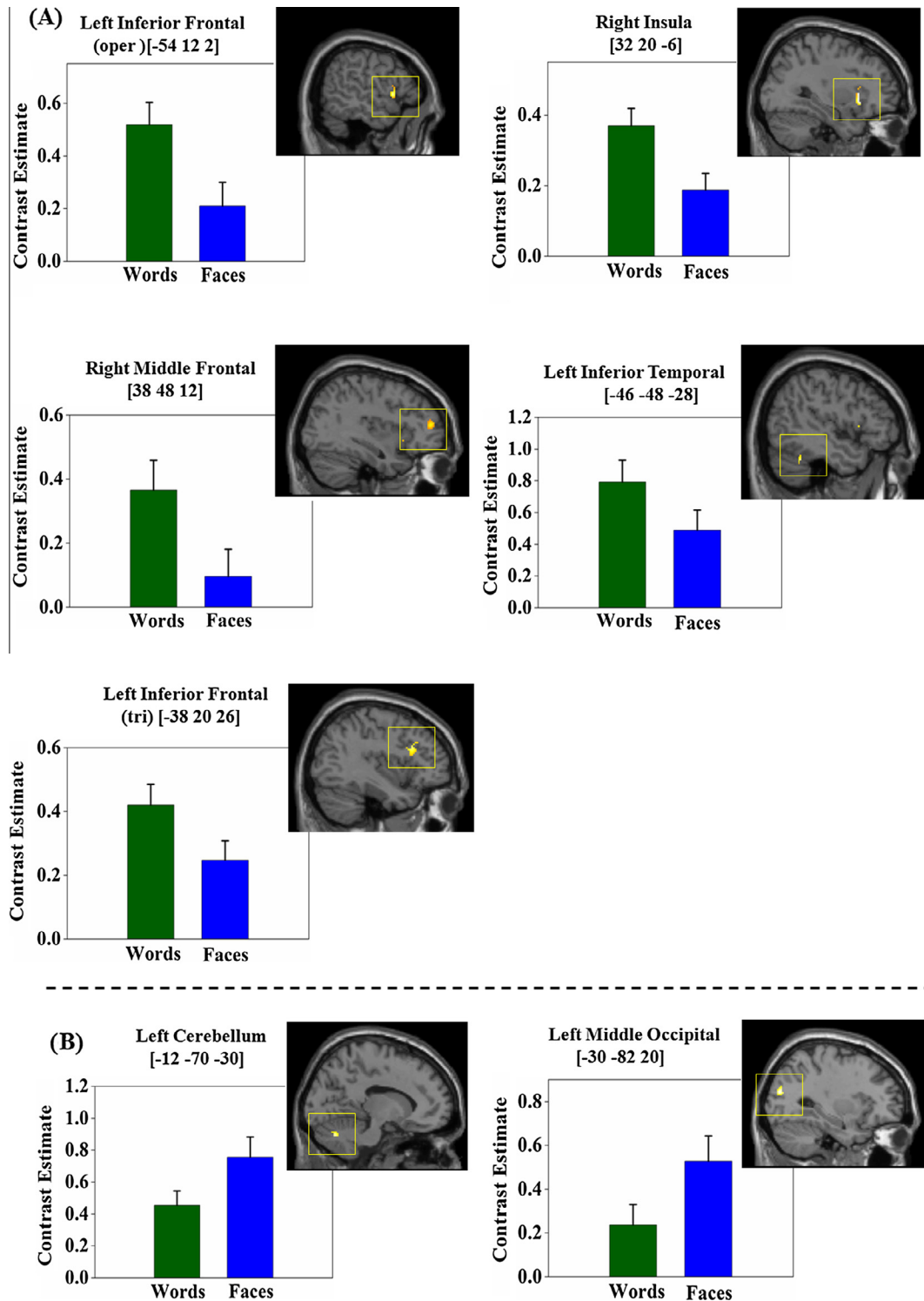


Fig. 4. Contrast estimates for words and faces in (A) word-specific and (B) face-specific ROIs. Vertical bars in the graphs indicate SEM.

image WM have shown that Crus I is modality-independent (Hautzel et al., 2009; Thurling et al., 2012). Crus I is reported to be involved in temporal updating of WM contents (Desmond & Fiez, 1998; Desmond, Gabrieli, Wagner, Ginier, & Glover, 1997) as well as in temporal organisation of various cognitive tasks serving as an internal timing device (Dreher & Grafman, 2002; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002).

Notably, in the present study we did not find any significant activations in the dorsolateral prefrontal cortex (DLPFC). DLPFC

has been frequently implicated in WM studies, and has been proposed to be involved in the monitoring and manipulation of actively maintained information within WM (Barch et al., 1997; Braver et al., 2001; Cohen et al., 1997; Hautzel et al., 2002; Ragland et al., 2002). However, a closer survey of the literature reveals that DLPFC activity has primarily been reported during verbal identity WM tasks (Barch et al., 1997; Braver et al., 2001; Cabeza, Dolcos, Graham, & Nyberg, 2002; Dima, Jogia, & Frangou, 2014; Ragland et al., 2002; Rodriguez-Jimenez et al., 2009). As

such, it is feasible that DLPFC is primarily recruited during WM for verbal stimuli. In support of this hypothesis, we observed significant activation of DLPFC in the middle frontal gyrus activated cluster for exclusive identity WM for words at a threshold of $p < 0.001$ and $T \geq 4$ (Table 4). Two *n*-back fMRI studies that directly compared encoding of verbal and visual stimuli reported task-specific DLPFC activation for both words and faces WM (Braver et al., 2001; D'Esposito et al., 1998). However, both these studies used a low-level fixation baseline. Thus, the relative absence of DLPFC activations in our study may be due to the high-level control condition, which was well matched for demands on context, attention, and decision-making.

4.2. Exclusive perception-specific regions in identity WM

In addition to delineating the core neural network subtending WM for identity monitoring, this study further mapped regions of the human brain showing stimulus-specific activation during verbal and visual categories.

4.2.1. Identity WM for words

We show that identity WM for verbal stimuli exclusively activated the left ventral IFG, corresponding specifically to the pars triangularis and pars opercularis that together form the Broca's area. Literature has elaborated a role for this region in semantic information processing (Binder, Desai, Graves, & Conant, 2009; Bookheimer, 2002; Poldrack et al., 1999; Rugg, Fletcher, Chua, & Dolan, 1999) and it has been reported to be involved in rehearsing the phonological information in an active state over short retention intervals (Axmacher et al., 2009; Paulesu et al., 1993). A recent meta-review that compared WM for verbal and visual stimuli showed that verbal tasks were significantly more likely to recruit left IFG pars triangularis (Rottschy et al., 2012).

Additionally, left ITG [−46 −48 −28] was found to be exclusively activated during verbal identity WM. Previous studies have shown ITG to be associated with verbal stimuli (Axmacher et al., 2009; Cohen et al., 2002; Fiebach, Rissman, & D'Esposito, 2006; Gaillard et al., 2006; Kiehl et al., 1999; Nobre, Allison, & McCarthy, 1994). A major part of the activated cluster included the posterior fusiform gyrus (also called the word form area), which has been implicated in reading and processing verbal stimuli (Cohen & Dehaene, 2004; Cohen et al., 2004; Polk et al., 2002; Puce, Allison, Asgari, Gore, & McCarthy, 1996). We also observed a significantly activated cluster in the right IFG/Insula [32 20 −6] for verbal identity WM. Previous studies have shown insular activation for verbal stimuli (Cohen et al., 1997; Jonides et al., 1997; Ragland et al., 2002; Sweet et al., 2008).

4.2.2. Identity WM for faces

We used unfamiliar faces as nonverbal visual stimuli to minimize verbal strategies of encoding and maintenance. In accordance with our hypothesis, identity WM network for faces stimuli exclusively encompassed the left middle occipital gyrus/lateral occipital complex – a region that has been shown to be involved in perception, successful recognition, and discrimination of visual stimuli, including manmade objects as well as faces (Grill-Spector, Kushnir, Hendler, & Malach, 2000; Haist, Lee, & Stiles, 2010; Katanoda, Yoshikawa, & Sugishita, 2000; Malach et al., 1995; Pourtois, Schwartz, Spiridon, Martuzzi, & Vuilleumier, 2009).

4.2.3. Identity WM for objects

In contrast to verbal words and nonverbal visual faces, encoding and retrieval of “verbalizable” objects can be implemented through both verbal and visual strategies (Paivio & Csapo, 1973). As such, we postulated that for identity WM of nameable objects, both brain regions involved in visual processing and those involved in

verbal processing would be recruited. Accordingly, we did not observe any exclusive activations for objects compared to both words and faces.

Our results therefore indicate that perception neural systems specialized in recognition and discrimination of respective verbal and visual stimuli are actively recruited in addition to the core fronto-parieto-cerebellar network for identity WM of specific stimuli.

4.3. Left lateralized WM network

Hemispheric asymmetries in identity WM in terms of type of stimulus content, e.g., verbal versus visual, have not been extensively studied. The few studies that have assessed lateralization have relied on visual inspection of functional activations contrasted between different conditions rather than using statistical tools. In this study, we have used the LI toolbox to assess hemispheric lateralization. We observed left hemispheric bias for identity WM for verbal as well as visual stimuli. Our findings are in line with some previous studies that failed to find any hemispheric dissociation (Hautzel et al., 2009; Nystrom et al., 2000). Our findings are also in accordance with previous literature that has demonstrated left hemispheric bias for verbal identity WM (D'Esposito et al., 1998; Fiez et al., 1996; Nystrom et al., 2000), which is supported by the fact that the core areas for language such as Broca's area are located in left hemisphere. Few studies that used both words and faces as stimuli for two-back WM have shown left sided activation for words and right sided activation for faces (Braver et al., 2001; Haut & Barch, 2006). However, both these studies used fixation as a baseline. It is thus feasible that the observed stimulus-specific lateralization in these studies may be indicative of stimulus perceptual bias; a large body of work has shown that language functions are left lateralized and face processing functions are right lateralized (Puce et al., 1996).

In closing, a few caveats of our study may be pointed out. First, we used a high-level baseline in our experimental design to ensure that the observed activations are attributable to specific neural systems for active WM maintenance of different stimuli and not simply to differences in sensory perception of these stimuli. However, it is important to note that the similarity between the memory and control tasks may have led to diminished differences in activations because even though the subjects were only asked to remember the target stimulus in the zero-back task and not asked to maintain previous stimuli in memory, the two-back task may have primed them to do so implicitly. Another possible caveat of our study is the use of faces as a nonverbal visual stimulus. Faces encapsulate complex visual, emotional, and social information, and therefore may not be the optimal stimuli for delineating identity WM for nonverbal visual stimuli. Further, there is some evidence to suggest that faces may invoke discrete neural systems. Future studies on identity WM with simple nonverbal visual stimuli such as Chinese characters (Andrade, Kemps, Werniers, May, & Szmalec, 2002) or abstract drawings (Bellhouse-King & Standing, 2007; Vogt & Magnussen, 2005) are needed to affirm the findings of this study. However, it is to be noted that all the face perception related neural networks are anticipated to be equally employed in the active and the high level baseline task of the present study, and consequently the observed activations are expected to solely correspond to the identity WM network for faces.

In conclusion, the present study demonstrates the existence of a stimulus-independent core identity WM network. This core WM system is likely to subtend common executive functions like attentional modulation, processing and integration of sensory information, as well as maintenance and retrieval processes. Furthermore, our findings indicate that in addition to the core fronto-parieto-cerebellar network, distinct perception neural systems are actively

recruited during identity WM for respective verbal and visual stimuli. These stimulus-dependent regions are likely to be involved in stimulus maintenance and stimulus-specific retrieval strategies (Axmacher et al., 2009; Fiebach, Rissman, & D'Esposito, 2006; Katanoda et al., 2000; Paulesu et al., 1993). Our findings are in line with a recent meta-review on WM that demonstrated a core WM network along with specific regions that were sensitive to task stimuli (Rottschy et al., 2012).

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