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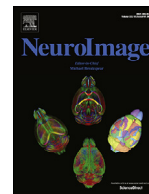**Permanent repository link:** https://openaccess.city.ac.uk/id/eprint/25941/

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Decoding verbal working memory representations of Chinese characters from Broca's area

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A R T I C L E   I N F O

A B S T R A C T

Representations of sensory working memory can be found across the entire neocortex. But how are verbal working memory (VWM) contents retained in the human brain? Here we used fMRI and multi-voxel pattern analyses to study Chinese native speakers (15 males, 13 females) memorizing Chinese characters. Chinese characters are uniquely suitable to study VWM because verbal encoding is encouraged by their complex visual appearance and monosyllabic pronunciation. We found that activity patterns in Broca's area and left premotor cortex carried information about the memorized characters. These language-related areas carried (1) significantly more information about cued characters than those not cued for memorization, (2) significantly more information on the left than the right hemisphere and (3) significantly more information about Chinese symbols than complex visual patterns which are hard to verbalize. In contrast, early visual cortex carries a comparable amount of information about cued and uncued stimuli and is thus unlikely to be involved in memory retention. This study provides evidence for verbal working memory maintenance in a distributed network of language-related brain regions, consistent with distributed accounts of WM. The results also suggest that Broca's area and left premotor cortex form the articulatory network which serves articulatory rehearsal in the retention of verbal working memory contents.

Introduction

There has been increasing interest in the neural basis of working memory (WM) storage in recent years (Christophel et al., 2017b; D'Esposito and Postle, 2015; Leavitt et al., 2017; Miller et al., 2018). This work, however, mainly focused on visual and other sensory forms of working memory to identify storage using fMRI and multi-voxel pattern analysis (MVPA). Recent studies used this approach, for example, to identify cortical regions representing low-level visual features such as orientation (Ester et al., 2015; Stephenie A. Harrison and Tong, 2009) and color (Serences et al., 2009), motion information (Emrich et al., 2013a; Riggall and Postle, 2012), auditory information (Kumar et al., 2016; Linke and Cusack, 2015), tactile patterns (Schmidt and Blankenburg, 2018), spatial locations (Jerde et al., 2012) and object information (Lee et al., 2013). Work on verbal working memory, however, is scarce

and lacks specificity for the remembered verbal content. Recent work using fMRI and MVPA, for example, employed English words and pseudowords as stimuli, but decoded the contrast between stimulus-domains (verbal versus nonverbal) instead of decoding the actual memorized content (Lewis-Peacock et al., 2012; Yue et al., 2019). Using EEG, a different group of researchers was able to decode which of two letters ('L' & 'T') subjects were currently memorizing (Polanía et al., 2011), but could not ascertain whether they were reading out visual or verbal working memory due to the limitations of the stimulus set. Thus, where in the human brain the contents of verbal working memory are stored has remained an open question.

This question is part of an ongoing debate between traditional views of working memory which localize storage to a central store in frontal regions (Goldman-Rakic, 1995) and views allocating storage to a distributed network of regions spanning the entire neocortex (Christophel et al., 2017b; Fuster, 1995; Postle, 2006; Zimmer, 2008).

The traditional view was challenged by recent MVPA work which decoded stimulus-specific WM contents in different posterior brain areas such as visual cortex (Emrich et al., 2013a; Stephenie A. Harrison and Tong, 2009; Riggall and Postle, 2012), auditory cortex (Kumar et al., 2016; Linke and Cusack, 2015), hMT+ (Christophel and Haynes, 2014; Emrich et al., 2013a), the frontal eye fields (FEF; Jerde et al., 2012) and posterior parietal cortex (Christophel et al., 2012; Christophel and Haynes, 2014; Jerde et al., 2012). Notably, some recent studies found content-specific working memory storage of objects (Lee et al., 2013), orientation (Ester et al., 2015) and auditory stimuli (Kumar et al., 2016) in both lateral prefrontal and posterior sensory regions. This recent work gave credence to a long-standing alternative perspective which postulated distributed representations in both posterior and frontal regions (Christophel et al., 2017b; Fuster, 1995; Postle, 2006; Zimmer, 2008). These findings raised a question whether these dual representations of memorized contents are redundant. Instead, we have argued for a division of labor where anterior regions represent abstract, semantic or verbal representations of memorized contents, while sensory regions maintain non-verbal sensory details of stimuli (Christophel et al., 2017b). Critically, our account of working memory storage predicts that verbal working memory storage in anterior regions is predominantly limited to left-hemispheric areas involved in language perception and production.

Here, we thus aimed at identifying neural circuits representing verbal working memory contents to (1) identify verbal working memory stores to allow for further exploration of verbal storage specifically and to (2) add to our understanding of the distribution of working memory storage in general. We asked Chinese native speakers to perform a difficult delayed match-to-sample task in a MRI scanner. Prior work indicates that Chinese characters which feature monosyllabic pronunciation combined with a complex visual appearance, are predominantly memorized verbally rather than visually (Hue and Erickson, 1988; Zhang and Simon, 1985). Thus, Chinese characters are uniquely suitable for the study of verbal working memory as compared to roman letters or words. We measured BOLD activity throughout the brain using fMRI while subjects memorized well-known simplified Chinese characters over an extended delay. Critically, we employed retro-cues to distinguish between mnemonic activity and activity related to reading and encoding the sample characters (Albers et al., 2013; Christophel et al., 2012; S. A Harrison and Tong, 2009; Schmidt et al., 2017; Sprague et al., 2014). Then we probed the entire human brain for brain patterns representing the individual memorized characters using a cross-validated multi-voxel pattern analysis (cvMANOVA; Allefeld and Haynes, 2014) and a searchlight approach (Kriegeskorte et al., 2006).

Materials and methods

Participants

Thirty healthy right-handed literate native speakers of simplified-Chinese (age between 18 and 35 years old) who had been raised in mainland China with normal or corrected-to-normal vision participated in the experiment. Handed-ness was self-reported. All participants had completed at least 12 years of school education in China which ensured their familiarity with frequently used Chinese characters. The sample size was chosen based on our experience with content-specific visual working memory signals (Christophel et al., 2012; Christophel and Haynes, 2014), but was increased considerably. Subjects gave informed consent and the study was approved by the local ethics committee. Two participants were excluded due to poor behavioral performance (Figure S1a). The final sample included 15 males and 13 females (age 27.25 ± 0.78 years old).

Stimuli

The stimuli used in this study were simplified Chinese characters with high familiarity among native Chinese speakers and comparable visual complexity (Figure b). Simplified Chinese characters have been officially used in mainland China and Singapore since the 1950s. The familiarity was ensured by drawing stimuli from the 'List of Frequently Used Characters in Modern Chinese' (Ministry of Education of the People's Republic of China, 1988), which contains the 3,500 most frequently used Chinese characters with between 1 and 23 strokes. The number of strokes of which a given character is composed is often regarded as a way to measure its visual complexity (Zimmer, 2008). Here, we decided for characters with 12 strokes, because 12-stroke characters are sufficiently complex while at the same time being frequent enough to provide a sufficient number of characters in the frequent list. Images for all characters were taken from a database provided by the Mojikyo institute (http://www.mojikyo.org/), with the same size and font. In addition, five native Chinese speakers were required to evaluate how well they knew every character with 12 strokes and its pronunciation (in total 320 characters with 12 strokes from the list). Only characters, which were rated as 'exact recognition' by all five native speakers, were selected for the stimulus pool. Furthermore, Chinese characters with symmetric structure (such as which means 'crystal') were left out due to their comparatively low visual complexity. As a result, 240 well-known simplified Chinese characters with 12 strokes were selected for the stimulus pool for this study.

To allow for subsequent fMRI multi-voxel pattern analysis, a limited number of sample stimuli were chosen for each participant to remember. Individual sample sets of 10 Chinese characters were generated based on criteria that characters of the same sample set presented different pronunciations (neither common consonants nor common vowels), low pixel-by-pixel correlation (Pearson correlation ≤ 0.1) and similar proportions of black pixels (difference ≤ 10%). A different sample set was generated for every participant. During scanning, stimuli were presented via a projector.

Experimental design

We used a retro-cue based match-to-sample task with a 10 s delay period (**Figure a**). A trial began with the sequential presentation of two sample stimuli. Each sample stimulus was shown for 500 ms, followed by a fixation period of 200 ms. Then a retro-cue ('1' or '2') was presented on a background of a black and white checkerboard for 500 ms. The retro-cue instructed subjects whether to remember the first or the second sample stimulus in each trial (cued & uncued sample; Sperling, 1960). This was followed by the presentation of a blank screen (with only the fixation point) for 9.5 s, resulting in an overall delay of 10 s. Then a sequence of three test screens was shown, each for 200 ms, separated by 300 ms. Each test screen contained two test characters. Subjects were required to find the retro-cued sample character among six test characters. This difficult variant of a match-to-sample task required subjects to identify the memorized item out of a larger set of stimuli (chance level: 16.67%) to minimize ceiling effects. After the offset of the third test screen, they had 1400 ms to respond by pressing the corresponding button. A pair of MR-compatible button boxes with 2 × 4 buttons (using the first three buttons on both sides) was employed to collect six possible response options. Participants were required to fixate throughout the trial.

All test stimuli were partly occluded to discourage subjects from memorizing only a small part of the character. Randomly, two out of nine patches that covered the whole stimulus space were occluded for all test characters in each trial. Critically, subjects deliberately received no instruction on how subjects should memorize the stimuli to avoid biasing them in favor verbalization as we aimed at avoiding verbalization that might have played no functional role in retaining the stimuli. Subjects were simply informed of the sequence of events and which buttons were needed to indicate the matching character. In addition, they were told to attend more carefully to the first stimulus in each trial to minimize recency effects.

The total duration of a trial was 14 s, followed by a variable inter-trial interval of 2–8 s (average: 4.8 s). Every subject completed an fMRI session of 4 runs, with 50 trials per run. Every Chinese character from the sample set was presented five times per run and 20 times in total as the cued sample. The trial order was randomized. The experiment was programmed using Matlab (Mathworks, Natick, MA) and Cogent 2000 (http://www.vislab.ucl.ac.uk/cogent_2000.php).

Please note that this design does not include any variation of sample size (Braver et al., 1997; Chen and Desmond, 2005; Cohen et al., 1997; Kirschen et al., 2010; Rypma et al., 1999) or the class of memorized content (i.e. verbal versus nonverbal content D'Esposito et al., 1998; Nystrom et al., 2000; Paulesu et al., 1993) nor does it have trials where subjects do not have to memorize any samples for extended periods of time (Collette et al., 1999; Crosson et al., 1999; Koelsch et al., 2009; Schumacher et al., 1996; Smith et al., 2001). This limitation prohibits us from running univariate comparisons between task conditions which are comparable with prior work.

Data acquisition

Functional MRI was measured on a Siemens 3 Tesla Trio scanner at the Berlin Center for Advanced Neuroimaging (BCAN). Both structural MRI data (T1-weighted MPPRAGE: 192 sagittal slices; TR = 1900 ms; TE = 2.52 ms; flip angle = 9°; FOV = 256 mm) and functional BOLD images (T2*-weighted gradient-echo EPI: 32 contiguous slices; whole neocortex; TR = 2 s; TE = 30 ms; voxel size = 3 × 3 × 3 mm; matrix size = 64 × 64 × 32; slice gap = 0.6 mm; descending order; flip angle = 90°; FOV = 192 mm) were acquired during the scanning. In each of the four experimental runs, 473 functional images were collected per participant. The onset of each trial was locked to the onset of the acquisition of an fMRI image to reduce temporal variability in the data analysis. All data is available upon request.

Statistical analysis

We employed cross-validated MANOVA (Allefeld and Haynes, 2014) a form of multivariate pattern analysis combined with searchlights (Kriegeskorte et al., 2006) to estimate brain regions holding content-specific information about Chinese symbols during the delay throughout the brain. Preprocessing was restricted to motion correction only, in order to maintain the fine spatiotemporal properties of the fMRI activity and therefore maximize the sensitivity of MVPA. Statistical analysis of fMRI data was performed using SPM8 (Friston K. J. et al., 1994) and cvMANOVA (Allefeld and Haynes, 2014).

The purpose of MVPA is to assess whether multivariate fMRI data contain information about differences between experimental conditions, i.e. whether the experimental manipulation induces different multivariate distributions in the data. Conventional classifier-based MVPA (Haynes and Rees, 2006) quantifies a multivariate effect by the accuracy of a classifier in distinguishing data belonging to different experimental conditions. Instead, cvMANOVA is based on multivariate analysis of variance (MANOVA; Timm, 2004) and quantifies the amount of multivariate variance explained by a specific contrast, in units of the multivariate error variance. To do so, it uses the multivariate form of the general linear model with the same regressors as would be used in univariate fMRI analysis. It has a number of advantages over classifier-based approaches: It replaces binary classification with a continuous measure of patterned differences, performs a parameter-free analysis based on a probabilistic encoding model of the data (the multivariate general linear model) and results in an interpretable and unbiased estimate of multivariate effect size (explained variance). Moreover, because cvManova employs a cross-validated variant of a likelihood-ratio statistic, it can be shown to be more sensitive than classification accuracy (see Fig. 3d in Allefeld and Haynes, 2014). For these reasons, cvMANOVA has been used throughout our recent work (Christophel et al., 2018, 2017). Other

than standard MANOVA, cvMANOVA uses leave-one-session-out cross-validation to obtain an unbiased estimate of the explained multivariate variance, called *pattern distinctness D* (Allefeld and Haynes, 2014). A consequence of this is that if the true amount of explained variance is 0, estimated values of *D* vary around 0 (for more details, please see Allefeld and Haynes, 2014). Notably, we employed a multivariate analysis approach to increase sensitivity and cannot make any inferences about the multivariate nature of the underlying signals (Hebart and Baker, 2018).

We modeled the delay-period activity in response to the memorized sample stimulus in each trial using 5 finite impulse response (FIR) regressors representing 5 fMRI scans acquired during the delay period (10 s delay at a TR of 2 s). For 10 memorized sample Chinese characters this resulted in 50 regressors (plus the constant regressor) for each of the four runs. We wanted to know whether the difference between the 10 memorized characters induced a difference in the multivariate distribution of the data in any one of the 5 FIR bins. For a given FIR bin, the corresponding contrast matrix contained 9 component contrasts (Is there a difference between character 1 and 2, character 2 and 3, […], character 9 and 10?). These were repeated for all FIR bins, leading to 5 × 9 = 45 component contrasts overall. The resulting contrast matrix had the following form (showing only the 5 component contrasts for the comparison character 1 vs 2):

$$C' = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & 0 & \cdots \\ 0 & 1 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & 0 & \cdots \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & -1 & 0 & 0 & \cdots \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & -1 & 0 & \cdots \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & -1 & \cdots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots \end{pmatrix}$$

Each row of C' had 50 entries corresponding to the 50 regressors, and there were 45 rows corresponding to the 45 component contrasts. Taken together, this contrast implemented the null model that in none of the 5 FIR bins there was a change in the multivariate distribution between the 10 conditions (memorized characters). cvMANOVA estimates the amount of multivariate variance in the data that goes beyond this null model and therefore quantifies evidence that there is indeed an effect of the memorized character. cvMANOVA was combined with searchlight analysis (Kriegeskorte et al., 2006). For this the analysis was applied to a set of voxels within a spherical mask with radius of 5 voxels that was centered on a given voxel, and this was repeated for each voxel throughout the brain in turn. We increased the searchlight radius as compared to our prior work to (a) to increase sensitivity and (b) to account for potential variation in function-anatomy association in more anterior regions (Grodzinsky and Santi, 2008; Schlaepfer et al., 1995). This resulted in a statistical parametric map of pattern distinctness values SPM{*D*} which reflected the local information content of the experimental data. These *D*-images were co-registered to the anatomical image, normalized using unified segmentation and smoothed with a Gaussian kernel of 3 mm FWHM. The resulting maps were then statistically assessed using a one-sample one-sided *t*-test against zero across subjects. Please note that one-sample t-tests do not provide population inference (Allefeld et al., 2016). Brain regions with values of pattern distinctness significantly larger than zero contain information about memorized Chinese characters during the delay period, which therefore can be considered as potential storage areas for verbal working memory.

To further interrogate these findings, we used a number of planned comparisons assessing whether the areas found carried information (1) selectively attributable to working memory, (2) selectively in the left hemisphere and (3) selectively during verbal rather than visual working memory. For this, we performed statistical comparisons using data from the cluster peaks of the main analysis showing the strongest effect. In detail, we used the (up to) three peaks with the highest T-value for each cluster (shown in Table S1), extracted D for these peaks from the respective searchlight maps and averaged them for each cluster. We focused these analyses on peaks rather than clusters to minimize effects

of thresholding on the data compared. Please note that while the peaks are identified as individual voxels, they represent D calculated from hundreds of voxels used in the searchlights in individual subject space. First, to test whether perceptual activity elicited by merely perceiving and reading the samples had leaked into delay period, we also performed a variant of the main analysis using those samples that were presented at the beginning of the trial but were not cued for memorization. This analysis was identical to the main analysis which focused on the memorized samples, but all labels were reassigned to represent the not cued item. Thus, the model for the uncued condition was identical to the cued condition, except that the FIR regressors modeled not the memorized character but the not cued character. Critically, this analysis focused on the same 5 delay period time points as the main analysis. Second, we also asked whether the regions found showed signs of lateralization. Searchlight multivariate pattern analyses regularly produce asymmetric patterns of results (Christophel et al., 2015, 2012; Christophel and Haynes, 2014). This asymmetry, however, can be a result of thresholding. For this reason, arguing for lateralization requires explicit testing (Davidson and Irwin, 1999). Here, we compared data extracted from cluster peaks with data from their right hemispheric counterparts by mirroring these peaks on the sagittal center plane in mni space (x = 0).

Third and finally, we directly compared our results to data from two previously published studies where subjects memorized complex visual pattern stimuli with little verbal content (Christophel et al., 2012; Christophel and Haynes, 2014). The analysis was identical to the main analysis for memorized Chinese characters above, but used data, time stamps and sample labels from these previously published data sets. Full detail for these additional studies is reported in the respective publications (Christophel et al., 2012; Christophel and Haynes, 2014). The studies shared a very similar overall design (same MRI scanner, trial-scanner time locking, two samples, masks and retro cues, similar delay, trial, run and experiment duration) but varied in minorly in scanning parameters (acquisition order, slice gap, flip angle), number of samples used per subject and the task at the end of the delay.

Results

Behavioral results

Behaviorally, two participants were excluded because of their poor performance compared to other participants (performance more than two standard deviations below the group average; **Fig. S1a**). The remaining 28 subjects reached on average an accuracy of 87.64% (SEM ± 1.17%) and a reaction time of 735 ms (SEM ± 26 ms).

MVPA analysis results

Patterns of brain activity during maintenance were analyzed using a multivariate pattern analysis approach (searchlight-based cvMANOVA; Allefeld and Haynes, 2014; Kriegeskorte et al., 2006) to identify brain regions encoding content-specific information about Chinese symbols.

We first asked which brain regions held significant stimulus-information during the delay. We found three brain regions with signals that held significant information about memorized Chinese symbols during the delay period (one-sample one-sided t-test, $P_{FWE} < 0.05$ cluster-level corrected, with cluster-defining threshold of $P < 0.001$; $N = 28$; see **Fig. 2** Figure 1a & **Table S1**). One brain region covers the pars orbitalis and pars triangularis of the left inferior frontal gyrus (BA 45, 46 & 47; cluster-level corrected $P_{FWE} = 0.038$), overlapping with the anterior part of what is generally defined as Broca's area (Pulvermüller and Fadiga, 2010). Another cluster is in the left premotor cortex (lPMC; BA 6, 8 & 9; cluster-level corrected $P_{FWE} < 0.001$), located anterior to the primary motor cortex and covers a major part of the precentral gyrus and the posterior part of the middle frontal gyrus in the left hemisphere. The last cluster is in early visual cortex in both the left (Brodmann area 17 & 18; cluster-level corrected $P_{FWE} < 0.001$) and the right hemisphere (Brodmann area 17, 18 & 19; cluster-level corrected $P_{FWE} = 0.004$).

We then asked whether the information that we found could be uniquely attributed to mnemonic processing. This is a necessary step, as information about a memorized item during the delay period might be a result of merely perceptual representations of the sample stimuli which persist long after stimulus offset due to hemodynamic lag. For this, we made use of the retro-cue information embedded in our design. We tested whether the regions reported above carried more information about the memorized (cued) characters as compared to characters which could be forgotten (uncued) after the retro-cue was presented. An area involved exclusively in the perception of a given character but not in the memorization would carry similar information for the cued and the uncued stimulus. Due to hemodynamic lag, this perceptual information might 'leak' into the delay and therefore mask as mnemonic activity. In contrast, memory storage would be indicated by significantly larger information for the memorized stimulus over the delay period. Testing this difference directly on all three regions (**Fig. 1**b), we found that Broca's area and left promotor cortex showed significantly more information for memorized contents qualifying them as working memory stores (two-sided paired t-test; in Broca's area: $P = 0.004$; in lPMC: $P < 0.001$). Early visual cortex, however, showed similar levels of information for cued and uncued symbols and is thus unlikely to be involved in the retention of Chinese characters (two-sided paired t-test; $P = 0.543$).

As a third step, we asked whether the information we found was limited to the left hemisphere as one might expect for language-driven representations. Both anterior Broca's area and premotor cortex were found to carry information only in the left hemisphere in this study. Explicitly testing for lateralization (**Fig. 1**c), we found that the corresponding regions in the right hemisphere did not contain significant stimulus information even at reduced thresholds, while significantly more information was found in the left than in the right hemisphere (two-sided paired t-test between hemispheres; in Broca's area: $P = 0.046$; in lPMC: $P < 0.001$).

Finally, we asked whether the regions we found to carry mnemonic representations in the current study were exclusively involved in verbal working memory. To investigate this question, we compared our results with data from two previous studies investigating the retention of complex visual patterns that were hard to verbalize: complex color patterns (Christophel et al., 2012) and complex motion patterns (Christophel and Haynes, 2014). We employed the same MVPA analyses to compare the memory storage of verbal and visual information in these regions. The sample size was 28 in this study, and 17 in both previous studies on non-verbal working memory. Therefore, we conducted a two–sided two-sample t-test on parametric maps of pattern distinctness in identified brain areas holding WM contents of Chinese characters (**Fig. 1**d). Both anterior Broca's area and lPMC held significantly more delay-period information for Chinese characters than for complex visual patterns (Chinese characters versus color patterns, in Broca's area: $P < 0.001$ and in lPMC: $P = 0.003$; Chinese characters versus motion patterns, in Broca's area: $P = 0.001$ and in lPMC: $P = 0.003$).

Notably, information regarding non-verbal patterns was indiscernible from 0 in both Broca's area and lPMC, with the exception that lPMC held significant information about complex color patterns, but significantly less than information about Chinese symbols (two-sided one-sample t-test; color patterns in Broca's area: $P = 0.494$ and in lPMC: $P < 0.001$; motion patterns in Broca's area: $P = 0.804$ and in lPMC: $P = 0.082$).

Discussion

The present study employed an information mapping approach to identify brain regions in 28 native Chinese speakers that maintained content-specific information about Chinese characters during a 10 s delay period. We found three brain regions holding significant information about memorized Chinese characters. Only anterior Broca's area and left
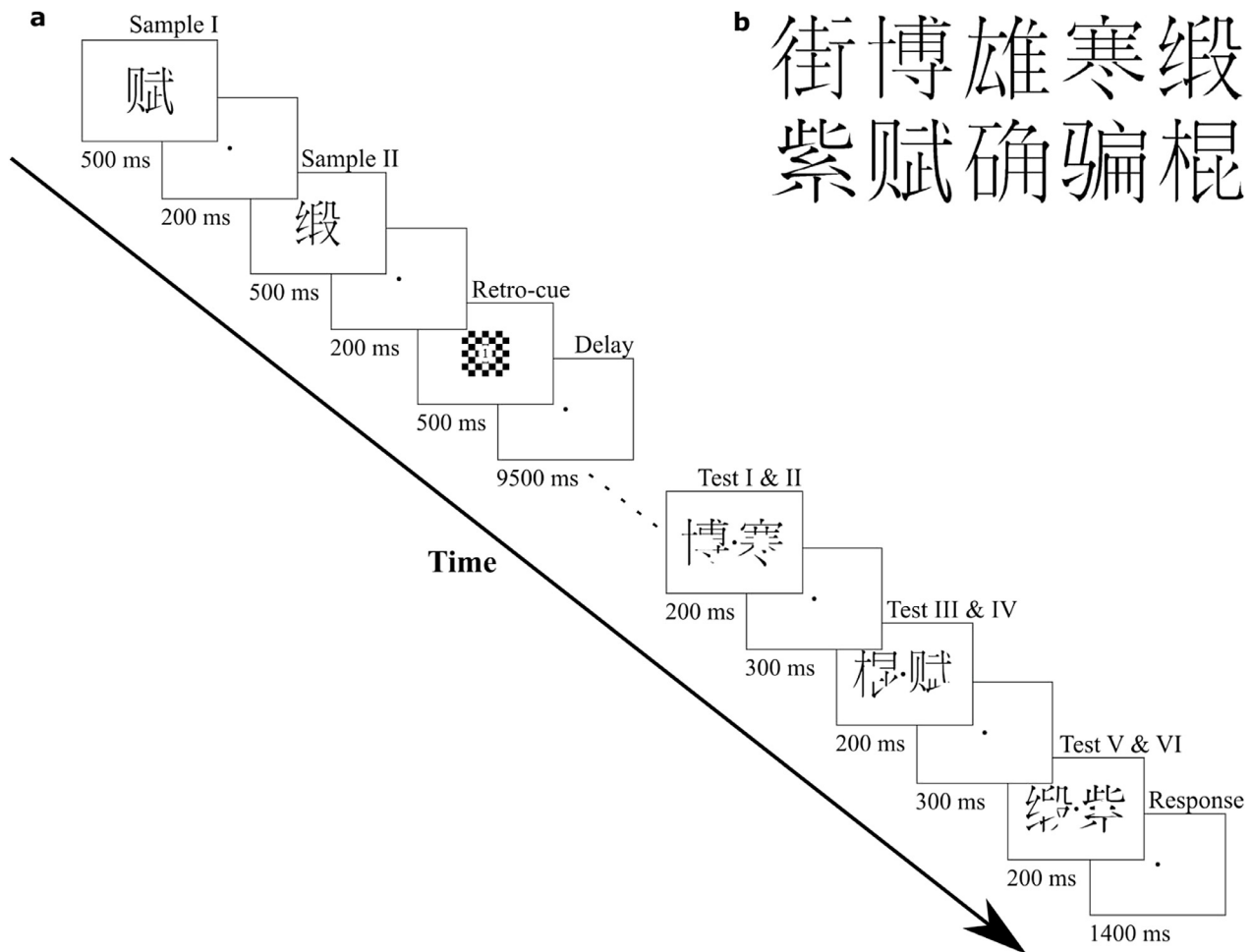
Fig. 1. (**a**) The paradigm of the retro-cue based match-to-sample task over an extended delay period. In each trial subjects were presented sequentially with two sample stimuli. This was followed by a retro-cue ('1' or '2') on a background of a black and white checkerboard, indicating whether the first or the second sample stimulus should be memorized (cued versus uncued stimulus). Then a blank screen with only the fixation point was presented for 9.5 s, resulting in an overall retention delay of 10 s (analysis time window). Afterwards, six test stimuli were presented in three sequential screens and subjects were asked to choose the cued stimulus by pressing the corresponding button. Test stimuli were partly occluded at random positions in each trial to prevent subjects from remembering only parts of the characters. (**b**) An individual sample set of ten Chinese characters with different pronunciations and comparable visual complexity was generated for each subject. Pronunciations of the monosyllabic Chinese characters are 'jiē bó xióng hán duàn zǐ fù què piàn gùn' in the illustrated sample set.

premotor cortex (lPMC) retained working memory contents while early visual cortex appeared to have no preference for the memorized over the not-memorized character and is thus unlikely to be involved in memorization. To our knowledge, this is the first study to decode stimulus-specific representations from Broca's area using fMRI and MVPA.

While the neural machinery at the heart of human capabilities to produce and understand speech is more intricate than we can give justice to, (for recent reviews see Armeni et al., 2017; Hickok and Poeppel, 2007; Houde and Nagarajan, 2011; Poeppel, 2012; Tourville and Guenther, 2011), it is clear that Broca's area plays a central role. It was originally believed that damage to Broca's area was sufficient to impair speech production (Broca, 1861). Later work demonstrated that this set of symptoms requires damage extending into the insula, motor cortex, subcortical structures and parts of the white matter (Alexander et al., 1990; Ardila et al., 2016; Dronkers et al., 2007; Mohr et al., 1978). Damage that is limited to Broca's area leads to a milder form typically referred to as 'minor Broca aphasia' (Ardila et al., 1988; Mohr et al., 1978). This neuropsychological evidence for a central role of Broca's area is supported by fMRI evidence for its involvement in language processing (Just et al., 1996; Kinno et al., 2008). Our results are consistent with the predominance of left-hemispheric areas like Broca's area in right-handed participants as a hallmark of language processing (Pulvermüller and

Fadiga, 2010). Notably, there is evidence which points to some involvement of right-hemispheric analogues of typical language related areas in human speech (Tourville and Guenther, 2011; Zangwill, 1967). Finally, it is worth noting that while our results overlap with what is typically referred to as Broca's area in prior work, there is considerable variation in the localization of Broca's area between studies and even subjects (Goucha and Friederici, 2015; Grodzinsky and Santi, 2008; Keller et al., 2009). More anterior and dorsal portions of the ventral prefrontal cortex have been implicated in abstracted and semantic working memory storage (Christophel et al., 2017b; Lee et al., 2013; Schmidt et al., 2017), but also rehearsal and mnemonic control (Fegen et al., 2015; Zanto et al., 2011). The relationship between Broca's area and these neighboring regions is a question for future research.

Premotor cortex has classically been shown to be important for the planning, the preparation, the selection and the initiation of movement (Wise, 1985). Stimulation of the left premotor cortex, however, also induces transient speech disturbances (Duffau et al., 2003). Further, recent TMS and fMRI evidence suggest its involvement in silent articulation and language comprehension (Iacoboni, 2008; Schomers et al., 2015).

Previous evidence exists supporting the participation of Broca's area and left premotor cortex in working memory as part of the dorsal stream of language processing (Hickok and Poeppel, 2007; Jacquemot and
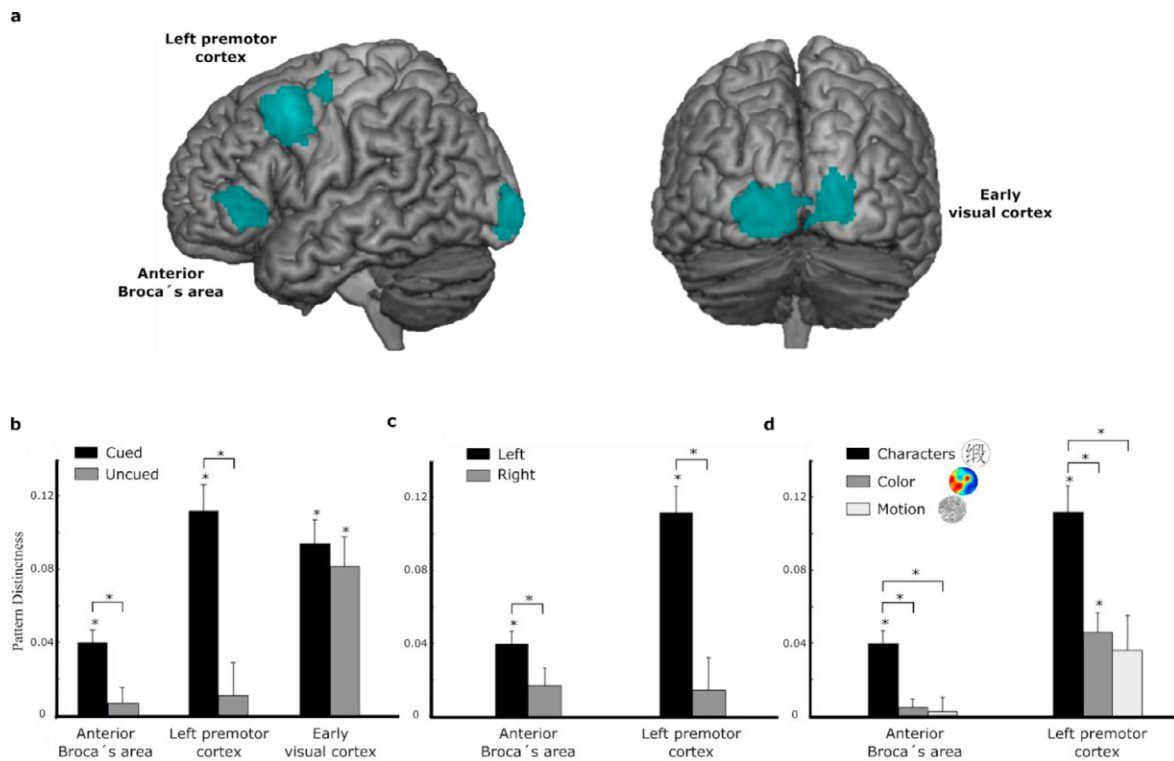
Fig. 2. Content-specific representations of Chinese characters during the delay period (Pattern distinctness D), revealed by a searchlight-based multi-voxel pattern analysis (cvMANOVA). **(a)** Brain regions with significant stimulus-specific information during the delay period (see Table S1; one sample one-sided t-test with P_{FWE} < 0.05; N = 28). **(b)** Content-specific information about cued (memorized) and uncued (presented but not cued to be memorized) samples retained in identified brain regions carrying delay-period contents. Regions encoding a comparable amount of information for cued and uncued samples were assumed to be involved in the perception than the retention process, and therefore were excluded from further analyses. **(c)** Comparison of the decoded information between the left and the right hemisphere. **(d)** Comparison of the current study with two previous working memory studies on complex visual patterns that were hard to verbalize (N= 28, 17 and 17; complex color patterns see Christophel et al., 2012; Christophel and Haynes, 2014). Data shown in **(b–d)** represent pattern distinctness in the peaks of the respective cluster (see **Table S1**) and **(for c)** their contralateral mirrors. Please note, that the data for memorized samples (black bars) is the same in Fig. 2b–d. Error bars represent between-subjects SEM; * above bars refers to two-sided one-sample t-test with P < 0.05; * above brackets indicates two-sided paired t-test **(in b, c)** or two-sided two-sample t-test **(in d)** with P < 0.05.

Scott, 2006). Lesion work suggested that damage to the left premotor cortex can lead to severe impairment in rehearsal and deficits in verbal short-term memory (Vallar et al., 1997). Previous fMRI research has further provided evidence for the involvement of language-related regions of the neocortex in working memory. For example, a number of studies reported increases in BOLD activity with increasing verbal working memory load in left inferior prefrontal cortex, premotor cortex, inferior parietal regions and superior temporal gyrus amongst other regions (Braver et al., 1997; Chen and Desmond, 2005; Cohen et al., 1997; Kirschen et al., 2010; Rypma et al., 1999; Yue et al., 2019). Activity differences in overlapping regions was also found when comparing verbal working memory to non-mnemonic control tasks (Collette et al., 1999; Crosson et al., 1999; Koelsch et al., 2009; Schumacher et al., 1996). Furthermore, recent fMRI work showed linearly increased brain activity with rising verbal rehearsal rate in premotor and inferior frontal areas (Fegen et al., 2015). Finally, a number of studies investigated verbal working compared to other non-verbal working memory contents using both univariate (Nystrom et al., 2000; Paulesu et al., 1993) and multivariate (Yue et al., 2019) methods. Reporting robust differences in premotor cortex, superior temporal areas, posterior parietal cortex and inferior frontal gyri (Nystrom et al., 2000; Paulesu et al., 1993; Yue et al., 2019), this work demonstrates that these areas at least have information about the general type of material that is remembered and are candidates for working memory storage. As a note of caution, however, prior work suggests that regions can show activity changes that are not stimulus-selective during working memory and thus not exhibit

stimulus-specific activity patterns (Emrich et al., 2013b; Riggall and Postle, 2012).

While it is plausible that regions where we do not find significant stimulus-selective information but which are implicated in prior work are involved in non-storage processes like stimulus unspecific attentional and control functions, it is also possible that our design and analysis approach might have led us to miss additional representations. In particular, in our searchlight analysis no significant stimulus-specific representation was estimated in posterior parietal brain regions that have been implicated in language processing and verbal working memory by neuropsychological investigations (Warrington et al., 1971; Warrington and Shallice, 1969) and superior temporal areas. We further did not find significant mnemonic activity patterns in regions of the left fusiform gyrus typically referred to as the visual word form area (VWFA; Cohen et al., 2000; Dehaene and Cohen, 2011; Dehaene et al., 2002) further suggesting that working memory storage in this study is predominantly depending on non-visual representations. The current study cannot exclude the possibility of other regions and strategies being involved in the retention of verbal material, as some subject indicated that they memorized using a visual or spatial strategy in addition to verbal encoding (see Figure S1). It is possible that additional regions represent memorized contents when auditory-verbal material is used (Yue et al., 2019) or when a larger set size encourages the use of additional regions to minimize interference within a given cortical circuit (Christophel et al., 2018). Alternatively, it is possible that our study lacked the statistical power to discover stimulus-selective activity pat-

terns which are less pronounced than the ones reported in the current study.

Anterior Broca's area and left premotor cortex contain significantly more delay-period information for Chinese characters than for complex visual patterns. Further, they carry little delay-period information for visual stimuli, with the exception that left premotor cortex stored significant information for complex color patterns. It is unclear whether the limited involvement of the premotor cortex in the storage of color patterns can be attributed to its general involvement in visual memory (e.g. active refreshment of visual stimuli during the delay) or the occasional use of verbalization strategies for complex color patterns. Generally, we cannot exclude the possibility that the language-related regions found in the current study could also carry information about complex visual stimuli if, for example, verbalization of these stimuli would be encouraged or other parameters of the designs were changed. Finally, a more comprehensive approach to dissociate mnemonic contents stored in cortical regions during working memory would take a wide swath of available data and compare information for all studied forms of contents and task-contexts across the entire human brain.

Participants furthermore reported a dominance of verbal (incl. acoustic and semantic) strategies in memorizing cued Chinese characters during the delay period in a post-study questionnaire (**Figure S1b**). These results suggest that visually displayed characters are memorized verbally, and that Broca's area and left premotor cortex serve as working memory stores specific to verbal rather than visual material. Although one cannot completely exclude the possibility that Chinese characters are memorized occasionally visually, it is unlikely that visual WM storage takes place in Broca's and lPMC. Instead, it is reasonable to infer that the two areas (as part of the articulatory network on the dorsal stream of language processing; Hickok and Poeppel, 2007) contributes to maintenance of verbal language information, possibly through articulatory rehearsal.

Notably, the searchlight-sphere in the current study centered in Broca's area (peak$_{MNI}$ = [−56, 34, −4], radius = 15 mm) overlaps with evidence for putatively 'visual' working memory storage of orientation in ventrolateral PFC (peakMNI = −37, 30, −2], radius = 8 mm; Ester et al., 2015). In addition, a recent fMRI study revealed content-specific tactile information in premotor cortex during working memory (Schmidt and Blankenburg, 2018). The evidence reported here might suggest that verbal working memory might play a role in the maintenance of these kinds of stimuli which have been originally thought of as 'low-level' sensory as suggested by prior behavioral and theoretical work (Postle, 2006; Postle et al., 2005; Simons, 1996).

Baddeley's influential 'phonological loop' model suggests that the function of verbal working memory storage is accomplished through the tight interplay between two systems: a sensory component and a motor component (Baddeley, 1992; Baddeley et al., 1984). The former captures the phonological input and decays over time, and the latter assists to maintain the memorized contents via articulatory rehearsal (Baddeley, 1992; Baddeley et al., 1984). While our design cannot discern the exact neural coding schemes used to retain verbal material, one could speculate that Broca's area and premotor cortex compose the articulatory network that serves for articulatory rehearsal (see also Hickok and Poeppel, 2007).

Our findings of verbal WM contents stored in Broca's area and left premotor cortex show little overlap with originally proposed dorsolateral prefrontal (DLPFC) regions for working memory storage (Goldman-Rakic, 1995). Although both regions lie within the frontal lobe, Broca's area is located inferior and premotor cortex located posterior to DLPFC. Thus, our findings provide no evidence in favor of a central working memory store localized in DLPF. Instead, they provide evidence favoring a 'distributed' account of working memory storage (Christophel et al., 2017b; Postle, 2006; Zimmer, 2008). Under this view, both sensory and non-sensory brain regions are able to carry persistent content-selective representations. For sensory memory, primate electrophysiology and human imaging studies have identified such persistent stimulus-

selective activity in regions covering the entire neocortex (for a review, see Christophel et al., 2017b). This study extends this data by revealing that verbal WM maintenance depends on a coordinated recruitment of distributed language-related regions in the anterior areas, but fails to identify representations in posterior language-specific areas. Notably, some distributed accounts of working memory (D'Esposito and Postle, 2015; Postle, 2006; Zimmer, 2008) further ascribe the role of attention allocation and control to prefrontal cortices. Please note that the current study cannot ascertain whether any particular region is involved in these processes.

For this study, we decided to use Chinese characters as stimuli instead of Latin script and (for example) English language stimuli. This choice was motivated by prior work suggesting a predominant use of verbal working memory for memorizing Chinese script and the possibility to discourage verbal encoding by varying the visual complexity of the sample characters used (Sun et al., 2011). Univariate evidence, however, suggests that studying verbal working memory with Latin script can lead to very similar results. For example, recent work (Kim et al., 2011) indicates that verbal working memory for Korean and English language stimuli activates an overlapping set of regions.

Finally, it is worth noting that the working memory task employed here is quite distant from real-life applications of working memory, where the environment is typically cluttered with distracting information, where working memory contents are usually retained while performing other tasks, where often more than one verbal stimulus is retained and where tasks regularly require combining or manipulating memorized information. Thus, further research is needed to establish whether the regions reported here fulfill the same roles in these real-life situations.

Conclusions

This is the first study using MVPA to directly examine the stimulus-specific storage of verbal working memory. Our findings show that verbal WM storage relies on a distributed network of language-related brain areas in the left hemisphere: anterior Broca's area and left premotor cortex. As part of the articulatory network for language processing, they might serve as a neural substrate for articulatory rehearsal in verbal working memory maintenance.

Data and code availability statement

For *'Decoding verbal working memory representations of Chinese characters from Broca's area'* by Yan, Christophel, Allefeld and Haynes.

Data availability

The behavioral and MRI data in this study are available from the corresponding authors upon reasonable request.

Code availability

Matlab source code for the toolbox cvMANOVA is available at https://github.com/allefeld/cvmanova/releases. We used the version v1 that was initially released on 2013.12.20 for this study.

Declaration of Competing Interest

None.

Credit authorship contribution statement

Chang Yan: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft, Visualization. **Thomas B. Christophel:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - review & editing, Supervision.

Carsten Allefeld: Methodology, Software, Writing - review & editing. **John-Dylan Haynes:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.

References

Albers, A.M., Kok, P., Toni, I., Dijkerman, H.C., de Lange, F.P., 2013. Shared representations for working memory and mental imagery in early visual cortex. Curr. Biol. 23, 1427–1431.

Alexander, M.P., Naeser, M.A., Palumbo, C., 1990. Broca's area aphasias: aphasia after lesions including the frontal operculum. Neurology 40, 353–353.

Allefeld, C., Görgen, K., Haynes, J.-D., 2016. Valid population inference for information-based imaging: from the second-level t-test to prevalence inference. Neuroimage 141, 378–392.

Allefeld, C., Haynes, J.-D., 2014. Searchlight-based multi-voxel pattern analysis of fMRI by cross-validated MANOVA. Neuroimage 89, 345–357.

Ardila, A., Bernal, B., Rosselli, M., 2016. Why Broca's area damage does not result in classical Broca's aphasia. Front. Hum. Neurosci. 10, 249.

Ardila, A., Rosselli, M., Ardila, O., 1988. Foreign accent: an aphasic epiphenomenon? Aphasiology 2, 493–499.

Armeni, K., Willems, R.M., Frank, S.L., 2017. Probabilistic language models in cognitive neuroscience: promises and pitfalls. Neurosci. Biobehav. Rev. 83, 579–588.

Baddeley, A., 1992. Working memory. Science 255, 556–559.

Baddeley, A., Lewis, V., Vallar, G., 1984. Exploring the articulatory loop. Q. J. Exp. Psychol. Sect. A 36, 233–252.

Braver, T.S., Cohen, J.D., Nystrom, L.E., Jonides, J., Smith, E.E., Noll, D.C., others, 1997. A parametric study of prefrontal cortex involvement in human working memory. Neuroimage 5, 49–62.

Broca, P., 1861. Remarks on the seat of the faculty of articulated language, following an observation of aphemia (loss of speech). Bull. Soc. Anat. 6, 330–357.

Chen, S.H.A., Desmond, J.E., 2005. Cerebrocerebellar networks during articulatory rehearsal and verbal working memory tasks. NeuroImage 24, 332–338.

Christophel, T.B., Allefeld, C., Endisch, C., Haynes, J.-D., 2017. View-independent working memory representations of artificial shapes in prefrontal and posterior regions of the human brain. Cereb. Cortex 28, 2146–2161.

Christophel, T.B., Cichy, R.M., Hebart, M.N., Haynes, J.-D., 2015. Parietal and early visual cortices encode working memory content across mental transformations. Neuroimage 106, 198–206.

Christophel, T.B., Haynes, J.-D., 2014. Decoding complex flow-field patterns in visual working memory. Neuroimage 91, 43–51.

Christophel, T.B., Hebart, M.N., Haynes, J.-D., 2012. Decoding the contents of visual short-term memory from human visual and parietal cortex. J. Neurosci. 32, 12983–12989.

Christophel, T.B., Iamshchinina, P., Yan, C., Allefeld, C., Haynes, J.-D., 2018. Cortical specialization for attended versus unattended working memory. Nat. Neurosci. 21, 494–496.

Christophel, T.B., Klink, P.C., Spitzer, B., Roelfsema, P.R., Haynes, J.-D., 2017b. The distributed nature of working memory. Trends Cognit. Sci. 21, 111–124.

Cohen, J.D., Perlstein, W.M., Braver, T.S., Nystrom, L.E., Noll, D.C., Jonides, J., Smith, E.E., 1997. Temporal dynamics of brain activation during a working memory task. Nature 386, 604–608.

Collette, F., Salmon, E., Van der Linden, M., Chicherio, C., Belleville, S., Degueldre, C., Delfiore, G., Franck, G., 1999. Regional brain activity during tasks devoted to the central executive of working memory. Cognit. Brain Res. 7, 411–417.

Crosson, B., Rao, S.M., Woodley, S.J., Rosen, A.C., Bobholz, J.A., Mayer, A., Cunningham, J.M., Hammeke, T.A., Fuller, S.A., Binder, J.R., 1999. Mapping of semantic, phonological, and orthographic verbal working memory in normal adults with functional magnetic resonance imaging. Neuropsychology 13, 171–187.

Davidson, R.J., Irwin, W., 1999. Neuroanatomy of emotion and affective style. Trends Cognit. Sci. 3, 11.

D'Esposito, M., Aguirre, G.K., Zarahn, E., Ballard, D., Shin, R.K., Lease, J., 1998. Functional MRI studies of spatial and nonspatial working memory. Cognit. Brain Res. 7, 1–13.

D'Esposito, M., Postle, B.R., 2015. The cognitive neuroscience of working memory. Annu. Rev. Psychol. 66, 115–142.

Dronkers, N.F., Plaisant, O., Iba-Zizen, M.T., Cabanis, E.A., 2007. Paul Broca's historic cases: high resolution MR imaging of the brains of Leborgne and Lelong. Brain 130, 1432–1441.

Duffau, H., Capelle, L., Denvil, D., Gatignol, P., Sichez, N., Lopes, M., Sichez, J.-P., Van Effenterre, R., 2003. The role of dominant premotor cortex in language: a study using intraoperative functional mapping in awake patients. NeuroImage 20, 1903–1914.

Emrich, S.M., Riggall, A.C., LaRocque, J.J., Postle, B.R., 2013a. Distributed patterns of activity in sensory cortex reflect the precision of multiple items maintained in visual short-term memory. J. Neurosci. 33, 6516–6523.

Emrich, S.M., Riggall, A.C., LaRocque, J.J., Postle, B.R., 2013b. Distributed patterns of activity in sensory cortex reflect the precision of multiple items maintained in visual short-term memory. J. Neurosci. 33, 6516–6523.

Ester, E.F., Sprague, T.C., Serences, J.T., 2015. Parietal and frontal cortex encode stimulus-specific mnemonic representations during visual working memory. Neuron 87, 893–905.

Fegen, D., Buchsbaum, B.R., D'Esposito, M., 2015. The effect of rehearsal rate and memory load on verbal working memory. NeuroImage 105, 120–131.

Friston, K.J., Holmes, A.P., Worsley, K.J., J.-P., Poline, Frith, C.D., Frackowiak, R.S.J., 1994. Statistical parametric maps in functional imaging: a general linear approach. Hum. Brain Mapp. 2, 189–210.

Fuster, J.M., 1995. In: Memory in the Cerebral Cortex: An Empirical Approach to Neural Networks in the Human and Nonhuman Primate, 72. MIT Press, pp. 227–228.

Goldman-Rakic, P.S., 1995. Architecture of the prefrontal cortex and the central executive. Ann. N.Y. Acad. Sci. 769, 71–84.

Goucha, T., Friederici, A.D., 2015. The language skeleton after dissecting meaning: a functional segregation within Broca's Area. NeuroImage 114, 294–302.

Grodzinsky, Y., Santi, A., 2008. The battle for Broca's region. Trend Cognit. Sci. 12, 474–480.

Harrison, Stephenie A., Tong, 2009. Decoding reveals the contents of visual working memory in early visual areas. Nature 458, 632–635.

Harrison, S.A, Tong, F., 2009. Decoding reveals the contents of visual working memory in early visual areas. Nature 458, 632–635.

Haynes, J.-D., Rees, G., 2006. Decoding mental states from brain activity in humans. Nat. Rev. Neurosci. 7, 523–534.

Hebart, M.N., Baker, C.I., 2018. Deconstructing multivariate decoding for the study of brain function. Neuroimage 180, 4–18.

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

Houde, J.F., Nagarajan, S.S., 2011. Speech production as state feedback control. Front. Hum. Neurosci. 5, 82.

Hue, C.-W., Erickson, J.R., 1988. Short-term memory for Chinese characters and radicals. Mem. Cognit. 16, 196–205.

Iacoboni, M., 2008. The role of premotor cortex in speech perception: evidence from fMRI and rTMS. J. Physiol.-Paris, Links Interact. Lang. Mot. Syst. Brain 102, 31–34.

Jacquemot, C., Scott, S.K., 2006. What is the relationship between phonological short-term memory and speech processing? Trends Cognit. Sci. 10, 480–486.

Jerde, T.A., Merriam, E.P., Riggall, A.C., Hedges, J.H., Curtis, C.E., 2012. Prioritized maps of space in human frontoparietal cortex. J. Neurosci. 32, 17382–17390.

Just, M.A., Carpenter, P.A., Keller, T.A., Eddy, W.F., Thulborn, K.R., 1996. Brain activation modulated by sentence comprehension. Science 274, 114–116.

Keller, S.S., Crow, T., Foundas, A., Amunts, K., Roberts, N., 2009. Broca's area: nomenclature, anatomy, typology and asymmetry. Brain Lang. 109, 29–48.

Kim, K.K., Byun, E., Lee, S.K., Gaillard, W.D., Xu, B., Theodore, W.H., 2011. Verbal working memory of Korean–English bilinguals: an fMRI study. J. Neurolinguist. 24, 1–13.

Kinno, R., Kawamura, M., Shioda, S., Sakai, K.L., 2008. Neural correlates of noncanonical syntactic processing revealed by a picture-sentence matching task. Hum. Brain Mapp. 29, 1015–1027.

Kirschen, M.P., Chen, S.H., Desmond, J.E., 2010. Modality specific cerebro-cerebellar activations in verbal working memory: an fMRI study. Behav. Neurol. 23, 51–63.

Koelsch, S., Schulze, K., Sammler, D., Fritz, T., Müller, K., Gruber, O., 2009. Functional architecture of verbal and tonal working memory: an FMRI study. Hum. Brain Mapp. 30, 859–873.

Kriegeskorte, N., Goebel, R., Bandettini, P., 2006. Information-based functional brain mapping. PNAS 103, 3863–3868.

Kumar, S., Joseph, S., Gander, P.E., Barascud, N., Halpern, A.R., Griffiths, T.D., 2016. A brain system for auditory working memory. J. Neurosci. 36, 4492–4505.

Leavitt, M.L., Mendoza-Halliday, D., Martinez-Trujillo, J.C., 2017. Sustained activity encoding working memories: not fully distributed. Trends Neurosci. 40, 328–346.

Lee, S.-H., Kravitz, D.J., Baker, C.I., 2013. Goal-dependent dissociation of visual and prefrontal cortices during working memory. Nat. Neurosci. 16, 997–999.

Lewis-Peacock, J.A., Drysdale, A.T., Oberauer, K., Postle, B.R., 2012. Neural evidence for a distinction between short-term memory and the focus of attention. J. Cogn. Neurosci. 24, 61–79.

Linke, A.C., Cusack, R., 2015. Flexible information coding in human auditory cortex during perception, imagery, and STM of complex sounds. J. Cognit. Neurosci. 27, 1322–1333.

Miller, E.K., Lundqvist, M., Bastos, A.M., 2018. Working memory 2.0. Neuron 100, 463–475.

Ministry of Education of the People's Republic of China, 1988. List of Frequently Used Characters in Modern Chinese.

Mohr, J., Pessin, M., Finkelstein, S., Funkenstein, H., Duncan, G., Davis, K., 1978. Broca aphasia: pathologic and clinical. Neurology 28, 311–324.

Nystrom, L.E., Braver, T.S., Sabb, F.W., Delgado, M.R., Noll, D.C., Cohen, J.D., 2000. Working memory for letters, shapes, and locations: fMRI evidence against stimulus-based regional organization in human prefrontal cortex. Neuroimage 11, 424–446.

Paulesu, E., Frith, C.D., Frackowiak, R.S., 1993. The neural correlates of the verbal component of working memory. Nature 362, 342.

Poeppel, D., 2012. The maps problem and the mapping problem: Two challenges for a cognitive neuroscience of speech and language. Cognit. Neuropsychol. 29, 34–55.

Polanía, R., Paulus, W., Nitsche, M.A., 2011. Noninvasively decoding the contents of visual working memory in the human prefrontal cortex within high-gamma oscillatory patterns. J. Cognit. Neurosci. 24, 304–314.

Postle, B.R., 2006. Working memory as an emergent property of the mind and brain. Neuroscience 139, 23–38.

Postle, B.R., D'Esposito, M., Corkin, S., 2005. Effects of verbal and nonverbal interference on spatial and object visual working memory. Mem. Cogn. 33, 203–212.

Pulvermüller, F., Fadiga, L., 2010. Active perception: sensorimotor circuits as a cortical basis for language. Nat. Rev. Neurosci. 11, 351–360.

Riggall, A.C., Postle, B.R., 2012. The relationship between working memory storage and elevated activity as measured with functional magnetic resonance imaging. J. Neurosci. 32, 12990–12998.

Rypma, B., Prabhakaran, V., Desmond, J.E., Glover, G.H., Gabrieli, J.D.E., 1999. Load-dependent roles of frontal brain regions in the maintenance of working memory. Neuroimage 9, 216–226.

Schlaepfer, T.E., Harris, G.J., Tien, A.Y., Peng, L., Lee, S., Pearlson, G.D., 1995. Structural differences in the cerebral cortex of healthy female and male subjects: a magnetic resonance imaging study. Psychiatry Res.: Neuroimaging 61, 129–135.

Schmidt, T.T., Blankenburg, F., 2018. Brain regions that retain the spatial layout of tactile stimuli during working memory – A 'tactospatial sketchpad'? NeuroImage 178, 531–539.

Schmidt, T.T., Wu, Y., Blankenburg, F., 2017. Content-specific codes of parametric vibrotactile working memory in humans. J. Neurosci. 37, 9771–9777.

Schomers, M.R., Kirilina, E., Weigand, A., Bajbouj, M., Pulvermüller, F., 2015. Causal influence of articulatory motor cortex on comprehending single spoken words: TMS evidence. Cereb. Cortex 25, 3894–3902.

Schumacher, E.H., Lauber, E., Awh, E., Jonides, J., Smith, E.E., Koeppe, R.A., 1996. PET evidence for an amodal verbal working memory system. Neuroimage 3, 79–88.

Serences, J.T., Ester, E.F., Vogel, E.K., Awh, E., 2009. Stimulus-specific delay activity in human primary visual cortex. Psychol. Sci. 20, 207–214.

Simons, D.J., 1996. In sight, out of mind: when object representations fail. Psychol. Sci. 7, 301–305.

Smith, E.E., Geva, A., Jonides, J., Miller, A., Reuter-Lorenz, P., Koeppe, R.A., 2001. The neural basis of task-switching in working memory: effects of performance and aging. Proc. Natl. Acad. Sci. 98, 2095–2100.

Sperling, G., 1960. The information available in brief visual presentations. Psychol. Monogr.: Gen. Appl. 74, 1–29.

Sprague, T.C., Ester, E.F., Serences, J.T., 2014. Reconstructions of information in visual spatial working memory degrade with memory load. Curr. Biol. 24, 2174–2180.

Sun, H., Zimmer, H.D., Fu, X., 2011. The influence of expertise and of physical complexity on visual short-term memory consolidation. Q. J. Exp. Psychol. 64, 707–729.

Tourville, J.A., Guenther, F.H., 2011. The DIVA model: a neural theory of speech acquisition and production. Lang. Cognit. Process. 26, 952–981.

Vallar, G., Di Betta, A.M., Silveri, M.C., 1997. The phonological short-term store-rehearsal system: patterns of impairment and neural correlates. Neuropsychologia 35, 795–812.

Warrington, E.K., Logue, V., Pratt, R.T.C., 1971. The anatomical localisation of selective impairment of auditory verbal short-term memory. Neuropsychologia 9, 377–387.

Warrington, E.K., Shallice, T., 1969. The selective impairment of auditory verbal short-term memory. Brain 92, 885–896.

Wise, S.P., 1985. The primate premotor cortex: past, present, and preparatory. Annu. Rev. Neurosci. 8, 1–19.

Yue, Q., Martin, R.C., Hamilton, A.C., Rose, N.S., 2019. Non-perceptual regions in the left inferior parietal lobe support phonological short-term memory: evidence for a buffer account? Cereb. Cortex 29, 1398–1413.

Zangwill, O.L., 1967. Speech and the minor hemisphere. Acta Neurol. Psychiatr. Bel. 67, 1013–1020.

Zanto, T.P., Rubens, M.T., Thangavel, A., Gazzaley, A., 2011. Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. Nat. Neurosci. 14, 656–661.

Zhang, G., Simon, H.A., 1985. STM capacity for Chinese words and idioms: chunking and acoustical loop hypotheses. Memory Cognit. 13, 193–201.

Zimmer, H.D., 2008. Visual and spatial working memory: from boxes to networks. Neurosci. Biobehav. Rev. 32, 1373–1395.