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Characterizing the neural correlates of modality-specific and modality-independent accessibility and availability signals in memory using partial-least squares

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ABSTRACT

Previous studies have shown that information that currently cannot be retrieved but will be retrieved on a subsequent, more supported task (i.e. is available but not accessible) has a distinct neural signature compared with non-available information. For verbal paired-associates, an availability signal has been revealed in left middle temporal cortex, an area potentially involved in the storage of such information, raising the possibility that availability signals are expressed in modality-specific storage sites. In the present study subjects encoded pictures and sounds representing concrete objects. One day later, during fMRI scanning, a verbal cued-recall task was administrated followed by a post-scan recognition task. Items remembered on both tasks were classified as accessible; items not remembered on the first but on the second task were classified as available; and items not remembered on any of the tasks were classified as not available. Multivariate partial-least-squares analyses revealed a modality-independent accessibility network with dominant contributions of left inferior parietal cortex, left inferior frontal cortex, and left hippocampus. Additionally, a modality-specific availability network was identified which included increased activity in visual regions for available pictorial information and in auditory regions for available sound information. These findings show that availability in memory, at least in part, is characterized by systematic changes in brain activity in sensory regions whereas memory access reflects differential activity in a modality-independent, conceptual network, thus indicating qualitative differences between availability and accessibility in memory.

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Introduction

Most people have experienced alterations in their ability to remember a specific fact or a name, such that information that first could not be accessed suddenly comes to mind. Thus, despite not remembered in the first place, the information was apparently available in memory. Tulving and Pearlstone (1966) first introduced the distinction between *accessible* versus *available* information in memory. Their experimental design involved two consecutive tests: free recall followed by cued-recall. Items that could not be retrieved on the first test but on the second test were defined as available but not accessible, whereas items retrieved on the first as well as the second test were termed accessible. The available information could thereby be differentiated from apparently forgotten information, i.e. items that were neither retrieved on the first nor the second test.

In a recent fMRI study, Habib and Nyberg (2008) identified neural correlates of accessibility and availability in memory for verbal paired associates. Using the same terminology as Tulving and Pearlstone (1966) but utilizing different tasks, items were classified as remembered/accessible, inaccessible but available, and forgotten/not available. Activity in a network of regions was higher for available than forgotten items, including the medial temporal cortex, left lateral middle temporal cortex, and parietal cortex. Based on previous suggestions (e.g., Miyashita, 2004), Habib and Nyberg (2008) proposed that the left lateral temporal region might be implicated in the storage of paired-associate information in memory. By this view, availability in memory would, at least in part, be expressed in material-/modality-specific brain regions as defined by the encoding conditions.

Successful retrieval of episodic information (i.e. memory access) has also been associated with differential activation in modality-specific regions (e.g., Nyberg et al., 2000; Wheeler et al., 2000; Vaidya et al., 2002). However, largely, successful retrieval from long-term memory appears to be characterized by modality-independent brain networks (e.g., Nyberg et al., 1996a, b; Sohn et al., 2005; Vandenberghe et al., 1996; McIntosh et al., 1997; Henson et al., 1999a; Wagner et al., 2005). Moreover, in keeping with the observation by Habib and Nyberg (2008)

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that memory access was specifically associated with left inferior frontal gyrus, retrieval success has been linked to left frontal regions for both verbal and pictorial information (Nyberg et al., 2000).

In the present study we directly tested whether the encoding modality would jointly influence availability and accessibility signals. Participants were presented with pictures and sounds representing concrete objects during the initial encoding phase of the experiment. On the next day, during fMRI scanning, they were presented with words corresponding to previously encoded sounds and pictures, and indicated if the words reminded them of the previously studied items (cued-recall). Following the scanning session, outside the scanning room, subjects were administrated a Yes/No recognition test in which all encoded sounds and pictures were presented intermixed with new items. This particular combination of tests captures the gist of the original Tulving and Pearlstone design (see also Habib and Nyberg, 2008), with a more difficult/less supported task being followed by a more supportive task (recognition with copy cues). It should be noted, though, that the distinction between availability and accessibility put forth in this study is one of several dual-process models of memory retrieval that potentially could account for the observed effects. For example, accessibility might correspond to recollection whereas an availability signal could be seen as reflecting a weaker oldness or familiarity signal that translates into a remember response on the subsequent more supported task.

We used a multivariate spatiotemporal partial-least-squares (ST-PLS) analysis (McIntosh et al., 2004; McIntosh and Lobaugh, 2004), supplemented with univariate voxel-based statistical parametric mapping (SPM; cf., McIntosh et al., 1996; McIntosh et al., 2004; Addis et al., 2009) to test whether the availability/accessibility signals would be seen in modality-specific brain regions. If the original study modality was to have an influence on both availability and accessibility, the analysis should reveal common material-specific networks for both available and accessible information. Possible alternative outcomes would be that a modality-specific network would only be associated with accessibility (cf., e.g., Nyberg et al., 2000) or only with availability. Support in favor of the latter possible outcome would be consistent with the notion that memory access is primarily based on conceptual information (Habib and Nyberg, 2008, cf., Moscovitch and McAndrews, 2002).

Methods

Participants

Sixteen right-handed participants (mean age 25 years; age range 21–40; 10 females) received financial compensation for their participation. All participants had normal or corrected to normal vision and were in good general health with no prior history of neurological or psychiatric complaints (none of the subjects reported drug/alcohol abuse). Informed consent was signed by all participants and the study was approved by the ethics committee at Umeå University. Two subjects were outliers due to low recall rates (less than 5 %) and were therefore excluded from the analysis. One additional subject was eliminated from the analysis due to extremely deviating brain scores, which could severely influence the multivariate analysis and induce the first principle component by itself. Thus, the final sample consisted of 13 participants.

Stimuli and procedure

The encoded stimuli consisted of unrelated sounds and pictures of easily identifiable objects such as animals, musical instruments, vehicles, etc. which were self-assembled from different sources on the internet. Pictures were colored photos. Sounds had variable duration between 2–4 s depending on their characteristic. Three separate phases (encoding, cued recall and recognition) were part of the experiment, but only the cued-recall test took place while measurement of brain activation was conducted with functional magnetic resonance imaging (fMRI). During the encoding phase, participants memorized 40 pictures and 40 sounds which were presented in separate lists in a randomized order across subjects. Each picture was presented for 2.5 s on a computer screen while each sound stimulus was played between 2–4 s, with an even distribution across that range, through regular headphones with individually adjusted volume. Due to a higher difficulty of remembering sounds compared to pictures, as revealed in pilot tests, the sound list was presented twice whereas the picture list was presented once. Subjects were explicitly instructed to memorize the pictures and sounds for a test that would be taken the following day.

Approximately 24 h after encoding, subjects performed a cued-recall test in the fMRI scanner. The cued-recall stimuli consisted of 240 nouns, of which 80 corresponded to the previously encoded pictures and sounds and the remaining 160 words (80 concrete/80 abstract) were unrelated (i.e. new words). Words were presented in white color on a black background on a computer screen located at the end of the scanner bore, and the subjects viewed the screen via a mirror placed directly above their head. Each word was presented for 2.5 s, followed by a fixation cross (duration 2 s). Circles indicating rest time periods were presented after every 10 words (duration 20 s). Thus, a mixed block-event-related design was used (e.g. rest blocks of 20 s and task blocks of 45 s) from which only items within-task blocks (10 cued-recall trials) were modeled as an event-related design for the following analysis (both in PLS and SPM). The cued-recall test was performed under intentional and incidental retrieval conditions. In the intentional condition, subjects were explicitly instructed to indicate whether they could remember a sound or picture corresponding to each word by pressing a button with their right ring finger as fast as possible (see Fig. 1). In addition, they categorized each word as concrete or abstract by pressing buttons with their index and middle fingers, respectively. In the incidental retrieval condition, they first categorized each word and if they happened to remember an item related to a presented word they indicated that with a button press. The manipulation of retrieval intentionality (including categorization) formed a basis for a separate study, reported elsewhere (Kompus et al., in press), and in the present study items from both retrieval conditions were classified with regard to availability and accessibility. Control analyses confirmed that the manipulation of retrieval intentionality did not have any effects on the results reported here.

After the cued-recall phase, outside the scanning room, subjects were administrated a Yes/No recognition test in which all encoded sounds and pictures (40 of each kind) were presented intermixed with 40 new items (20 sounds and 20 pictures). The pictures were presented on a computer screen and the sounds were presented through headphones. The subjects were required to press “1” or “2” on a keyboard to indicate whether or not they recognized sounds and pictures from the initial encoding phase (Day1).

Item classification

Items were post-hoc sorted according to encoding modality as well as retrieval success on both tests. Henceforth, we will refer to each item category as follows:

1. *Accessible Pictures* (*Picture Rc+Rn+*): Studied pictures correctly retrieved during both the cued-recall test and the recognition test.
2. *Accessible Sounds* (*Sound Rc+Rn+*): Studied sounds correctly retrieved during both the cued-recall test and the recognition test.
3. *Available Pictures* (*Picture Rc−Rn+*): Studied pictures that were not retrieved during the cued-recall test but were later recognized during the recognition test.

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4. *Available Sounds* (*Sound Rc−Rn+*): Studied sounds that were not retrieved during the cued-recall test but were later recognized.
5. *Forgotten items* (*Rc−Rn−*): Studied pictures and sounds that were neither recalled nor recognized. Note that this condition also included correctly rejected new concrete items as the number of forgotten items was low and did not allow for the formation of a unique category for forgotten sounds and pictures, respectively. Common to old forgotten and new concrete items was the apparent absence of memory traces emanating from the encoding phase. Items which were recalled but not recognized were rare (on average less than 2.8 items per subject) and were therefore excluded from the analysis.

fMRI data acquisition

Structural and functional images were collected using a 3 T Philips Achieva scanner. Functional T2*-weighted images (31 slices with 4.65 mm thickness) were acquired with a single-shot gradient echo EPI sequence (TR = 1512 ms, TE = 30 ms, FOV = 22 cm, pixel size = 3.44 mm, sense-factor = 2.6) utilized for blood oxygen level-dependent contrast assessment. Structural high-resolution T_1 images (170 slices, 1 mm thickness, FOV = 24 cm) were collected following the functional image acquisition.

Registration of the responses was performed utilizing Lumitouch fMRI optical response keypads (photon control Inc., Canada).

fMRI data analysis

Functional images were preprocessed utilizing the Statistical Parametric Mapping software (SPM5, Wellcome Department of Cognitive Neurology, London, UK). As a first step, the images were realigned and unwarped to compensate for subject movement during scanning. Secondly, the realigned data were linearly normalized to the Montreal Neurological Institute (MNI) template using trilinear interpolation. Ultimately the normalized data were spatially smoothed with a three-dimensional Gaussian kernel of 6 mm full-width-at-half-maximum (FWHM) to suppress the effects of noise. The preprocessed data were analyzed using two different approaches: (1) multivariate spatiotemporal partial-least squares, and (2) univariate statistical parametric mapping.

PLS analysis

The analysis was performed on preprocessed data using spatio-temporal Partial-Least Squares (PLS; McIntosh et al., 2004,McIntosh and Lobaugh, 2004; McIntosh et al., 1996), determining time-varying distributed patterns of the brain as a function of the task. PLS is an assumption-free approach in terms of the shape and time course of the hemodynamic response function, as well as regarding how conditions will collate to form patterns. In general, PLS as a multivariate approach is more sensitive than univariate techniques, particularly for fMRI data in which correlations among dependent measures exist (cf., Harris, 1975). PLS is connatural to Principle

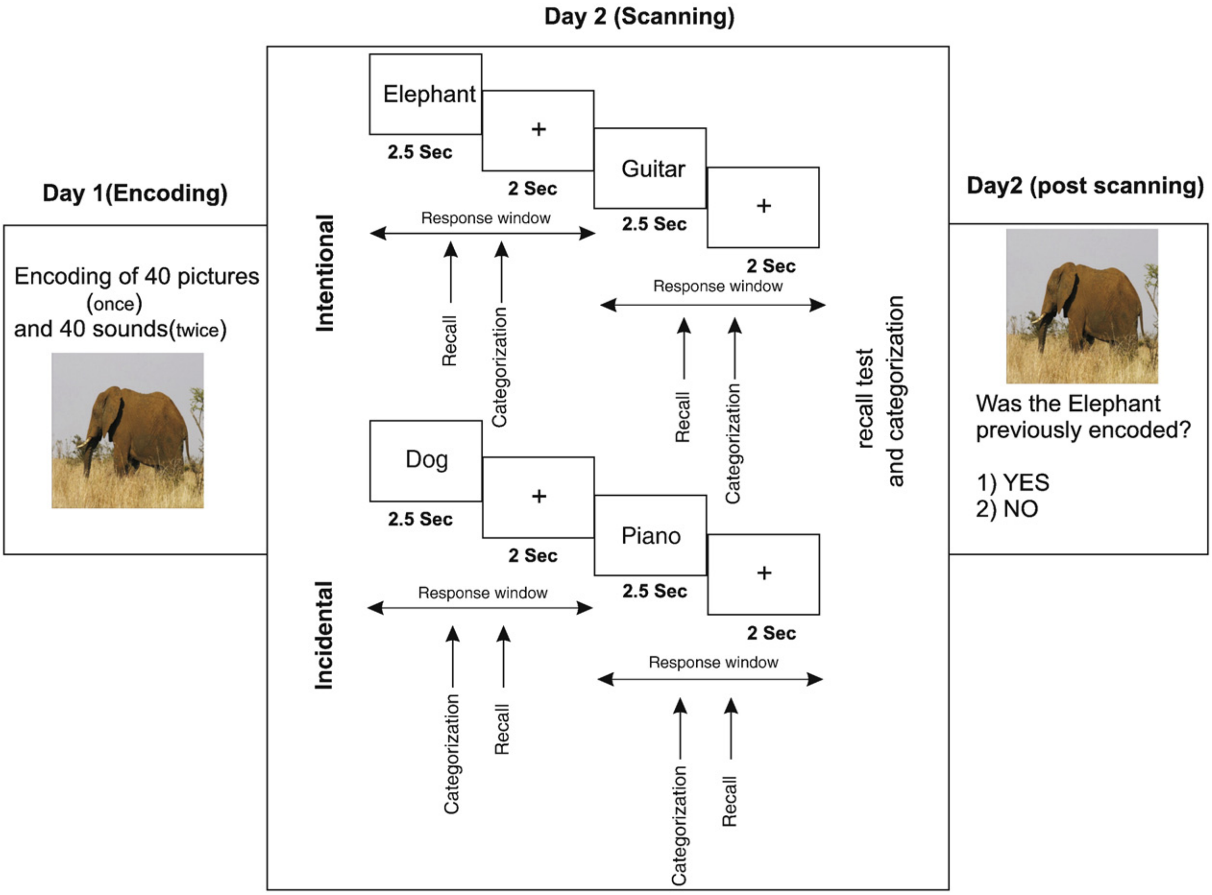

Fig. 1. Schematic illustration of the experimental design. During the first day, participants were instructed to memorize sounds and pictures. One day after, during scanning, words (1/3 matched to previously encoded sounds and pictures whereas 2/3 were unrelated, new words) were presented to participants for 2.5 s follow by 2 s inter-stimulus-intervals when a plus sign was shown. Participants indicated whether or not the word had been presented the day before (as a picture or sound), and made a semantic abstract/concrete judgment (see Methods). After scanning, a post-recognition test (yes/no) was conducted where the actual sounds and pictures were presented along with new items.

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Component Analysis (PCA; Friston et al., 1993) with the additional constraint that PLS decomposes the "part" of the covariance matrix that is attributable to the experimental design (McIntosh et al., 2004). In addition, PLS assesses activation changes across all regions of the brain simultaneously rather than in a voxel-by-voxel manner. Simultaneous analysis of spatial and temporal patterns is a noteworthy feature of this multivariate technique.

The spatiotemporal analysis proceeded in stages. First, a data matrix was constructed by separately including each individual's fMRI trial onsets for each condition of interest. For each condition, a 12 s (8 lags × 1.5 s/TR = 12 s) temporal window was specified for the Hemodynamic Response Function (HRF) to be manifested. The specified window would include BOLD signal changes from up to 3 trials, but control analyses revealed that trials following a specific available/accessible trial, within the specified 12 s temporal window, would in virtually all cases (97%) be new items. Thereby, any influence on the BOLD signal of availability/accessibility due to the following trials (within a 12 s temporal window) would be trivial. Processing during the cued-recall test was modeled as 500 ms post-stimulus onset. The data matrix containing MR signal was normalized within trials to the first scan of each trial, thereby denoting the percent signal changes of each voxel at each time point from the onset of each trial. The main purpose of the normalization was to improve the signal to noise ratio by reducing the effect of the low-frequency environmental noise while keeping the amplitude of the BOLD signal intact.

Subsequently, the constructed data matrix, containing subjects and conditions in the rows and voxel intensities for all time points in the columns, was subjected to a within-task mean centering procedure by which the grand mean (mean of each column) was subtracted from the value of each voxel in that column, producing the rotated version of the covariance matrix between the data and design matrix (containing orthonormal contrasts). Singular value decomposition (SVD) was performed on the centered deviation matrix to reveal orthogonal latent variables (LV). Each LV contains voxel and design saliencies reflecting the brain activation related to the experimental design. The amount of total variance each LV accounts for, termed the eigenvalues, was derived by the square of the singular values for each LV. In addition, brain scores and design scores were extracted for each LV. The former reflects how much each subject contributes to the pattern of each LV, obtained as the result of the dot product of each subject's image volume and the voxel saliencies of each LV. The latter reflected the contrasts expressing the effect of each particular LV, calculated by the dot product of a subject's image volume and the design saliencies of each LV. Eventually, brain scores were calculated for each time point and subsequently averaged within the group, yielding temporal brain scores (mean brain score versus time points) by which contrasts across conditions for each LVs were identified (Figs. 2 & 3).

Five different LVs (in agreement with the number of tasks) were decomposed. Statistical significance of LVs was evaluated by permutation tests. Permutation tests involved reordering the rows of the data matrix and recalculating the latent variables of the reordered matrix utilizing the same singular value decomposition approach at each permutation. Ultimately, the number of times the permuted singular value exceeds the original singular value yields the probability of the significance of original LVs (McIntosh et al., 2004, McIntosh et al., 1996). In the present study, 500 permutations were conducted to assess the statistical significance of each LV. Additionally, 100 bootstrap tests (estimation of standard error at the voxel level) were conducted to assess the reliability of voxel saliencies (at each time point) contributing to each LV. This was accomplished by using sampling with replacement followed by estimation of standard error of the saliencies after bootstrap sampling (McIntosh et al., 2004; McIntosh et al., 1996). Bootstrap ratio (BSR), which is the ratio of voxel saliencies over estimated standard error, was computed for each voxel. Voxels with BSR > 2.8 (approximately *z*-score corresponding to $P<0.005$ two-tailed, or a 95 % confidence interval) were judged to be reliable. Since saliencies are identified by a single analytic step there is no need for multiple comparisons corrections. All the reported clusters comprised at least 5 contiguous voxels and were consistently activated across at least four lags.

SPM analysis

The data were modeled voxel-wise using a general linear model (GLM), implemented in SPM5, including all five categories of items (See item classification). All five regressors, constructed as a delta function with a 500 ms post-stimulus onset, were convolved with a canonical HRF. In order to attenuate the low-frequency signal drift and serial (temporal) correlation, a high-pass filter (cut-off, 128 s) and a first order autoregressive model, AR(1), were used, respectively. Contrast images from each individual were taken into the second level random effects analysis (voxel-wise one-sample t test, df = 12) to delineate inter-subject variability. To investigate a modality-specific effect that was common for availability and accessibility, contrasts comparing the available and accessible sounds versus available and accessible pictures and vice versa were set up. In the order (Sound Rc+Rn+, Sound Rc−Rn+, Picture Rc+Rn+, Picture Rc−Rn+, Forgotten Rc−Rn−) the noted contrasts were (1, 1, −1, −1, 0), and (−1, −1, 1, 1, 0), respectively. To further determine whether there would be reactivation of sensory regions for accessible or available items, the contrasts comparing the effect of available sounds versus available pictures (0, 1, 0, −1, 0) and accessible sounds versus accessible pictures (1, 0, −1, 0, 0) were estimated, separately. The statistical threshold was set at $P<0.005$, uncorrected (extent threshold 5 voxels).

Behavioral method

Behavioral data analysis

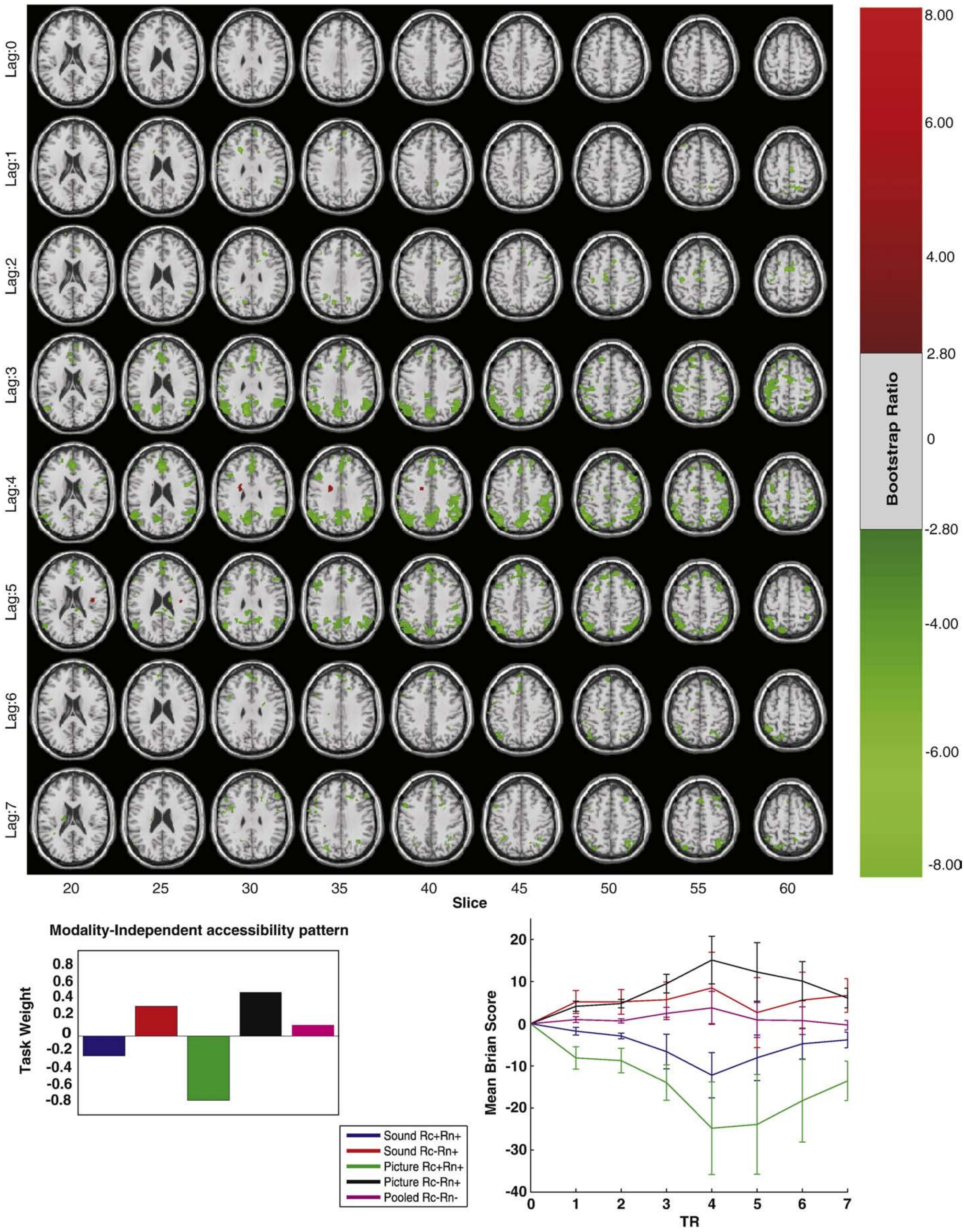
Behavioral data were analyzed by measures of reaction time and accuracy, using Statistica Toolbox (version 9). The accuracy (hit rates vs. false alarm rates) across both recall and recognition tests was evaluated using *t*-test. Additionally, mean reaction times for categorization response were evaluated by one-way ANOVA followed by a post-hoc Fisher test. Note that reaction times were computed for the categorization response, with reference to the onset of the categorization decision, which was part of all item categories whether or not the item elicited a memory response.

Results

Behavioral results

During the cued-recall test subjects correctly recalled 54.31% (43.45 ± 13 item) of the encoded items. During the recognition test, subjects correctly recognized 76.81% (61.45 ± 10 item) of the studied items. Thus, as expected, additional mnemonic responses were

Fig. 2. Singular image, task weight and temporal brain score for first latent variable(LV1).On the singular image, the Y axis represents the time(in TR) from stimulus onset and the X axis represents the approximate location of an axial slice in MNI space. The reliable activations, based on a bootstrap technique, are highlighted as the ratio of the voxel saliencies over estimated standard error. The singular image is overlaid on a standard MRI template. The temporal brain score (bottom right) of LV1 expresses changes in task-related brain activation across the lag window (8 TR) across all brain regions. LV1 ($p<0.0001$) indicates a material-independent accessibility pattern with maximum differentiation of both picture Rc+Rn+ and sound Rc+Rn+ from other conditions at 3–4 lag. The task weight (bottom left) reflects the contrast expressing the effect of LV1.



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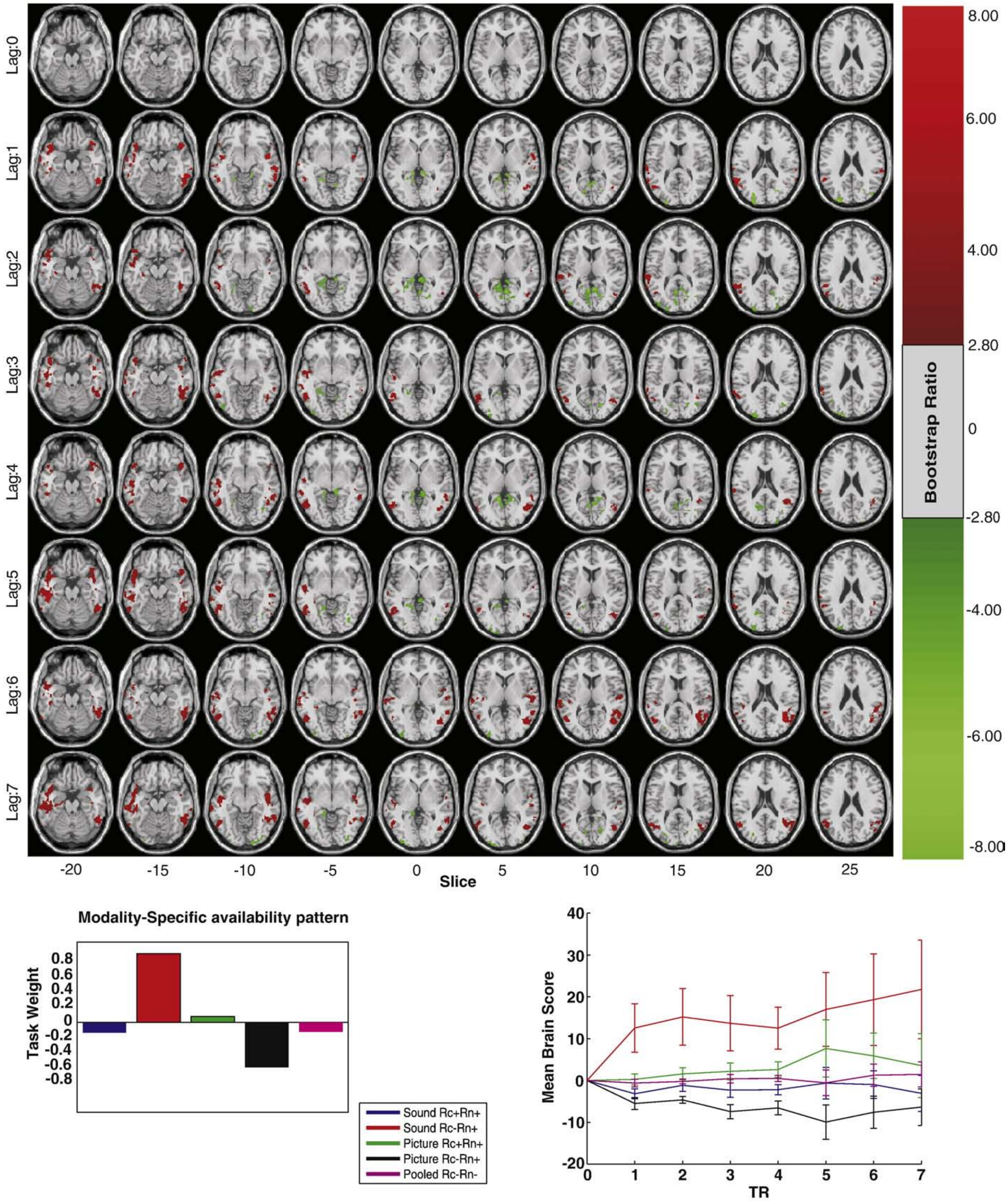

Fig. 3. Singular image, task weight and temporal brain score for the second latent variable (LV2) reflecting modality-specific availability (for details, see Figure legend 2).

elicited during the second, more supported recognition test, which made it possible to examine availability during the first test. On both tests, the average proportion of false alarms was < 1% and hit rates were significantly greater than false alarm rates (t (13) = 10.7, and 20.9, respectively, $P<0.001$). Of all the encoded items (40 sounds/40 pictures), the percentage of items falling into each category given in

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the item classification section was: Picture Rc+Rn+ = 14.15/40 = 35.38 % (14.15 ± 7.5), Picture Rc−Rn+ = 13.23/40 = 33.07 % (13.23 ± 4.5), Sound Rc+Rn+ = 23.61/40 = 59.02% (23.61 ± 8.5), Sound Rc−Rn+ = 10.46/40 = 26.15% (10.46 ± 6), and Forgotten Rc−Rn− (excluding new items) = 11.76/80 = 14.70% (11.76 ± 9). Thus, a reasonable number of items went into each item category of interest for pictures and sounds. There were very few sound/picture items which were recalled but not recognized (see Nilsson et al., 1988), so these items were excluded from the analysis. Additionally, there were very few items for which the participants did not give any response (≈ 1.38%); these items were also excluded from the analysis. Control analyses (see brain imaging results) confirmed that differences in the number of items that fell into each category had a trivial effect on brain activation patterns.

Mean reaction times for the categorization response across the item categories were assessed by one-way ANOVA (with Fisher test for post-hoc comparison); Sound Rc+Rn+ (1820 ± 86 ms), Picture Rc+Rn+ (1876 ± 108 ms), Sound Rc−Rn+ (1412 ± 143 ms), Picture Rc−Rn+ (1371 ± 89 ms) and Forgotten Rc−Rn− items including new items (1200 ± 80 ms). A significant effect of condition was revealed by the ANOVA (F (4,65) = 24.67, $P<0.001$). Post-hoc Fisher test revealed that the reaction times for Sound Rc−Rn+ was significantly shorter than for Sound Rc+Rn+ ($P<0.001$) but longer than Forgotten Rc−Rn− ($P<0.01$). The reaction times for Picture Rc−Rn+ was also significantly shorter than for Picture Rc+Rn+ ($P<0.001$) but longer than Forgotten Rc−Rn− ($P<0.01$). The reaction times did not differ between accessible sounds and pictures ($P=0.26$).

Brain imaging results

Two significant LVs were identified in the task PLS analysis. LV1 ($P<0.0001$) accounted for 41.1% of the cross-block covariance (covariance between the design and data). This LV reflected a modality-independent accessibility pattern in which both sound Rc+Rn+ and picture Rc+Rn+ were differentiated from sound Rc−Rn+ and picture Rc−Rn+, with the maximum difference at TR 3–4 (Fig. 2). There was no significant difference between the forgotten and available patterns, indicating that this LV differentiated between items that were successfully recalled and items that were not. Confidence intervals (95%) around the temporal brain scores for LV1 confirmed a consistent differentiation of modality-independent accessible items from available and forgotten items on a subject-by-subject basis for most of the time points. Additionally, LV1 reflected a weak differentiation between sound Rc+Rn+ and picture Rc+Rn+ at early lags (see confidence interval of lag 1,2 of mean brain score for LV1). The singular image of LV1 is presented at the top of Fig. 2 and consists of loadings at all the brain voxels at all time points. Reliable time points and voxels, rendered by the bootstrap technique, are represented in red and green, corresponding to positive and negative directions of LV1, respectively. Table 1 summarizes the significant regional saliencies in LV1. The positive saliencies correspond to greater activity associated with the available/forgotten items (i.e. non-recalled items) and included the right middle temporal gyrus, right inferior temporal gyrus and right rolandic operculum. The negative saliences reflected accessibility, and included the superior frontal gyrus, superior temporal gyrus, cerebellum, and the superior and inferior parietal lobule, bilaterally. An increased accessibility signal was

Table 1
Regions from LV1 showing modality-independent accessibility.

Region	Hem	BA	PLS (X,Y,Z)	BSR	LAG	SPM(X,Y,Z)	SPM T
				Neg			
Inferior parietal	L	40	(−40,−52,58)	−10.24	1,2,3,4,5,6,7	(−40,−52,58)	8.10
Olfactory	L	25	(−10,14,−16)	−9.49	1,3,4,5,6	(−6,10,−12)	4.12
Inferior Parietal	L	39	(−48,−60,52)	−9.34	3,4,5,6,7	(−40,−56,50)	5.52
Middle frontal	L	11	(−24,52,−16)	−8.57	3,4,5,7	(−30,54,10)	5.44
Superior frontal	L	10	(0,62,4)	−8.08	1,2,3,4,5	(−4,54,6)	4.52
Inferior parietal	L	7	(−32,−60,38)	−8.04	2,3,4,5,7	–	nd
Middle temporal	L	21	(−68,−22,−14)	−7.48	2,3,4,5	(−66,−24,−12)	5.18
Superior parietal	L	_	(−34,−68,60)	−7.46	1,3,4,5,6,7	–	nd
Superior frontal	R	9	(14,42,52)	−7.38	2,3,4,5,6	(18,46,42)	5.26
Precuneus	L	7	(−2,−78,42)	−7.18	2,3,4,5,6,7	(−8,−72,42)	5.67
Superior parietal	R	5	(22,−56,58)	−7.14	1,2,3,4,5,6	(28,−64,64)	5.20
Superior temporal	R	38	(28,20,−26)	−6.89	3,4,5,6	(30,15,−24)	5.98
Inferior frontal	L	46	(−46,46,−8)	−6.81	4,5,6,7	–	nd
Superior frontal	L	10	(−6,52,6)	−6.71	1,2,3,4,5,6	(−6,52,6)	7.65
Inferior frontal	L	–	(−54,32,28)	−6.65	1,2,3,4,5,6,7	(−49,34,24)	3.98
Superior frontal	L	9	(−4,52,38)	−6.19	4,5,6,7	(−6,49,46)	4.56
Cerebelum	L	–	(−22,−36,−40)	−5.82	2,3,4,5,6,7	(−26,−34,−44)	6.98
Cerebelum	R	–	(46,−66,−30)	−5.73	4,5,6,7	(38,−60,−28)	6.53
Superior parietal	L	–	(−36,−50,60)	−5.70	1,3,4,5,6	(−36,−50,60)	4.20
Superior frontal	L	10	(−8,54,6)	−5.68	1,2,3,4,5,6	(−8,54,6)	6.55
Inferior frontal	R	47	(40,36,−18)	−5.52	4,5,6,7	(40,42,−10)	6.07
Superior frontal	L	32	(0,28,42)	−5.10	2,3,4,5,6	(−6,32,42)	5.32
Inferior frontal	L	44	(−42,20,34)	−5.08	2,3,4,5,6,7	(−40,18,34)	3.98
Hippocampus	L	–	(−24,−34,0)	−5.02	4,5,6,7	(−18,−36,4)	4.39
Superior temporal	L	38	(−50,18,−20)	−4.89	1,4,5,6	(−52,12,−18)	7.62
Inferior parietal	R	39	(52,−52,40)	−4.72	2,3,4,5,7	(52,−52,40)	5.55
Amygdala	R	34	(28,0,−10)	−4.52	1,2,3,4,7	(24,−6,−12)	4.10
Middle frontal	L	46	(−38,26,38)	−3.62	2,3,4,5	(−40,32,36)	3.98
Inferior parietal	R	40	(54,−38,54)	−3.54	1,3,4,5	(54,−38,54)	4.87
Hippocampus	L	–	(−22,−26,−8)	−3.50	1,2,3,4,5	(−20,−30,−6)	4.98
Superior frontal	R	6	(20,2,56)	−3.31	1,3,4,5,6	(18,6,64)	4.23
Middle frontal	L	9	(−18,52,26)	−3.21	2,3,4,5,6,7	–	nd
				Pos			
Middle temporal	R	38	(50,10,−24)	5.15	1,2,5,7	–	nd
Inferior temporal	R	20	(54,−44,−14)	4.37	1,2,3,6	–	nd
Rolandic	R	48	(40,−12,22)	4.29	1,2,3,5,7	–	nd

Hem = hemisphere; BA = Brodmann area; BSR = Bootstrap ratio; LAG = Active time points; SPM (X,Y,Z) and T values taken from the closest region from PLS peak within 12 mm.

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also observed in the left hippocampus, left middle frontal gyrus, left precuneus, amygdala, and inferior frontal gyrus bilaterally. The average hemodynamic response function (HRF) for selected regional maxima is shown in Fig. 4, where it can be seen that the HRF closely mimicked the temporal brain scores for the LV. These regions were selected based on their close correspondence with previous findings on accessibility

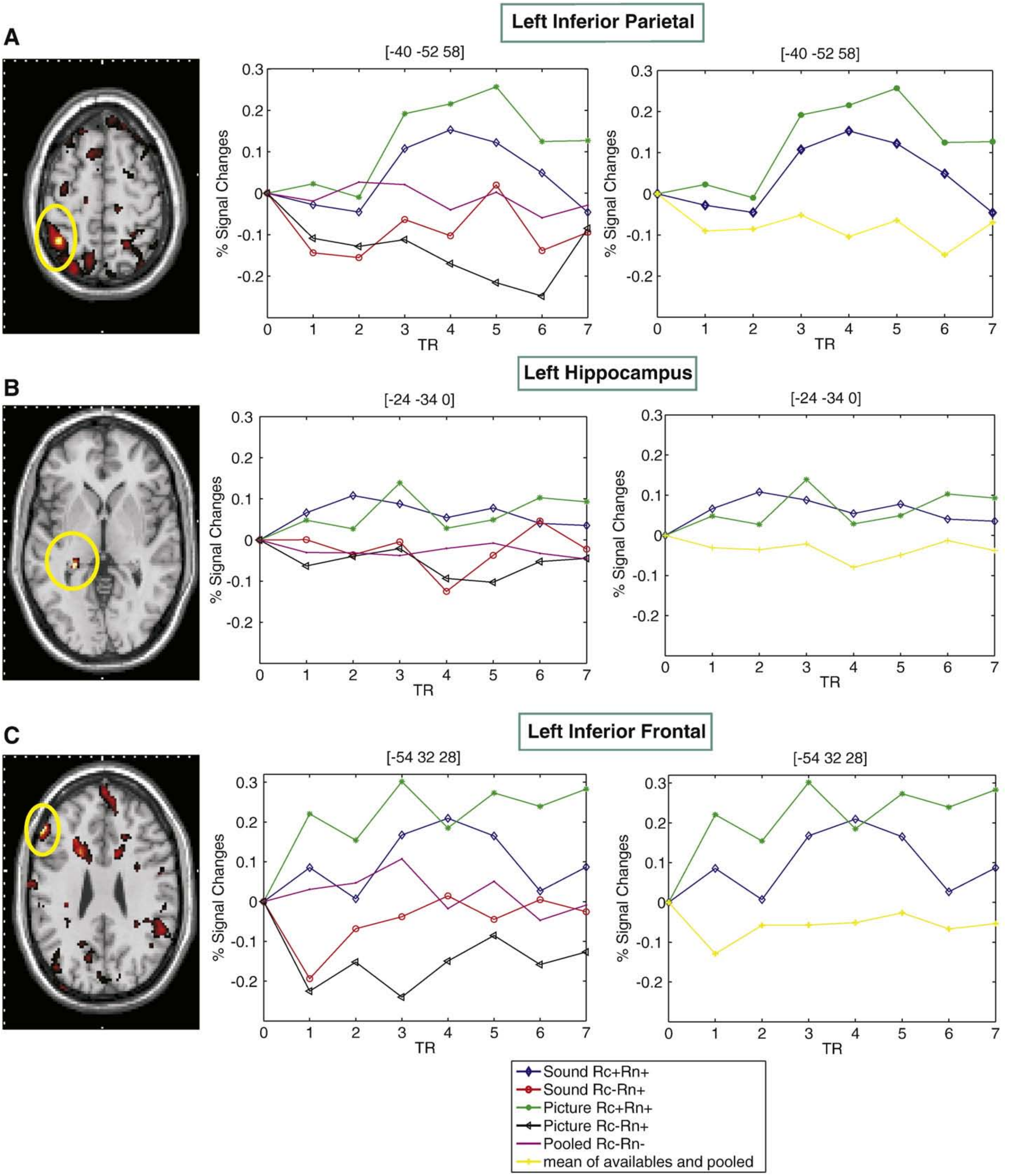

Fig. 4. Activations reflecting a general accessibility signal. Regions indicating increased activity for an accessibility signal (Table 1) are overlaid on the MNI brain template (leftmost column). The second column presents signal changes, proportional to the first TR, across the lags of each selective region. The third column present the same signal changes as in the second column, for the sound/picture available and pooled items averaged together. (A) Left Inferior Parietal. (B) Left Hippocampus. (C) Left Inferior Frontal.

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(Habib and Nyberg, 2008), but it should be stressed that the singular spatiotemporal patterns should not be only restricted to few regions and time points that survive the bootstrap threshold as the pattern as a whole will provide a better relation to the design parameters than any individual region can provide by itself.

LV2 ($P<0.01$), accounting for 30.9 % of the cross-block covariance, reflected a modality-specific availability pattern in which sound Rc− Rn+ and picture Rc−Rn+ were differentiated from the other conditions during all lags with the maximal differentiation at lag 5–7, whereas the three other conditions were roughly at zero as shown by the temporal brain score (Fig. 3). Additionally, the mean brain score of LV2 reflects a consistent differentiation of available sounds and pictures on a subject-by-subject basis. The significant regional activations of LV2, reflecting modality-specific availability, are summarized in Table 2. LV2 identified regions predominantly located in auditory and visual cortex, reflecting increased activity for available sounds and pictures, respectively (for select examples, see Fig. 5). The positive saliencies, which characterized sound availability, were left-lateralized, including the left inferior, middle, and superior temporal gyrus. In addition to modality-specific regions, sounds engaged left parahippocampus and inferior frontal gyrus, bilaterally. The negative saliencies, reflecting picture availability, were expressed in the occipital cortex, lingual gyrus, and the left fusiform gyrus.

To control for any influence of the intentionality manipulation on the result, we reanalyzed the data-set from the intentional condition only. Despite being based on fewer observations per category, this analysis revealed roughly the same patterns, at approximately the same significance levels, as the one reported above. Additionally, to control for number of items falling into each category, two control analyses were conducted. First, the data-set were reanalyzed using only the old forgotten items but excluding the new items from this category. Despite being based on less observation in the forgotten category, the same patterns were revealed. Second, a non-rotated PLS was used to test the potential influence of a greater number of items in the forgotten condition versus the other conditions, as well as accessible sound condition versus other conditions. The permutation test revealed that these patterns were not statistically significant ($P=0.9$). In this context it should be noted that the multiple regression approach implemented in SPM is more robust to differences in the number of items falling into each category. Given the high similarity between SPM and PLS pattern, any influence of the number of items falling into each category was apparently minor.

To substantiate the effects identified by LV1 and LV2, a univariate second-order random effects SPM analysis (cf., McIntosh et al., 2004, Addis et al., 2009) was conducted on subject specific parameter estimate images coding modality-independent accessibility and modality-specific availability contrasts, separately. The statistical maps yielded by *t*-tests were threshold at $P<0.005$ uncorrected, to facilitate the comparison with PLS. The *t*-scores for local maxima of the SPM analysis, located within the same anatomical gyrus as the PLS local maxima, that fell within 12 mm (twice the FWHM of the smoothing kernel) of the PLS peaks revealed by LV1 and LV2 are given in the last column of Tables 1 and 2, respectively. Voxels identified as reliable by PLS but not detected by SPM, were termed “not detected” (indicated by “nd”). As can be seen from the table, there was a strong overlap between PLS and SPM for the modality-independent

Table 2
Regions identified by LV2 showing modality-specific availability.

Region	Hem	BA	PLS(X,Y,Z)	BSR	LAG	SPM(X,Y,Z)	SPM T
	Sound						
Inferior temporal	L	20	(−46,−28,−20)	8.13	1,5,6,7	(−48,−20,−22)	3.10
Parahippocampus	L	20	(−26,−16,−24)	7.92	1,5,6,7	(−20,−10,−28)	3.90
Middle temporal	L	20	(−42,0,−26)	6.63	2,3,4,5,6,7	(−46,0,−26)	3.13
Middle temporal	L	37	(−52,−58,4)	6.29	3,5,6,7	(−52,−64,4)	3.09
Inferior temporal	L	37	(−52,−54,−4)	6.01	2,3,4,5,7	(−48,−52,−4)	3.45
Inferior temporal	R	37	(58,−56,−20)	5.87	1,3,5,6,7	(52,−58,−16)	3.17
Middle temporal	L	22	(−50,−50,22)	5.84	1,2,3,5	–	nd
Inferior temporal	L	37	(−52,−52,−10)	5.12	1,2,3,4,5,6	(−48,−52,−4)	3.45
Middle temporal	L	37	(−44,−64,−2)	5.01	2,4,5,6	–	nd
Middle temporal	L	22	(−60,−50,20)	4.62	1,2,3,5	(−66,−48,18)	3.57
Inferior temporal	R	20	(56,−42,−14)	4.59	1,3,5,6,7	–	nd
Supra Marginal	R	40	(56,−38,42)	4.49	2,3,4,5,6,7	–	nd
Inferior frontal	R	38	(38,26,−18)	4.40	1,2,3,4,5	–	nd
Middle temporal	L	21	(−46,−2,−24)	4.39	2,3,5,6,7	(−46,0,−26)	3.13
Middle temporal	L	–	(−56,12,−24)	4.39	2,3,4,6	–	nd
Middle temporal	L	21	(−62,−2,−24)	4.35	1,3,4,5,6	–	nd
Superior temporal	R	38	(32,10,−28)	4.15	2,3,5,6	–	nd
Inferior Frontal	L	11	(−22,28,−10)	4.10	1,2,4,7	(−24,34,−6)	4.54
Middle temporal	R	37	(48,−66,6)	4.00	1,2,4,6,7	–	nd
Middle temporal	L	–	(−58,10,−22)	3.97	1,2,3,4,5,6	–	nd
Superior temporal	L	48	(−42,8,−18)	3.77	1,2,3,4,5,7	–	nd
Middle temporal	L	48	(−48,−20,−4)	3.75	3,5,6,7	–	3.54
Middle temporal	L	22	(−52,−10,−10)	3.74	2,3,4,5,7	(−52,−14,−14)	6.28
Inferior temporal	R	20	(44,−12,−26)	3.50	1,2,5,6,7	(44,−12,−26)	5.03
Middle temporal	R	21	(60,−48,−2)	2.94	4,5,6,7	–	nd
	Picture						
Calcarine	R	17	(20,−72,10)	−7.47	2,3,4,7	–	nd
Middle occipital	L	18	(−20,−96,16)	−4.70	1,2,3,5,7	(−20,−97,14)	7.00
Superior occipital	R	18	(26,−92,18)	−4.01	1,2,3,4	–	nd
Lingual	R	17	(6,−58,10)	−3.79	1,2,4,5	(6,−60,10)	3.31
Fusiform	L	19	(−30,−66,−6)	−3.37	3,4,5,6,7	–	nd
Superior occipital	L	18	(−22,−92,28)	−3.35	1,2,3,4	–	nd
Lingual	L	17	(−6,−72,6)	−3.11	1,2,3,5	–	nd
Calcarine	L	17	(−6,−60,8)	−2.99	1,2,4,5	–	nd
Middle occipital	R	39	(40,−72,20)	−2.98	2,3,4,5	–	nd
Superior occipital	R	18	(24,−88,30)	−2.95	1,2,3,4	–	nd

Hem = hemisphere; BA = Brodmann area; BSR = Bootstrap ratio; LAG = Active time point;
SPM T values taken from the closest region from PLS peak.

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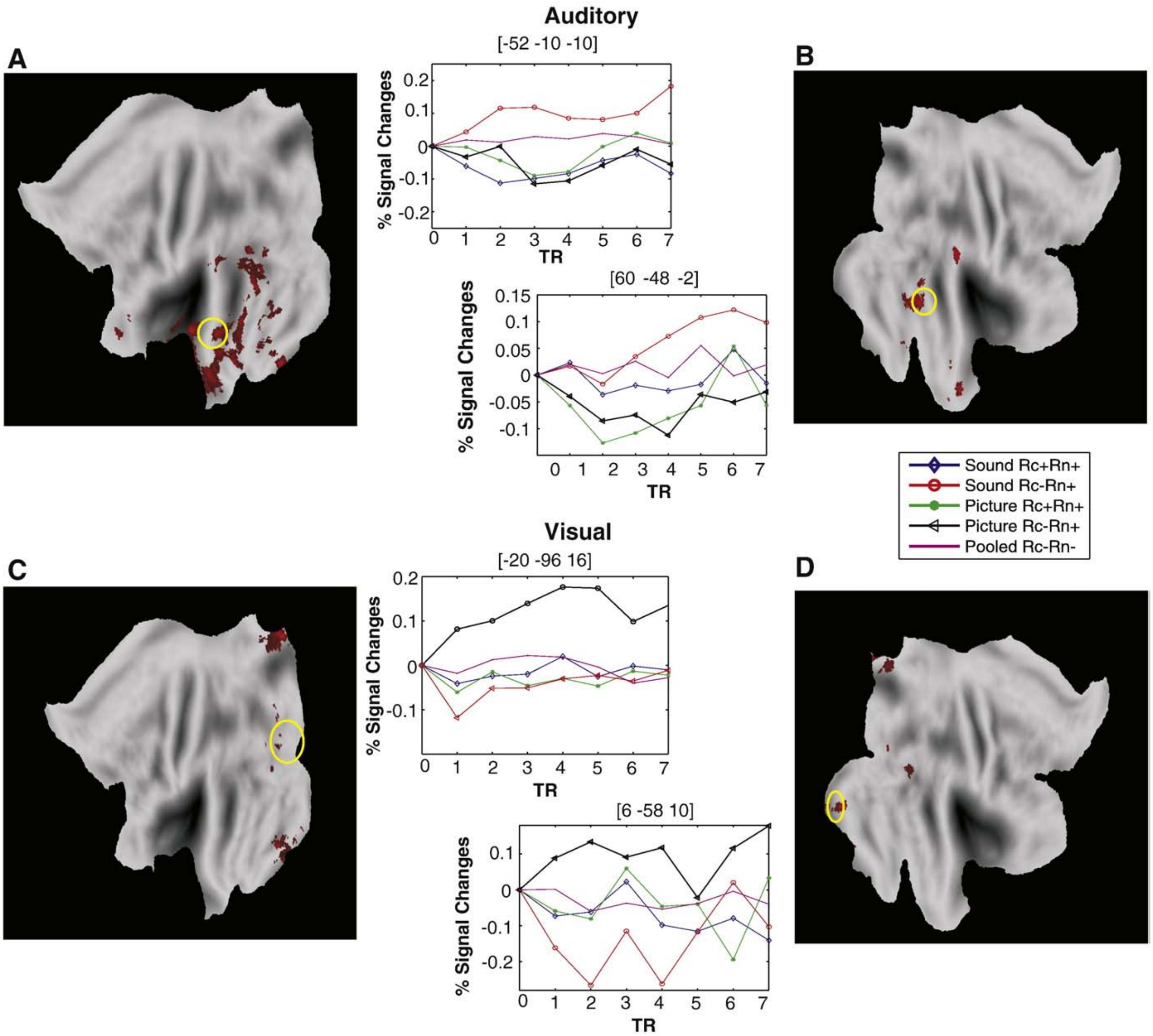

Fig. 5. Activations corresponding to a material-specific availability network are mapped on a flat brain template. The leftmost column represents the auditory and visual availability networks in the left hemisphere whereas the rightmost column reflects the same network in the right hemisphere. Percent signal change of selected regions (yellow circle) are plotted in the middle. (A) Left Middle Temporal [−52,−10,−10]. (B) Right Middle Temporal [60,−48,−2]. (C) Left Middle Occipital [−20,−96,16]. (D) Right Lingual [6,−58,10].

accessibility signal. The overlap was less pronounced for LV2, modality-specific availability, but the two sets of analyses converged on an availability signal in occipital cortex for pictures and an availability signal for sounds in temporal cortex. Moreover, in keeping with the failure to observe a modality-specific effect that was common for availability and accessibility in the PLS analysis, a planned SPM contrast (available and accessible sounds versus available and accessible pictures) did not reveal any significant effects.

Taken together, the PLS analysis revealed a modality-independent accessibility network (plus a weak modality-specific accessibility across early lags), not influenced (at least across most of the lags) by the original encoding conditions (pictures vs. sounds), along with a modality-specific availability network. In Fig. 6, the brain scores from the two LV's are projected into the same space. As is apparent, there is a clear separation between accessibility (green and blue symbols) and availability (i.e. LV1; red and black symbols), and a modality-specific effect on availability (red vs. black symbols) but not accessibility (i.e. LV2; overlap between green and blue symbols). Importantly, the plot in Fig. 6 also provides information on within-category stability (i.e. whether the effect holds for all/most of the individuals), and it can be seen that the separation of accessibility from availability is highly robust at the individual subject level.

Discussion

The present results support previous findings (Habib and Nyberg, 2008) of a distinct brain signature of available but currently non-accessible information relative to apparently forgotten and new (non-studied) information. The reaction time data converged with the imaging results in showing that the reaction times were about 200 ms longer for available than forgotten items during the cued-recall task—despite the fact that neither item class elicited a memory response. Moreover, the results provided support for the hypothesis that the availability signal would be expressed in modality-specific regions

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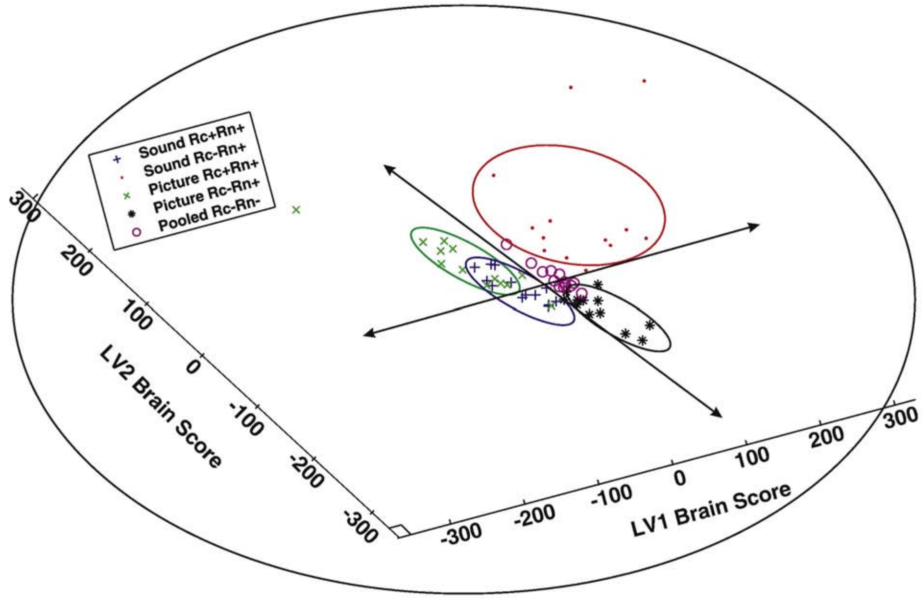

Fig. 6. Brain score plot of the two significant LVs against each other across 13 subjects. This plot elucidates the dissociation between sound/picture accessibility versus the other conditions on one dimension, where accessible items show a high tendency of grouping together regardless of modality. On the other dimension, there is a dissociation between sound availability and picture availability, which reinforces the existence of a modality effect for available but not for accessible items.

with a dominant contribution of left inferior, middle, and superior temporal regions for available sound information, and of the occipital cortex, lingual gyrus, and the left fusiform gyrus for pictorial information. Beyond modality-specific regions, availability of sounds was expressed in left parahippocampus and inferior frontal gyrus, bilaterally. Parahippocampus was previously reported as one of the main regions in a distributed pattern of brain activity, signaling availability of previously stored information (Habib and Nyberg, 2008, see also Cabeza et al., 2001). For pictures, the availability patterns was more limited to posterior, visual regions, but at a more liberal threshold ($B.R > 2.5$) a response was found in bilateral middle frontal gyrus. Indeed, the availability network was more extensive for sounds than for pictures. The reason for this is unclear but one likely explanation is that sounds were presented twice during the encoding phase. Speculatively, due to additional encoding opportunities, sounds might have been encoded in a richer way which in turn affected the availability signal (it also led to the highest levels of memory access).

A key finding of this study was that study modality did not have a corresponding influence on accessibility as it had on availability. Instead, the analysis revealed a modality-independent accessibility pattern (LV 1) that was distinct from the modality-specific availability networks (LV 2). The effect of accessibility was extensive but dominated by activity increases in left frontal cortex, left parietal cortex, and left hippocampus. These regions have been found to reflect retrieval success in earlier studies (e.g., Nyberg et al., 1996b, 2000 Konishi et al., 2000; Henson et al., 1999a; Sanders et al., 2000; Wagner et al., 2005), and in the previous study by Habib and Nyberg (2008) activity in these regions defined accessibility. LV1 also included additional regions, such as the precuneus and right prefrontal cortex, which previously have been related to successful episodic retrieval for a variety of different materials and encoding conditions (cf., e.g., Henson et al., 1999b; Tulving et al., 1994). The accessibility network was thus mostly left-lateralized which is consistent with the research reviewed above. A second potential source of left-lateralization could be attributed to use of the verbal material during the cued-recall test, consistent with previous findings showing that verbal material is processed more efficiently in the left hemisphere during mnemonic tasks (e.g., Kelley et al., 1998; Wagner et al., 1998).

In the previous study by Habib and Nyberg (2008), a univariate analytic approach was used that explicitly tested for quantitative differences (forgotten<available<accessible). Correspondingly, the analysis revealed several regions in which a graded (quantitative) response pattern was seen (for additional support for quantitative neural differences related to recall and recognition performance, see Brassen et al., 2006), but, as noted, there were also some regions where the difference was significant between accessible–available but not between available–forgotten (i.e. indicating qualitative differences). Critically, by revealing separate accessibility and availability networks, rather than common modality-specific networks for accessible and available information, the outcome of the present multivariate PLS analysis is highlighting qualitative differences between availability and accessibility. Likely, this difference is established already at the time of encoding (cf., Blumenfeld and Ranganath, 2006; Jackson and Schacter, 2004; Staresina and Davachi, 2006) such that "deep" semantic/conceptual information was generated and incorporated into the memory trace for subsequently accessible items (Habib and Nyberg, 2008). By this view, had we probed for Remember vs Know responses at the final recognition task, the items that were accessible during cued recall would likely more frequently have been associated with *Remembering* compared to available items.

A critical role of semantic/conceptual information for successful retrieval (memory access) is in keeping with numerous previous empirical theories and theoretical accounts (for a review, see Roediger et al., 1989). Still, perceptual, modality-specific information has been shown to influence the activation pattern associated with successful episodic retrieval (e.g., Nyberg et al., 2000; Wheeler et al., 2000). The weak influence of the encoding format on subsequent retrieval patterns (i.e. modality-independent accessibility network in LV1) in the present study is likely due to some key aspects of the experimental design, notably the shift in study-test format from pictures/sounds to words. It should be noted, however, that a modality-specific trend was also observed across the early lags of LV1. Speculatively, this effect indicates that for both accessible and available information, a

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modality-specific signal is present during the early retrieval phase. Thereafter, recruitment of a modality-independent network will be dominant for accessible information, whereas for available information activity will continue to build-up in modality-specific regions. While not sufficient for eliciting a remember response, the build-up in modality-specific regions could underlie performance on implicit, perceptually-based tasks. An interesting question for future research is whether the availability signals observed here can be seen as some kind of a familiarity response. Indeed, it has been argued that a familiarity discrimination network requires highly processed sensory information as its input (Aggleton and Brown, 2006). By this view, modality-specific availability signals could be a foundation for familiarity responses. To address this issue, it will be necessary to combine methodologies for defining availability in memory and those for assessing the quality of mnemonic experiences (e.g. familiarity vs. recollection).

The use of a multivariate, data-driven statistical approach was instrumental for the present demonstration of a modality-independent (as well as weak modality-specific) accessibility network along with modality-specific availability networks. For the modality-independent accessibility pattern (LV1, Table 1), there was strong overlap among the peaks identified by the SPM and PLS analyses, but for the modality-specific availability patterns there were less consistency. The SPM analysis did reveal modality-specific regions, closely overlapping with peaks from the PLS analysis, but many more regions were revealed by PLS (there were no region detected by SPM but not by PLS). The difference between SPM and PLS can be attributed to many factors. First, PLS as a multivariate approach has greater sensitivity compared to the univariate SPM approach (Harris, 1975; Mardia et al., 1979; Norman et al., 2006). Second, PLS deals with association between the data with its effect as a whole, which reflects a cooperative interaction among the brain regions (all voxels over the whole brain partially contribute to the pattern), whereas in SPM a voxel-wise statistical assessment would be independently conducted to select only the most significant voxels. Third, in general, the permutation tests determining significance in PLS avoid the multiple comparisons problem, whereas correction for multiple comparison is one great concern in SPM. Fourth, common practice in SPM is to scrutinize carefully task/condition *differences* whereas PLS accommodates indices of *similarity* and *differences* by utilizing all experimental variables simultaneously. For instance, in this study, LV1 indicated that accessible sounds and pictures were most *similar* in modality-independent regions, while LV2 delineated *different* modality-specific regions that distinguished available sounds and available pictures.

Despite the usefulness of PLS for the present purpose, some methodological caveats should be noted. As stated in the methods section, PLS utilizes a mathematically elegant method, SVD, in order to extract mutually orthogonal patterns. However, it has been previously reported that SVD may not capture the true dependencies between the patterns (McIntosh and Lobaugh, 2004). Additionally, it is not unlikely that the patterns given by SVD would be either non-linear or difficult to interpret such that the extracted patterns (optimal contrasts) do not easily map on to *a priori* expectations. Hence, we utilized a post-hoc contrast procedure in SPM to aid and corroborate our interpretation of the PLS patterns.

A final methodological caveat is that it cannot be completely ruled out that task demands influenced the pattern of the first LV, differentiating access from available and forgotten item. This is because when remembering that an item mapped to a previously presented picture or sound, the participants responded a key press. The lack of this extra motor response in the available/forgotten categories likely accounted for the increased reaction time associated with access, and might have contributed to the paucity of positive saliencies of LV1. Importantly, though, the pattern of brain regions associated with accessibility was highly similar to what has previously been observed (Habib and Nyberg, 2008), suggesting that access at least was a dominating process contributing to the effect expresses by LV1.

In conclusion, this study provided evidence for a qualitative difference between availability and accessibility in memory by linking memory access to conceptual, modality-independent brain regions, and availability in memory to elevated activity in modality-specific brain regions.

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References

Addis, D.R., Pan, L., Vu, M.-A., Laiser, N., Schacter, D.L., 2009. Constructive episodic simulation of the future and the past: Distinct subsystemsof a core brain network mediate imaging and remembering. Neuropsychologia. 47, 2222–2238.

Aggleton, J.P., Brown, M.W., 2006. Interleaving brain systems for episodic and recognition memory. Trends Cognitive Sci. 10, 455–463.

Blumenfeld, R.S., Ranganath, C., 2006. Dorsolateral prefrontal cortex promotes long-term memory formation through its role in working memory organization. J. Neurosci. 26, 916–925.

Brassen, S., Weber-Fahr, W., Sommer, T., Lehmbeck, J.T., Braus, D.F., 2006. Hippocampal-prefrontal encoding activation predicts whether words can be successfully recalled or only recognized. Behav. Brain Res. 278, 171–271.

Cabeza, R., Rao, S.M., Wagner, A.D., Mayer, A.R., Schacter, D.L., 2001. Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. Proc. Natl. Acad. Sci. 98, 4805–4810.

Friston, K.J., Frith, C.D., Frackowiak, R.S.J., 1993. Principal component analysis learning algorithms—A neurobiological analysis. Proc. R. Soc. Lond. B Biol. Sci. 254, 47–54.

Habib, R., Nyberg, L., 2008. Neural correlates of availability and accessibility in memory. Cereb. Cortex 18, 1720–1726.

Harris, R.J., 1975. A primer for Multivariate statistics. Academic Press, New York.

Henson, R.N., Rugg, M.D., Shallice, T., Josephs, O., Dolan, R.J., 1999a. Recollection and familiarity in recognition memory: an event-related functional magnetic resonance imaging study. J. Neurosci. 19, 3962–3972.

Henson, R.N., Shallice, T., Dolan, R. J. 1999b. Right prefrontal cortex and episodic memory retrieval: a functional MRI test of the monitoring hypothesis. Brain 122: 1367–1381.

Jackson III, O., Schacter, D.L., 2004. Encoding activity in anterior medial temporal lobe supports subsequent associative recognition. Neuroimage 21, 456–462.

Kelley, W.M., Miezen, F.M., McDermott, K.B., Buckner, R.L., Raichle, M.E., Cohen, N.J., Ollinger, J.M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Petersen, S.E., 1998. Hemispheric asymmetry for verbal and nonverbal memory encoding in human dorsal frontal cortex. Neuron 20, 927–936.

Kompus, K., Eichele, T., Hugdahl, K., Nyberg, L., in press. Multimodal Imaging of incidental retrieval: the low route to memory. Journal of Cognitive Neuroscience.

Konishi, M.E., Wheeler, D.I., Donaldson, Buckner R.L., 2000. Neural correlates of episodic retrieval success. Neuroimage 12, 276–286.

Mardia, K., Kent, J., Bibby, J., 1979. Multivariate Analysis. Academic Press, New York.

McIntosh, A.R., Lobaugh, N.J., 2004. Partial least squares analysis of neuroimaging data: applications and advances. Neuroimage 23, S250–S263.

McIntosh, A.R., Bookstein, F.L., Haxby, J.V., Grady, C.L., 1996. Spatial pattern analysis of functional brain images using partial least squares. Neuroimage 3, 143–157.

McIntosh, A.R., Nyberg, L., Bookstein, F.L., Tulving, E., 1997. Differential functional connectivity of prefrontal and medial temporal cortices during episodic memory retrieval. Hum. Brain Mapp. 5, 323–327.

McIntosh, A.R., Chau, W., Protzner, A.B., 2004. Spatiotemporal analysis of event-related fMRI data using partial least squares. Neuroimage 23, 764–775.

Miyashita, Y., 2004. Cognitive memory: cellular and network machineries and their top-down control. Science 306, 435–440.

Moscovitch, D.M., McAndrews, M.P., 2002. Material-specific deficits in "remembering" in patients with unilateral temporal lobe epilepsy and excisions. Neuropsychologia 40, 1335–1342.

Nilsson, L.G., Law, J., Tulving, E., 1988. Recognition failure of recallable unique names: evidence for an empirical law on memory and learning. J. Exp. Psychol. Learn. Mem. Cogn. 14, 266–277.

Norman, K.A., Polyn, S.M., Detre, G.J., Haxby, J.V., 2006. Beyond mind-reading: multi-voxel pattern analysis of fMRI data. Trends Cognitive Sc. 10, 424–430.

Nyberg, L., McIntosh, A.R., Houle, S., Nilson, L.-G., Tulving, E., 1996a. Activation of medial temporal structures during episodic memory retrieval. Nature 380, 715–717.

Nyberg, L., McIntosh, A.R., Cabeza, R., Habib, R., Tulving, E., 1996b. General and specific brain regions involved in encoding and retrieval of events: what, where, and when. Proc. Natl. Acad. Sci. 93, 11280–11285.

Nyberg, L., Habib, R., McIntosh, A.R., Tulving, E., 2000. Reactivation of encoding-related brain activity during memory retrieval. Proc. Natl. Acad. Sci. 97, 11120–11124.

Roediger III, H.L., Weldon, M.S., Challis, B.H., 1989. Explaining dissociations between implicit and explicit measures of retention: A processing account. In: Roediger III, H.L., Craik, F.I.M. (Eds.), Varieties of memory and consciousness: Essays in honour of Endel Tulving. Erlbaum, Hillsdale, NJ, pp. 3–14.

Sanders, A.L., Wheeler, M.E., Buckner, R.L., 2000. Episodic recognition modulates frontal and parietal cortex activity. J. Cogn. Neurosci, Supplement. 28.

Sohn, M.H., Goode, A., Stenger, V.A., Jung, K.J., Carter, C.S., Anderson, J.R., 2005. An information-processing model of three cortical regions: Evidence in episodic memory retrieval. Neuroimage 25 (1), 21–33.

Staresina, B.P., Davachi, L., 2006. Differential encoding mechanisms for subsequent associative recognition and free recall. J. Neurosci. 26, 9162–9172.

Tulving, E., Pearlstone, Z., 1966. Availability versus accessibility of information in memory for words. J. Verb. Learn. Verb. Behav. 5, 381–391.

Tulving, E., Kapur, S., Craik, F.I.M., Moscovitch, M., Houle, S., 1994. Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography findings. Proc. Natl. Acad. Sci. 91, 2016–2020.

Vaidya, C.J., Zhao, M., Desmond, J.E., Gabrieli, J.D.E., 2002. Evidence for cortical encoding specificity in episodic memory: Memory-induced re-activation of picture processing areas. Neuropsychologia 40, 2136–2143.

Vandenberghe, R., Price, C., Wise, R., Josephs, O., Frackowiak, R.S., 1996. Functional anatomy of a common semantic system for words and pictures. Nature 383, 254–256.

Wagner, A.D., Poldrack, R.A., Eldridge, L.L., Desmond, J.E., Glover, G.H., Gabrieli, J.D.E., 1998. Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. NeuroReport 9, 3711–3717.

Wagner, A.D., Shannon, B.J., Kahn, I., Buckner, R.L., 2005. Parietal lobe contributions to episodic memory retrieval. Trends Cognitive Sc. 9, 445–453.

Wheeler, M.E., Petersen, S.E., Buckner, R.L., 2000. Memory's echo: vivid remembering reactivates sensory-specific cortex. Proc. Natl. Acad. Sci. 97, 11125–11129.

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