# A domain-general frontoparietal network interacts with domain-preferential intermediate pathways to support working memory task

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Working memory (WM) is essential for cognition, but the underlying neural mechanisms remain elusive. From a hierarchical processing perspective, this paper proposed and tested a hypothesis that a domain-general network at the top of the WM hierarchy can interact with distinct domain-preferential intermediate circuits to support WM. Employing a novel N-back task, we first identified the posterior superior temporal gyrus (pSTG), middle temporal area (MT), and postcentral gyrus (PoCG) as intermediate regions for biological motion and shape motion processing, respectively. Using further psychophysiological interaction analyses, we delineated a frontal–parietal network (FPN) as the domain-general network. These results were further verified and extended by a delayed match to sample (DMS) task. Although the WM load-dependent and stimulus-free activations during the DMS delay phase confirm the role of FPN as a domain-general network to maintain information, the stimulus-dependent activations within this network during the DMS encoding phase suggest its involvement in the final stage of the hierarchical processing chains. In contrast, the load-dependent activations of intermediate regions in the N-back task highlight their further roles beyond perception in WM tasks. These results provide empirical evidence for a hierarchical processing model of WM and may have significant implications for WM training.

*Key words*: frontal–parietal network; hierarchical model; kinetic stimulus; N-back; working memory.

## Introduction

Working memory (WM) refers to one's ability to maintain a limited set of information for a period and manipulate it in a goal-directed fashion (Baddeley and Hitch 1974; Baddeley 2012). This mechanism is crucial for a wide range of cognitive tasks (Rasmussen and Bisanz 2005; Nettelbeck and Burns 2010; Injoque-Ricle and Burin 2011). Given the importance of WM, a considerable number of studies have attempted to develop efficient means to improve it. Yet neither adaptive cognitive training programs nor noninvasive stimulation methods have yielded consistent results (Nilsson et al. 2017, Reinhart and Nguyen 2019, Wang et al. 2019a, 2019b, Sloan et al. 2020), implying the inadequate understanding of WM mechanisms.

Studies aiming to uncover the neural mechanisms of WM have reported that brain activations relating to information maintenance spread across almost the entire cerebral cortex (Christophel et al. 2017), i.e. the notion that specific brain regions are responsible for information storage is insufficient to understand WM. Recently, a hierarchical processing framework provided a new perspective to investigate WM (Nee and Brown 2013; D'Esposito and Postle 2015; Hasson et al. 2015;

Nee and D'Esposito 2016; Christophel et al. 2017; Badre and Nee 2018). The general principles of hierarchal neural models suggest a brain functional organization in which the primary sensory areas encode low-level features and the prefrontal areas encode the most abstract and categorical information from different modalities, with intermediate levels between the 2 ends (Hasson et al. 2015; Christophel et al. 2017). Taking this as a new perspective to consider the neural substrates of WM, a hierarchical neural organization (Fig. 1) is proposed in the present study to account for the ability to encode, maintain, and manipulate information in a goal-directed fashion, with the latter 2 aspects defining the core feature of WM from the classic view. Without any task goal, no information that relates to the current sensory inputs is intentionally maintained, despite that the neural circuits for processing sensory inputs are available (Fig. 1A). For a given WM task, a specific task goal would result in a top-down modulation from high-level circuits to select appropriate intermediate circuits, in order to progressively transform sensory inputs into a higher level of abstract representation that can be maintained and manipulated in a common network (Fig. 1B and C). Based on this model, we hypothesized
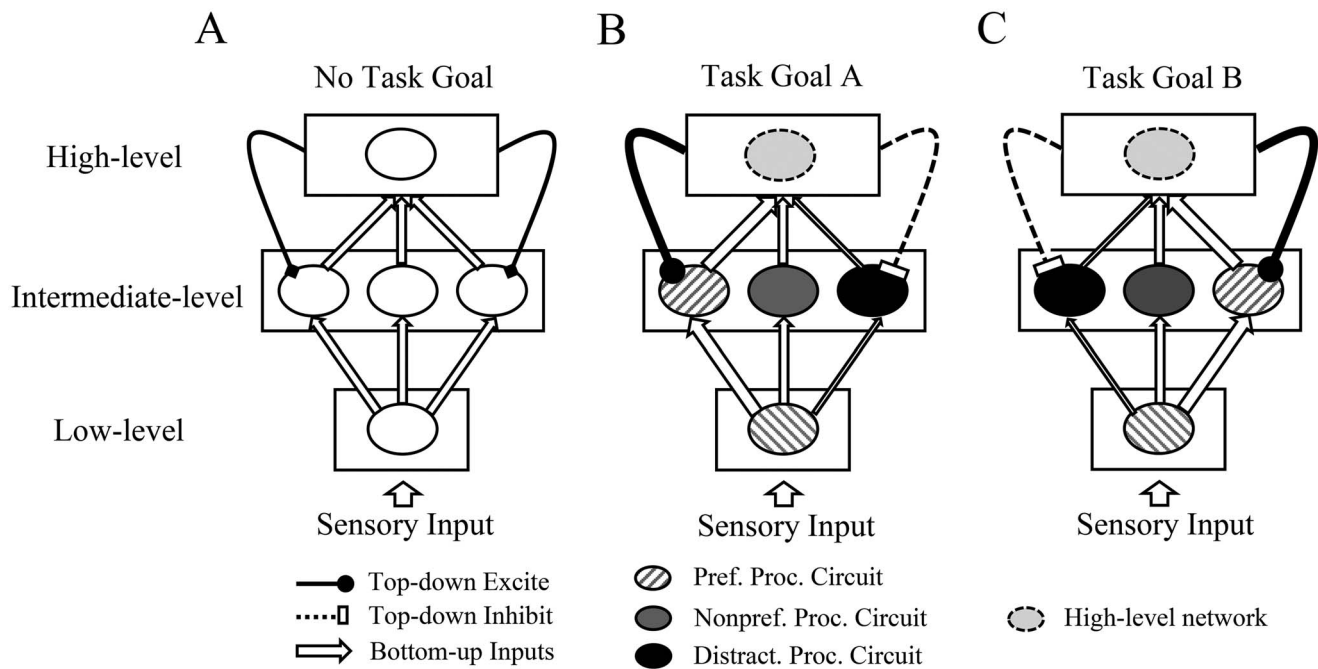
**Fig. 1.** Schematic of the hierarchical neural model to support WM tasks. The activation of a low-level circuit such as primary visual cortex propagates to intermediate-level circuits and finally to a domain-general high-level network, whereas no information is intentionally maintained without a specific task goal A). With the presence of task goals, the high-level network maintains the task rules and exerts top-down modulations on intermediate circuits accordingly B, C); in WM tasks, it also serves as the primary neural substrate to maintain trial-based information that has been hierarchically abstracted through multiple layers of intermediate circuits. *Abbreviations:* Pref. Proc. Circuit, preferential processing circuit; Nonpref. Proc. Circuit, non-preferential processing circuit; Distract Proc. Circuit, distract processing circuit.

that a domain-general network would interact with distinct domain-preferential intermediate pathways to support WM tasks with different stimuli or task goals. However, the direct evidence for this hypothesis is incomplete.

In order to investigate the neural substrate of WM from the hierarchical processing perspective outlined above, we used point-light constituted biological motion (BM) and circle shape motion (SM) as 2 kinetic stimulus types (Shen et al. 2014; Gao et al. 2015). Previous studies have shown that motion categories can be decoded from brain activations despite different incidental features (Wurm and Lingnau 2015; Wurm et al. 2016; Hafri et al. 2017), indicating that high-level abstract representations of motion can be derived from stimuli. As illustrated in Fig. 2A, when processing kinetic stimuli, participants first perceived low-level features of light-points, then the geometry and location of the points-constituted object were extracted, which formed a static image. Next, the representation of motion could be formed by integrating these static images, which is an additional abstraction step compared with previous studies using static stimuli. This abstraction procedure may thus induce more robust brain activations of intermediate pathways than static stimuli, and is more suitable to illustrate the intermediate neural substrates in WM tasks. The high-level abstract representation of BM, which portrays human actions, may produce a unique social attribute. In line with this conjuncture, the processing of BM requires the involvement of both the middle temporal area (MT) and superior temporal gyrus (STG; Pitcher and Ungerleider

2021). Although the MT is critical for general complex motion perception (Lingnau and Downing 2015; Liu and Pack 2017), the posterior STG (pSTG) acts as an essential component of social cognition network (Adolfi et al. 2017) with preferential responses to BM perception (Grossman et al. 2000; Sokolov et al. 2018). Therefore, we hypothesized that MT and pSTG play important roles at intermediate processing stages of BM WM. In contrast, the neural substrate supporting the intermediate processing of SM has not been identified, however, we hypothesized that different brain regions would be involved in this condition because no social attributes could be extracted. Among the many regions showing activation in WM tasks, the frontal–parietal network (FPN) demonstrates robust and consistent activation regardless of stimulus materials and paradigms (Collette and Van der Linden 2002; Owen et al. 2005; Rottschy et al. 2012; Dong et al. 2016). Therefore, this network, which may serve as the domain-general neural substrate in the WM hierarchy, could interact with the intermediate regions in a task-dependent fashion.

## Materials and methods
### Experimental design

Two typical WM task paradigms, the N-back and the delayed match to sample (DMS), were adopted with 2 types of kinetic stimuli as sensory inputs (Fig. 2). Since the participants perceived the cognitive load merely by the task cue and the stimuli were identical across different loads of the N-back paradigm, this
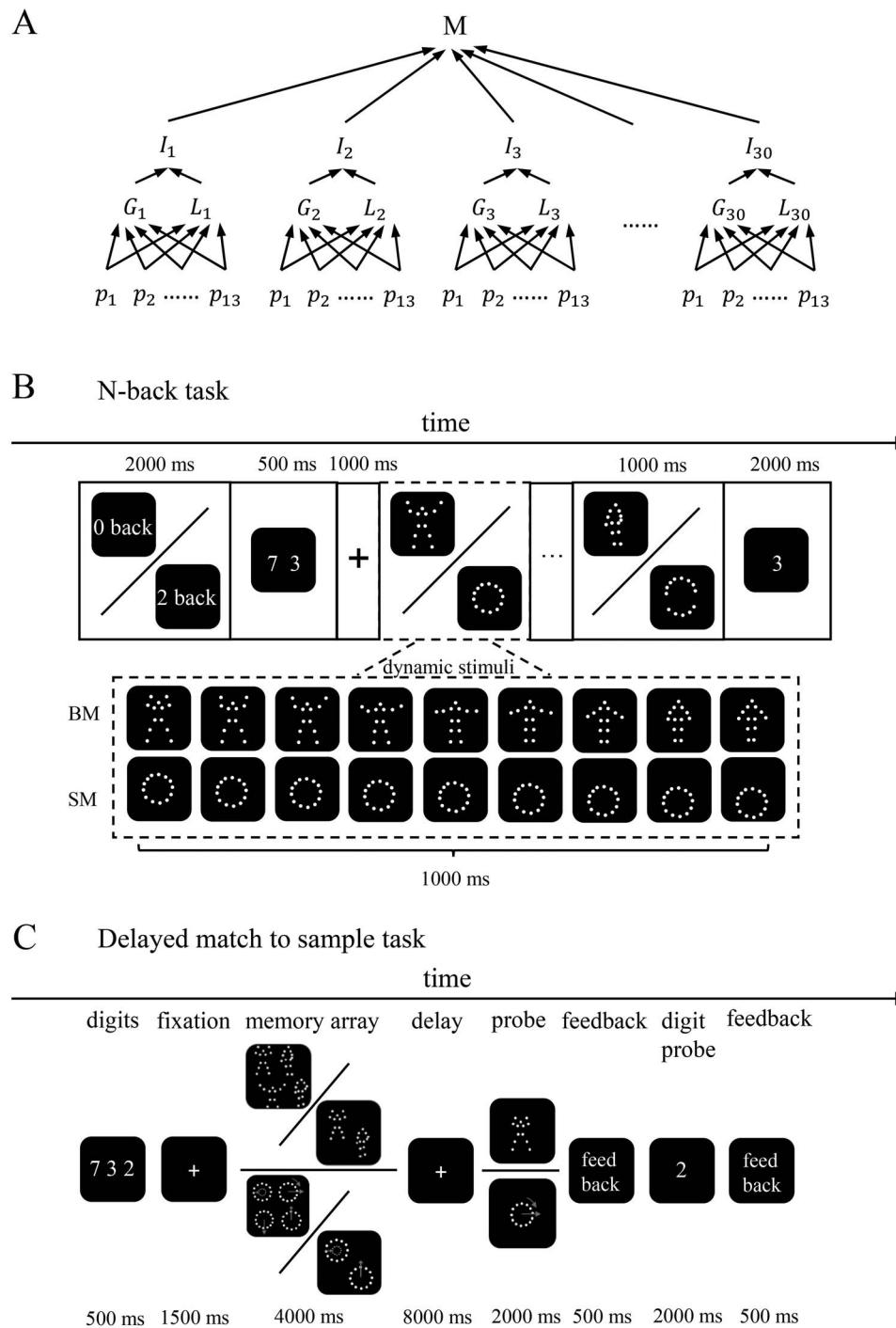
**Fig. 2.** fMRI task design. A) Schematic of the hierarchical abstract representation of a kinetic stimulus. The stimulus is composed of 13 light points (*p*). By integrating all of the light points, participants could extract the geometry (G) and location (L) of the points-constituted object, which formed a static image (I). The representation of motion (M) could be formed by integrating these static images. B) The kinetic N-back task design. C) The DMS task design. The BM stimuli simulated human body movements and SM stimuli were circle shape movements. Each movement was an animation consisting of 30 frames. *Abbreviations*: BM, biological motion; SM, shape motion.

configuration could be used to "test whether a given brain region was involved in information maintenance and/or manipulation by contrasting the activations between low and high N-back load conditions." In addition, the manipulation of stimulus materials would not only enable the assessment of "domain-preferential intermediate regions by contrasting brain activations of different sensory inputs under the same N-back load, but also the domain-general WM regions by jointly considering its stimulus-free regional activation and stimulus-dependent interregional connections with distinct intermediate regions." Therefore, to test our hypothesis of the hierarchical processing model for WM tasks (Fig. 1), we first used the N-back task to identify

intermediate regions, and then performed psychophysiological interaction (PPI) analyses to define domain-general regions (see details below). Lastly, we used the DMS task to verify the N-back results and further dissect the specific roles (e.g. perception, information maintenance, and/or manipulation) of these regions in WM tasks because the DMS paradigm could separate the process of maintaining information from sensory perception (also refers to "encoding") by a delayed interval, during which sensory input was absent.

## Subjects

Fifty-five participants were recruited for the N-back experiment. One participant did not finish the test and 7 were excluded because of large head motions (maximum displacement > 3 mm or 3°, or the number of time points with Framewise Displacement > 0.5 mm exceeded 10% of the total), leaving 47 participants for the final group-level analysis (18 males, age = 19.91±0.80).

The DMS data were composed of 2 subsets. An "old" subset (24 participants) was drawn from an earlier study on WM capacity, from which the DMS task data involving BM only have been disclosed (Lu et al. 2016), but the results involving both BM and SM conditions have never been published. A "new" dataset (22 participants) was further collected to enlarge the sample size. Eight and 4 participants were excluded because of large head motion from the "old" and "new" datasets, respectively, leaving 34 participants for the final sample (18 males, age = 23.28±2.55). The vision of all participants was normal or corrected to normal, and none reported a history of psychiatric disorders. This study was approved by the Ethic Committee of Zhejiang University. Informed consent was obtained from each participant before the study, and all participants were compensated for their time dedication.

## fMRI task details and behavioral data analyses

As illustrated in Fig. 2B, the N-back WM task consisted of 2 stimulus conditions, namely BM and SM. Each stimulus condition was composed of 2 memory loads (0-back and 2-back), with 4 blocks for each load and the order of blocks as pseudo-random. For the 0-back block, the participants were required to press a key when the actual stimulus was identical with the first stimulus displayed at the beginning of each 0-back block. Meanwhile, in the 2-back block, a response was required to be made when the actual stimulus matched the stimulus presented 2 trials earlier. The stimuli under BM N-back and SM N-back conditions were 13 light points simulating human body movements and circle shape movements, respectively, and each block consisted of 14 trials (stimuli). Each movement simulation was an animation of 30 frames displayed through Psychtoolbox on Matlab (R2017b) with a duration of 1 s. The monitor refresh rate was set to 60 Hz. Between the animations, there was a fixation lasting for 1 s. To avoid the linguistic encoding of kinetic stimuli, participants were asked to silently rehearse 2

digits randomly generated and presented before each block (Gao et al. 2015; Lu et al. 2016). A probe digit was presented at the end of the block to test the accuracy of digital rehearse. Each N-back block was followed by a short rest period of 12 s when a fixation was presented to allow the hemodynamic response to return to baseline. Notably, the point-light BM stimuli used in the present study contained animate entities and participants could perceive them with social attributes by integrating a series of visual inputs.

The DMS task used the same stimuli as the N-back task (Fig. 2C). Each participant underwent 6 task runs, including 3 runs of BM and 3 runs of SM condition. The order of BM and SM runs was counterbalanced between the subjects. Each condition was composed of 2 memory loads (2 sets and 4 sets), and trials of different loads were intermixed. Within each trial, 3 digits were presented on a black screen for 0.5 s, and then the memory array was displayed for 4 s after a 1.5-s fixation period. The participants were required to maintain the stimuli of memory array for a delay period of 8 s and respond according to whether the stimulus displayed in the following probe was one of the stimuli in the memory array (Fig. 2C). Similar to the N-back task, participants were asked to silently rehearse 3 digits presented at the beginning of each trial, and a probe digit was presented later. In each run, there were 6 baseline trials in which the digital rehearsal task was required, but the "memory array" was replaced by a white fixation.

For the N-back task, $d'$ was employed as the behavioral index for WM performance. The formula used to calculate $d'$ was as follows: $d' = Z_{Hit} - Z_{FA}$ (Haatveit et al. 2010), where *Hit* represents the percentage of target trials (animations) that were correctly responded, whereas *FA* represents the percentage of nontarget trials that were incorrectly answered. A high $d'$ value indicates that the signal/target can be reliably detected (Haatveit et al. 2010), and therefore means a better N-back WM ability. For the DMS task, the accuracy of each condition was calculated. A 2-way repeated measures analysis of variance (ANOVA) was conducted on each variable with stimulus-type (BM vs. SM) and load (0-back vs. 2-back and 2 sets vs. 4 sets for N-back and DMS, respectively) within-subject factors. The Bayes factor (BF) was calculated to confirm the reliability of the statistical inference. If the *P* value was smaller than 0.05 yet the BF was also small (e.g. < 3), the alternative hypothesis would not be accepted (Wu et al. 2018).

## Imaging acquisition and preprocessing

The N-back functional magnetic resonance imaging (fMRI) data and the "new" DMS data were acquired by a 3T Siemens Prisma scanner using a 20-channel coil. The functional images were collected using a T2*-weighted single-shot echo-planner imaging sequence with multiband acceleration (multiband factor = 4), and the collection parameters were as follows: TR/TE = 1,000 ms/34 ms,

flip angle = 50°, FOV = 230×230 mm², matrix = 92×92, voxel size = 2.5×2.5×2.5 mm³, and slice number = 52. Anatomical images were collected using a T1-weighted 3D magnetization-prepared rapid gradient echo sequence with the following parameters: TR/TE = 2,300 ms/2.32 ms; flip angle = 8°; FOV = 240×240 mm²; matrix = 256×256; voxel size = 0.94×0.94×0.9 mm³; and 208 slices in the sagittal panel.

The "old" DMS fMRI data were acquired by a GE 3T Signa HDxt scanner. The functional images were collected using a T2*-weighted single-shot echo-planner imaging sequence, and the collection parameters were as follows: TR/TE = 2,000 ms/30 ms; flip angle = 90°; FOV = 240×240 mm²; matrix = 64×64; voxel size = 3.75 ×3.75×5 mm³; and slice number = 33. No structural data were collected.

Both N-back and DMS fMRI data were preprocessed using AFNI (Cox 1996), ANTs (http://stnava.github.io/ANTs/), SPM12 (https://www.fil.ion.ucl.ac.uk/spm/), and DPABI (Yan et al. 2016). The fMRI data were subjected to slice acquisition time correction, motion correction, spatial normalization, and smooth (FWHM = 5 mm). Since no structural data were acquired for the "old" DMS experiment, the functional data of this dataset were normalized to MNI space using an EPI template. In the first level analysis of the N-back task, the general linear model (GLM) was used to obtain the activation maps of BM 0-back, BM 2-back, SM 0-back, and SM 2-back conditions for each participant, with the rest period as the baseline condition. For the DMS task, we separately modeled the encoding (4 s for the memory array period), maintenance (8 s for the delay period), response (2 s for the probe period), and feedback (0.5 s for the feedback period) periods for the correct trials of each WM load (i.e. 2 sets and 4 sets) and each stimulus type (i.e. BM and SM). In addition, 3 regressors for digit encoding, digit response, and digit feedback were included. The error trials were also modeled with additional regressors for encoding, response, and feedback periods.

## Statistical analyses of brain activation

In order to identify the stimulus-preferential intermediate processing regions, a 2-way repeated ANOVA on the N-back activation maps was conducted at the group level with stimulus-type (BM and SM) and load (0-back and 2-back) as within-subject factors. Brain regions showing significant stimulus-type main effect (BM vs. SM) were regarded as intermediate regions.

In order to identify a hypothetic domain-general WM network, the above resultant ROIs were used in voxel-wise PPI analyses. The differences in effective connectivity between BM and SM conditions were examined under the 2-back condition, as both stimulus-type preferential and domain-general WM processing were highly demanded under this condition. Based on our schematic model in which there is a set of brain regions receiving inputs from intermediate regions independent of low-level stimulus features, we propose

that such top-level domain-general regions would be these regions showing (i) stimulus-type "dependent connectivity" with stimulus-preferential intermediate regions, and (ii) stimulus-type "independent activation." We used PPI analysis to identify regions satisfying the first criterion. Technically, PPI describes the condition-dependent synchronization between a source region (e.g. MT) and a target region or voxel (see supplementary materials for methodological details). We first acquired voxel-wise PPI maps (i.e. differences in effective connectivity between BM 2-back and SM 2-back conditions) using intermediate regions as seeds (one PPI map for each seed region). To further identify regions that also satisfy the second criterion, we conducted a conjunction analysis on the PPI maps and a WM map acquired from an automated meta-analysis of 1,091 studies using Neurosynth (https://neurosynth.org/) by searching the term "working memory." The resultant regions constituted the hypothetic domain-general WM network (Supplementary Fig. S1). All voxel-wise fMRI statistics were corrected for multiple comparisons according to voxel-wise $P$-value < 0.001 and a minimum cluster size of 22 voxels based on 3dClustSim (using the average spatial smoothness parameters of the group with the mixed-model autocorrelation function, ACF) in AFNI (Cox et al. 2017).

In order to verify the results of the N-back task, ROI-wise ANOVA analyses on the DMS activations were conducted. As the 2 DMS datasets yielded similar results, we combined them and performed repeated ANOVA analyses with stimulus-type (BM and SM) and load (2 sets and 4 sets) as within-subject factors, and scanner as a categorical covariate for encoding and maintaining phases separately. The intermediate regions and domain-general regions identified above were used as ROIs. Post-hoc tests were further performed with Bonferroni correction $P$ < 0.05. If the intermediate regions and domain-general regions were identified appropriately, the main effect of stimulus-type was expected for intermediate regions but not for domain-general regions. In addition, we tested the load and stimulus-type main effects of the N-back task on domain-general ROIs using ROI-wise ANOVA analyses. As the stimulus-type main effect of intermediate regions was already revealed by voxel-wise whole brain analysis, we only tested the load effect in the subsequent ROI-wise analysis of the N-back task (using paired $T$-tests).

The ROI-wise analyses were conducted to further dissect the roles (e.g. encoding, information maintenance, and/or manipulation) of stimulus-type preferential and domain-general regions in WM tasks. As different loads of sensory inputs (2 sets vs. 4 sets) required different demands for stimulus encoding in the DMS task, we examined whether these regions were engaged in encoding by testing the load effect during the DMS encoding phase. Similarly, whether these regions were engaged in information maintenance was tested by the load effect during the delayed phase. Returning to the N-back task, the sensory input was the same for 0-back

and 2-back conditions, whereas the load of information maintenance and manipulation in WM was higher under the 2-back condition. The regions that supported pure perception would not show significant WM load effect in the N-back task. Therefore, we combined the activations in both N-back and DMS tasks to summarize the roles of intermediate and domain-general regions in WM tasks.

# Results
## Behavioral results
Regarding N-back performance, the repeated ANOVA analyses showed a significant main effect of load on $d'$, indicating a better performance of the 0-back load compared with the 2-back load ($F$ (1,46) = 71.16, $P < 0.001$, $\eta_p^2 = 0.61$, $BF_{10} > 1,000$). Neither the stimulus-type main effect nor stimulus-type by load interaction was significant (stimulus-type main effect: $F$ (1,46) = 2.08, $P = 0.156$, $\eta_p^2 = 0.04$, $BF_{10} = 0.41$; interaction effect: $F$ (1,46) = 1.40, $P = 0.244$, $\eta_p^2 = 0.03$, $BF_{10} = 0.35$). As for the DMS task, the repeated ANOVA results showed a significantly higher accuracy for the 2 sets than the 4 sets load ($F$ (1,33) = 15.62, $P < 0.001$, $\eta_p^2 = 0.32$, $BF_{10} = 5.69 \times 10^3$). The accuracy was higher under the BM condition relative to the SM condition but the effect size was small (Ferguson 2009; $F$ (1,33) = 5.46, $P = 0.026$, $\eta_p^2 = 0.14$, $BF_{10} = 5.91$). No significant stimulus-type by load interaction was found ($F$ (1,33) = 0.01, $P = 0.926$, $\eta_p^2 < 0.001$, $BF_{10} = 0.12$).

These results indicated that our manipulation of WM load was efficient and the task difficulty was comparable between BM and SM conditions, which means that the activation difference between BM and SM conditions could be attributed to the difference of stimulus processing.

ANOVA analyses demonstrated that the accuracy of digit rehearsal did not differ between BM and SM conditions, and neither the load main effect nor the stimulus-type by load interaction was found in the N-back and DMS tasks (mean accuracy > 0.88 for all conditions, minimum $P = 0.051$, maximum $\eta_p^2 = 0.09$, and maximum $BF_{10} = 0.98$). The results indicated that participants followed the task instructions well.

## Imaging results
### Identification of stimulus-type preferential intermediate regions
One-sample $T$-tests showed the activation of a wide range of brain regions in response to the N-back task. Specifically, the activated brain regions included the typical frontal–parietal WM network seen in many previous studies (Owen et al. 2005; Dong et al. 2016; Zhou et al. 2019; Fig. 3A). In the 2-way repeated measures of ANOVA with stimulus-type (BM and SM) and WM-load (0-back and 2-back) as within-subject factors to identify intermediate regions, significant main effects of the stimulus-type were mainly found at the bilateral occipitotemporal cortex, postcentral gyrus (PoCG), pre-central gyrus, and

inferior frontal gyrus (Fig. 3B, Supplementary Table S1). Among them, the bilateral occipitotemporal cortex and PoCG were the most significant clusters ($F$ statistics > 100; Supplementary Table S1). Further paired $T$-tests showed that the bilateral occipitotemporal cortex was activated at a higher level under the BM condition relative to that under the SM condition for both 0-back and 2-back loads, whereas PoCG displayed the opposite pattern (Fig. 3C, Supplementary Table S2). These results indicated that the PoCG and occipitotemporal cortex (including pSTG and MT) may serve as the intermediate processing regions abstracting distinct features for SM and BM WM, respectively.

### Identification of high-level domain-general regions and their connectivity patterns with intermediate regions under different task contexts
Although BM and SM stimuli shared similar low-level features, the brain regions underlying intermediate processes for BM and SM WM would show stronger interactions with the WM core network in a context-dependent way. To define ROIs (e.g. pSTG, MT, and PoCG) with higher specificity, we constrained brain regions exhibiting activation differences between BM and SM conditions with AAL parcellations for STG and PoCG, and using VisfAtlas (Rosenke et al. 2021) for MT. The resultant 6 ROIs (Fig. 4, L PoCG: 232 voxels; R PoCG: 293 voxels; L pSTG: 21 voxels; R pSTG: 262 voxels; L MT: 68 voxels; and R MT: 75 voxels) were used in PPI analyses. As shown in Fig. 4, the bilateral pSTG and MT indicated stronger connections with the FPN under the BM 2-back condition, as compared with that under the SM 2-back condition. In contrast, the PoCG showed stronger connections with the FPN under the SM 2-back condition, as compared with that under the BM 2-back condition. The above PPI results suggested that the FPN satisfies the first top-level network property, namely stimulus-type "dependent connection." Although, the FPN also satisfies the second property of stimulus-type free activation based on Fig. 3A and B, we conducted a conjunction analysis on the FPN maps acquired from our PPI analyses and the WM meta-analysis map (https://neurosynth.org/) for better generalization (Supplementary Fig. S2). The conjunction FPN (Supplementary Fig. S1) was frequently activated by various WM tasks, and displayed stimulus-type dependent connectivity patterns with intermediate regions (pSTG, MT, and PoCG), indicating that it meets the 2 criteria for a domain-general network.

### Verification of N-back results and dissecting roles of stimulus-type preferential intermediate regions and domain-general regions in WM tasks
In order to verify the results of the N-back task and further dissect the roles of stimulus-type preferential and domain-general regions in WM tasks, we extracted the activation values of bilateral pSTG, MT, PoCG and the hypothetic domain-general WM network (i.e. FPN regions including bilateral frontal, supplementary motor area
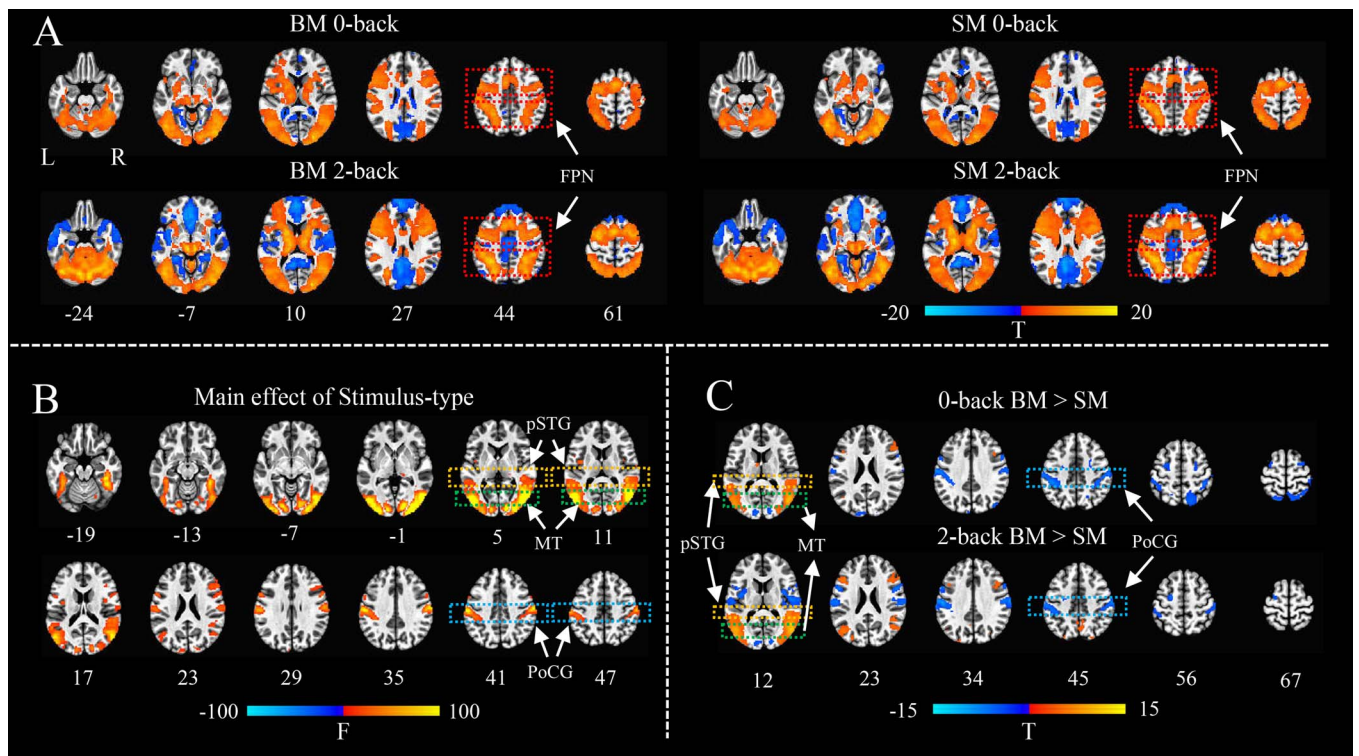
**Fig. 3.** Activation maps of the N-back task. A) Activation patterns showing that the FPN was engaged in all of the WM conditions. B) Regions showing significant stimulus-type main effect by ANOVA. C) Differences in activation between BM and SM conditions for 0-back and 2-back loads, showing higher activation in the pSTG and middle temporal visual area (MT) for BM vs. SM contrast and higher activation in the PoCG for SM vs. BM contrast. The activation maps were corrected for multiple comparisons with voxel-wise *P*-value < 0.001 and a minimum cluster size of 22 voxels. The boxes and arrows indicate the anatomical location of regions (red: FPN; yellow: pSTG; green: MT; and blue: PoCG), from which the domain-general and intermediate regions were identified in latter analyses. *Abbreviations:* BM, biological motion; SM, shape motion.

(SMA) and parietal regions; see Supplementary Fig. S1) and conducted repeated ANOVA analyses with stimulus-type (BM and SM) and load (2sets and 4sets) as within-subject factors, and scanner as a categorical covariate for the DMS task.

During the encoding phase, higher activation was not only shown for MT under the BM condition but also in response to high load under both BM and SM conditions (Table 1, Fig. 5B, Supplementary Table S3), whereas the PoCG displayed stronger activation under the SM condition relative to the BM condition for both low and high loads, and for high load only under the SM condition (Table 1 and Fig. 5D). As for pSTG, it was strongly activated under both BM and SM conditions, and the left pSTG displayed higher activation under the BM 4 sets relative to the BM 2 sets condition (Table 1 and Fig. 5F).

During the DMS maintenance phase, most intermediate ROIs except the left pSTG were suppressed. The left pSTG showed significant positive activation under the BM 4 sets condition, and the activation under this condition was significantly higher than that under the BM 2 sets condition (Fig. 5F). Returning to the N-back task, the stimulus-type main effects in these 3 regions had been examined (Fig. 3) but the load effects remained unknown. Therefore, we conducted paired *T*-tests to investigate whether these intermediate regions displayed load effects. ROI-level statistical analyses showed significantly higher response in MT and pSTG

for high load under the BM condition, and the left pSTG also presented a load effect under the SM condition (Fig. 5A and E). In contrast, the PoCG did not exhibit any significant load effect (Fig. 5C).

Regarding the domain-general FPN network, during the DMS encoding phase, the frontal and parietal regions not only displayed significant load effects but also higher activation under the SM condition (Fig. 6B and D), whereas the SMA only displayed a significant load effect (Fig. 6F). This result indicates that the FPN also plays prominent roles in encoding, and there are functional heterogeneities within this network. During the DMS maintenance phase, all FPN regions showed significant load effects under both BM and SM conditions but no or weak stimulus-type effect (Table 1 and Fig. 6B, D, and F). As the FPN regions were identified using PPI analyses, both the effects of stimulus-type and WM load in the N-back remained to be illustrated. ROI-based analyses revealed significantly higher responses in high WM load under both BM and SM conditions in all of the FPN regions (Table 1 and Fig. 6). Taken together, the sustained FPN activations during the DMS delayed phase and the N-back task indicated their critical role for information maintenance, whereas the FPN activations during the DMS encoding phase suggested that this network also plays important roles in the hierarchical processing chain. In short, as summarized in Fig. 7, our results provided proof-of-concept evidence to support the idea that
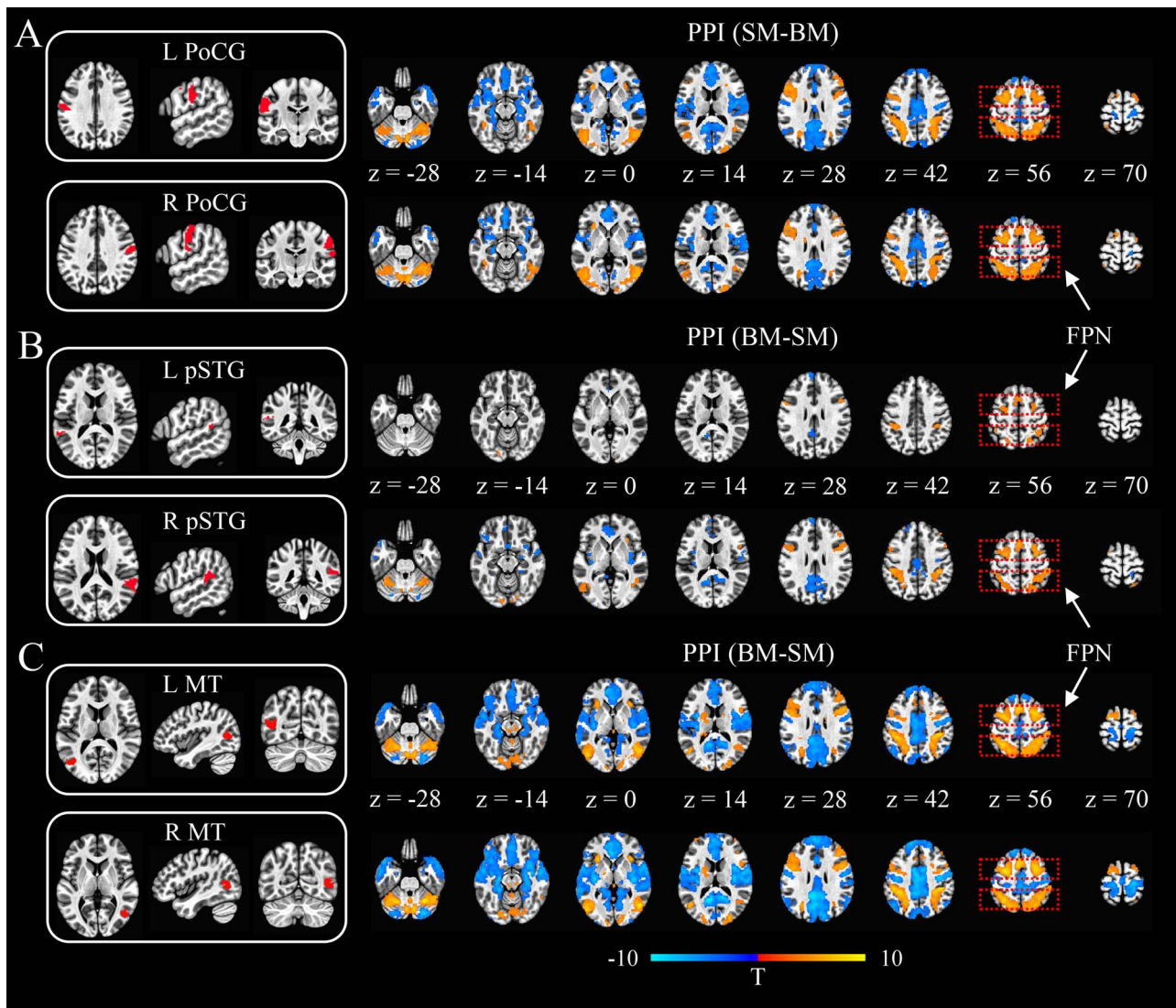
**Fig. 4.** Six intermediate regions and their effective connectivity maps. The 6 ROIs used in the PPI analysis were presented in the left panel. The effective connectivity difference of A) SM 2-back compared to BM 2-back condition and B), C) BM 2-back compared to SM 2-back condition were presented in the right panel. The PPI maps were corrected for multiple comparisons with voxel-wise P-value < 0.001 and a minimum cluster size of 22 voxels. The boxes and arrows indicate that the FPN shows the most robust PPI effect. *Abbreviations:* L, left; R, right; PoCG, postcentral gyrus; pSTG, posterior superior temporal gyrus; MT, middle temporal area; FPN, frontal–parietal network; BM, biological motion; SM, shape motion.

different intermediate neural pathways interact with a common domain-general FPN to support WM tasks.

## Discussion

In the present study, we examined the neural mechanisms of WM from a hierarchical processing perspective. Based on the comparison of activities between BM and SM WM using a novel N-back task, we identified pSTG, MT and PoCG as stimulus-type preferential intermediate processing regions. Further PPI analyses established context-dependent effective connectivity between FPN and the 3 intermediate regions. These results were validated and extended by an independent DMS task. Our findings provide evidence for a hierarchical processing model of WM, and may have significant implications for developing efficient interventions to improve WM, as discussed further below.

### Domain-general and stimulus-type preferential processing pathways of BM and SM

As FPN is consistently activated by various WM tasks (Zurowski et al. 2002; Owen et al. 2005; Rottschy et al. 2012; Zhou et al. 2019), including the present one (Fig. 3A), it is plausible to consider it as a WM domain-general network. Between the FPN and neural cortices receiving external inputs (e.g. the primary visual cortex for visual input), there must be multiple layers of networks through which input information is hierarchically processed from one layer to another. A top-down process is also necessary to modulate brain regions composed of intermediate layers based on task goals (Fig. 1B and C). Congruent with this conjecture, even though the low-level features such as brightness and color of the BM and SM conditions were comparable, we identified that pSTG, MT, and PoCG showed the most significant difference in activation, whereas the primary

**Table 1.** ROI-based analysis of N-back and DMS tasks.

| | DMS task | | | | N-back task | |
|---|---|---|---|---|---|---|
| | Encoding | | Maintenance | | | |
| | Load effect | Stimulus-type effect | Load effect | Stimulus-type effect | Load effect | Stimulus-type effect |
| Stimulus-preferential regions | | | | | | |
| Middle temporal (MT) | H > L (BM & SM) | BM > SM (H & L) | – | – | H > L (BM) | BM > SM (H & L) |
| Posterior superior temporal gyrus (STG) | H > L (BM) | – | H > L (BM) | – | H > L (BM & SM) | BM > SM (H & L) |
| Postcentral gyrus (PoCG) | H > L (SM) | SM > BM (H & L) | – | – | – | SM > BM (H & L) |
| Domain-general regions | | | | | | |
| Frontal cortex | H > L (BM & SM) | SM > BM (H & L) | H > L (BM & SM) | – | H > L (BM & SM) | SM > BM (L) |
| Parietal cortex | H > L (BM & SM) | SM > BM (H & L) | H > L (BM & SM) | SM > BM (H) | H > L (BM & SM) | SM > BM (L) |
| Supplementary motor area | H > L (BM & SM) | – | H > L (BM & SM) | – | H > L (BM & SM) | – |

The load and stimulus-type effects during the maintenance period were not marked for de-activated regions. *Abbreviations:* BM, biological motion; SM, shape motion; H, high WM load; L, low WM load.

visual and FPN were activated similarly between the 2 conditions (Fig. 3B and C), suggesting pSTG, MT, and PoCG as putative intermediate processing nodes for distinct abstract features of BM and SM, respectively. Indeed, the pSTG has been shown to play a critical role in the construction of meaningful biological movements from discrete light points (Grossman et al. 2000; Vaina et al. 2001), and is able to integrate multi-sensory information (Fernandino et al. 2016; Hasan et al. 2016). Meanwhile, the MT is responsive for complex motion discrimination and is also an essential region constituting the visual pathway of social perception (Pitcher and Ungerleider 2021).

In contrast, the SM condition induced a stronger activation in PoCG, suggesting that a different intermediate node was more engaged. Although the engagement of PoCG as a crucial region in SM WM condition is a relatively novel discovery, this finding is reliable because the effect could be replicated by an independent DMS dataset. In the literature, PoCG is often reported to show activation in tasks evoking one's somatic sensation (Stilla and Sathian 2008; Puckett et al. 2020), or emotion recognition (Pourtois et al. 2004). However, recent studies have indicated the important roles of sensory and motor cortical areas in the neural representation of concepts (Kiefer and Pulvermüller 2012; Fernandino et al. 2016). Thus, a post-hoc explanation of the activation of PoCG under the SM condition is to some extent related to the representation of movements with regular patterns such as translation and rotation. Participants may abstract these movement conceptions through somatic experiences, requiring the involvement of PoCG, though more research is warranted to test this speculation.

## Neural substrates for the hierarchical processing model of WM

Similar to the abstraction gradient in the lateral prefrontal cortex (LPFC) proposed by Nee et al. (Nee and D'Esposito 2016; Badre and Nee 2018), we consider that a stimulus can be processed through a chain of neural network with the abstraction level increasing with the frontal–parietal regions as the apex in this hierarchical process. Although stimuli for both the BM and SM conditions are in a visuospatial form with comparable low-level features, the abstraction procedure would involve some brain regions processing shared features and other brain regions processing non-shared features at different levels of abstraction. Brain regions with distinct degrees of contribution to BM and SM abstraction should show differences in local activation and stimulus-type dependent connectivity with the apex regions. As summarized in Fig. 7, different intermediate neural pathways interacted with the same domain-general FPN to support different WM tasks. The specific roles of these intermediate regions and domain-general FPN regions are detailed below.

During the DMS maintenance phase in our experiment, the activations in the frontal–parietal cortices were increased by WM load. This sustained activity of the delay period is related to the content relevant to the task goal, which has been the focus of previous WM studies (Christophel et al. 2012; Ester et al. 2015; Schmidt et al. 2017). Combined with previous reports that stimulus content could be decoded from frontal and parietal regions (Christophel et al. 2012; Ester et al. 2015), it is possible that these regions are primary neural correlates to maintain the memory of content (i.e. information that has been processed from a sensory stimulus to a highly abstract representation (Fig. 7)). Furthermore, the activation differences in these regions during the encoding phase of the DMS task (Fig. 6B and D) indicated that these regions not only function as nodes of storage, but also engage in information processing. Considering both activations in response to encoding and maintenance in the DMS task, the frontal and parietal regions may
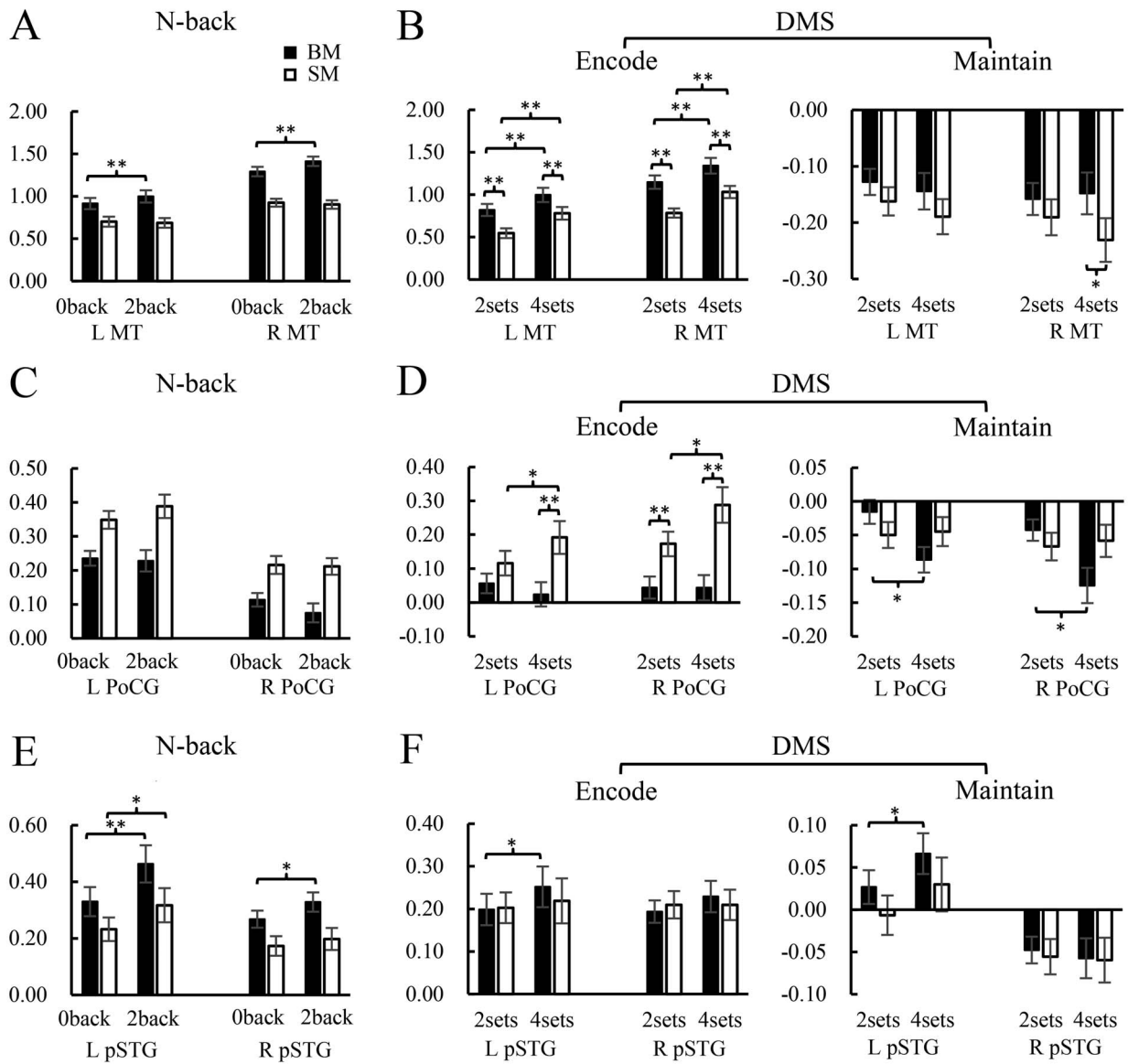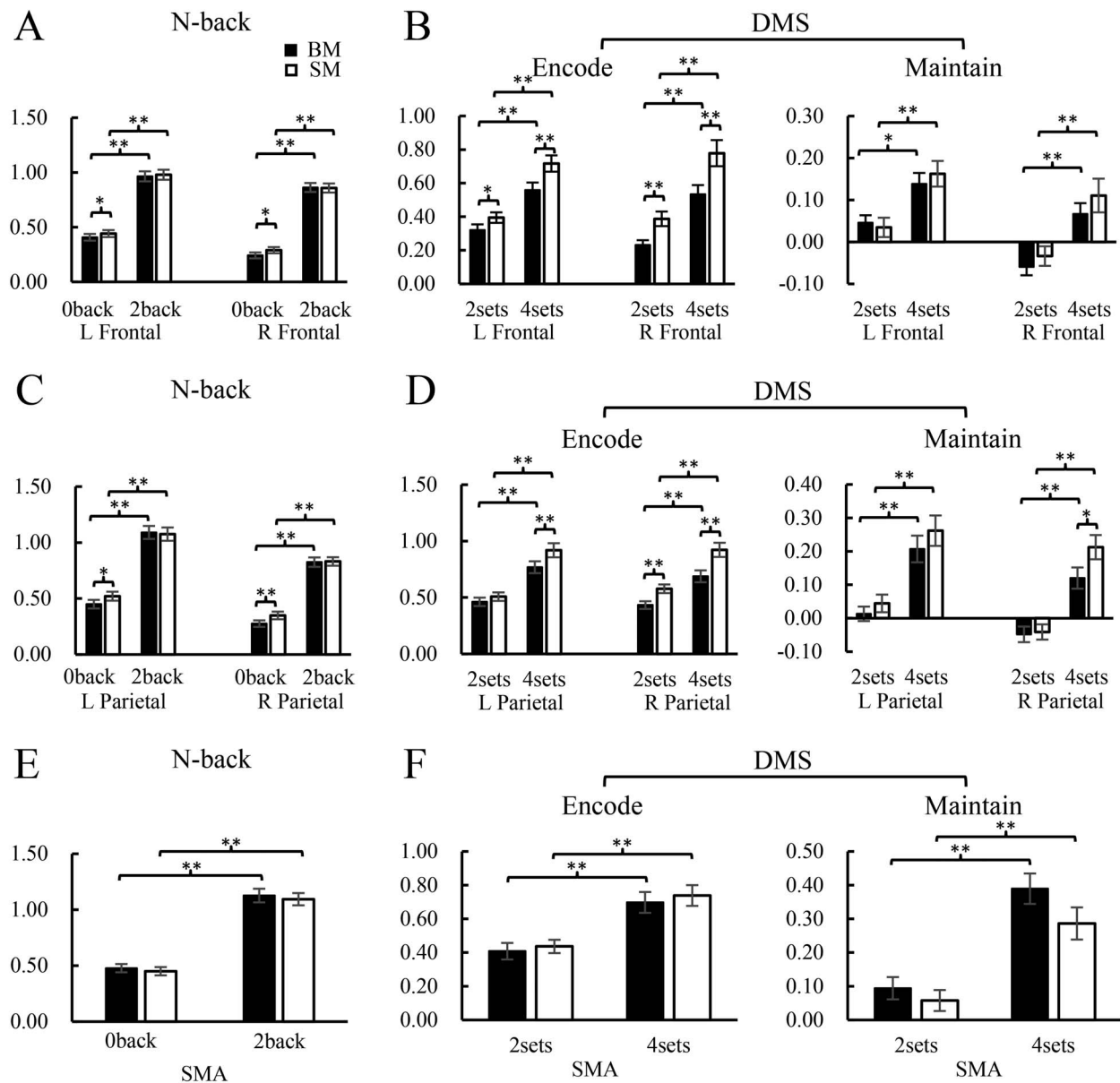
**Fig. 5.** ROI-based analyses of stimulus-type preferential regions. The vertical axis stands for fMRI activation strength. *Abbreviations:* BM, biological motion; SM, shape motion; DMS, delayed match to sample; MT, middle temporal; PoCG, postcentral gyrus; pSTG, posterior superior temporal gyrus. * $P < 0.05$, ** $P <= 0.001$. Note: The stimulus-type main effect of N-back task was previously revealed by whole-brain voxel-wise analysis.

serve as the neural correlates for late-stage processing and then the maintenance of the memory of content. On the other hand, the FPN regions are thought to represent task-general information that coordinate regions for stimulus-specific representations via top-down modulation (Sreenivasan et al. 2014; D'Esposito and Postle 2015). In particular, Nee et al. identified that participants represented and updated different levels of contextual information (e.g. task rules) with a rostrocaudal organization of the prefrontal cortex (Nee and Brown 2012, 2013; Badre and Nee 2018). Therefore, in addition to the memory of content, the memory of process (e.g. contextual information for the top-down modulation of intermediate circuits) is another type of information that was maintained in the frontal and parietal regions (Fig. 7). Moreover, the

activation of SMA was only dependent on cognitive load in all conditions in both tasks (Fig. 6E,F). Although, the SMA plays a critical role in preparing actions and representing planned operational sequence (Amador and Fried 2004; Nachev et al. 2008; Cona and Semenza 2017), the load-dependent activation of SMA during the maintenance phase of the DMS task indicated that this region could have more functions in WM than simple motor response, because the motor preparation for response was the same for high and low WM load conditions. Instead, the SMA might be the primary neural substrate underlying the mental operational sequences to manipulate information in WM tasks.

Regarding whether the stimulus-type preferential regions are engaged in information maintenance, the

**Fig. 6.** ROI-based analyses of domain-general regions. The vertical axis stands for fMRI activation strength. *Abbreviations:* BM, biological motion; SM, shape motion; DMS, delayed match to sample; SMA, supplementary motor area. * $P < 0.05$, ** $P < = 0.001$.

observed WM load effect in the N-back task indicated that both pSTG and MT play more roles beyond perception. As the sensory inputs were the same for 0-back and 2-back conditions, a higher pSTG/MT activation in response to the 2-back condition may reflect an enhanced top-down modulation or the engagement in WM maintenance. The top-down control over intermediary regions may "guide" these regions by invoking more postsynaptic neural activity to locally abstract/process in more detail such that the abstracted features can differentiate the current stimulus from previous ones. Notably, the pSTG displayed a stronger response to the high load condition of BM during the maintenance period (Fig. 5F). This pattern indicates that the pSTG may be also involved in information maintenance, which is consistent with previous studies

decoding the stimulus content from pSTG (Christophel et al. 2017; Erhart et al. 2021). In addition, it has been shown that sustained activation may be unnecessary for information maintenance (Riggall and Postle 2012). It is worthwhile for future studies to investigate how information maintained in FPN is different from that maintained in intermediate regions.

In the current study, we also observed a stronger functional coupling between MT and thalamus under the BM 2-back condition relative to the SM 2-back condition despite comparable activation between the 2 conditions. Since the thalamofrontal loop is important for WM maintenance (Bolkan et al. 2017; Hsiao et al. 2020), the abstracted task relevant information might be transmitted to this loop and thus induce stronger functional coupling between MT and thalamus. In addition,
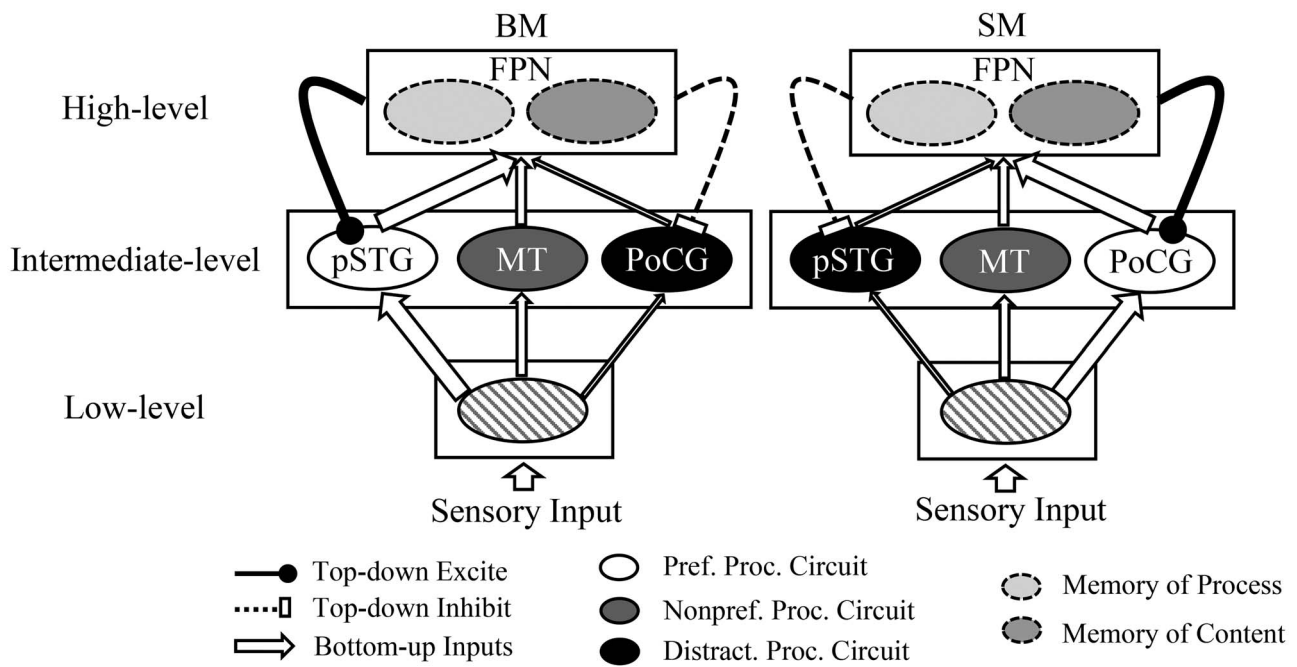
**Fig. 7.** Schematic of the hierarchical model of dynamic WM. Assumptive pathways of hierarchical information processing for biological motion A) and circle shape motion B). *Abbreviations*: BM, biological motion; SM, shape motion; pSTG, posterior superior temporal gyrus; MT, middle temporal area; PoCG, postcentral gyrus; Pref. Proc. Circuit, preferential processing circuit; Nonpref. Proc. Circuit, non-preferential processing circuit; Distract Proc. Circuit, distract processing circuit.

the medial dorsal thalamus is related to the recollection procedure (Danet et al. 2017). Given the relatively low demand for information maintenance and updating under the 0-back condition, the recollection process might be a primary factor inducing higher thalamic activation for BM. This is because the abstraction of BM would require or trigger more recollection processes to retrieve the experience associated with the BM stimulus (such as activities in social situations).

### The difference from hierarchical cognitive control and its implications for WM training

The hierarchical neural model proposed in the present study shares some principles similar to the hierarchical model of cognitive control, however, they have their own distinct features. Although cognitive control focuses more on behavioral adaptation in alignment with rules or goals, WM puts more emphasis on the mechanism of information maintenance and manipulation. Based on the evidence for the engagement of a rostrocaudal organization of LPFC when participants represent and update different levels of contextual information (e.g. task rules) in WM (Nee and Brown 2012, 2013), the hierarchical model proposed by Nee et al. indicates that the LPFC is the primary neural substrate for cognitive control (Nee and D'Esposito 2016; Badre and Nee 2018). In contrast, the current study focused on the hierarchical abstraction procedure of stimulus information and whether such abstracted content information can be eventually represented and manipulated by a domain-general network. Our results highlighted the FPN as the domain-general neural substrate for WM, which is

consistent with previous meta-analyses based on WM task induced activations (Owen et al. 2005; Rottschy et al. 2012). When examining the anatomic boundary of WM domain-general FPN reported in the present study and that of LPFC illustrated by Nee et al. (Badre and Nee 2018), we noticed that the FPN also included the caudal part of the LPFC for cognitive control. Although the representation of task rule in LPFC as retained information during the task can be considered as a type of maintained information described by WM, the few reports on rostral LPFC activation in WM is probably due the fact that most WM studies, including the present one, did not require subjects to switch between different levels of rules. In other words, WM tasks usually only necessitate contextual control underlined by caudal LPFC but not temporal control that engages rostral LPFC.

The findings of this paper shed light on the neural mechanisms of WM from a hierarchical perspective and may also have implications for understanding the transfer effects of WM training. First, the domain-general FPN may serve as the primary neural substrate of transfer effect. Indeed, the activation of FPN and its relationship with WM performance has been consistently reported (Owen et al. 2005; Dong et al. 2016; Liu et al. 2018), and our previous work has also shown that abacus-based mental calculation (AMC) training has a positive transfer effect on both verbal and spatial WM (Hu et al. 2011, Dong et al. 2016, Wang et al. 2019b). After AMC training, sustained activation in response to continuous mental spatial operation, which was not trained, was enhanced in the FPN (Zhou et al. 2019), and the activation of middle frontal cortex mediated the transfer

effect of AMC to a spatial WM task (Wang et al. 2019b). Second, the intermediate level of information processing also contributed to WM performance, which might account for the poor far-domain transfer effect of WM training. As the improvement of WM performance after a specific WM task training could be attributed to the increased efficiency of intermediate level processing, a near-transfer effect could be observed more often when the untrained task shared similar intermediate processing features with the trained task, however, a far-transfer effect was hardly seen because the intermediate pathways for the new tasks were not trained. In future studies, the training-induced transfer effects on WM should be dissected into gains in domain-general FPN and different layers of intermediate pathways.

## Conclusions

From a hierarchical processing perspective, the present study identified pSTG, MT and PoCG as stimulus-type preferential intermediate pathways of BM and SM WM information processing, respectively. Further analyses showed that the domain-general WM network, FPN, interacted with intermediate regions in a context-dependent manner. These results provide empirical evidence for the hierarchical model of WM and may have implications for future studies on designing effective intervention strategies to target different layers of the WM neural hierarchy.

## Supplementary material

Supplementary material can be found at *Cerebral Cortex* online.

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## References

Adolfi F, Couto B, Richter F, Decety J, Lopez J, Sigman M, Manes F, Ibanez A. Convergence of interoception, emotion, and social cognition: a twofold fMRI meta-analysis and lesion approach. *Cortex*. 2017:88:124–142.

Amador N, Fried I. Single-neuron activity in the human supplementary motor area underlying preparation for action. *J Neurosurg*. 2004:100:250–259.

Baddeley A. Working memory: theories, models, and controversies. *Annu Rev Psychol*. 2012:63:1–29.

Baddeley AD, Hitch G. Working memory. *Psychol Learn Motiv*. 1974:8:47–89.

Badre D, Nee DE. Frontal cortex and the hierarchical control of behavior. *Trends Cogn Sci*. 2018:22:170–188.

Bolkan SS, Stujenske JM, Parnaudeau S, Spellman TJ, Rauffenbart C, Abbas AI, Harris AZ, Gordon JA, Kellendonk C. Thalamic projections sustain prefrontal activity during working memory maintenance. *Nat Neurosci*. 2017:20:987–996.

Christophel TB, Hebart MN, Haynes J-D. Decoding the contents of visual short-term memory from human visual and parietal cortex. *J Neurosci*. 2012:32:12983–12989.

Christophel TB, Klink PC, Spitzer B, Roelfsema PR, Haynes JD. The distributed nature of working memory. *Trends Cogn Sci*. 2017:21:111–124.

Collette F, Van der Linden M. Brain imaging of the central executive component of working memory. *Neurosci Biobehav Rev*. 2002:26:105–125.

Cona G, Semenza C. Supplementary motor area as key structure for domain-general sequence processing: a unified account. *Neurosci Biobehav Rev*. 2017:72:28–42.

Cox RW. AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Comput Biomed Res*. 1996:29:162–173.

Cox RW, Chen G, Glen DR, Reynolds RC, Taylor PA. FMRI clustering in AFNI: false-positive rates. *Redux Brain Connect*. 2017:7:152–171.

Danet L, Pariente J, Eustache P, Raposo N, Sibon I, Albucher J-F, Bonneville F, Peran P, Barbeau EJ. Medial thalamic stroke and its impact on familiarity and recollection. *Elife*. 2017:6:e28141.

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

Dong S, Wang C, Xie Y, Hu Y, Weng J, Chen F. The impact of abacus training on working memory and underlying neural correlates in young adults. *Neuroscience*. 2016:332:181–190.

Erhart M, Czoschke S, Fischer C, Bledowski C, Kaiser J. Decoding spatial versus non-spatial processing in auditory working memory. *Front Neurosci*. 2021:15:637877.

Ester EF, Sprague TC, Serences JT. Parietal and frontal cortex encode stimulus-specific mnemonic representations during visual working memory. *Neuron*. 2015:87:893–905.

Ferguson CJ. An effect size primer: a guide for clinicians and researchers. *Prof Psychol Res Pract*. 2009:40:532–538.

Fernandino L, Binder JR, Desai RH, Pendl SL, Humphries CJ, Gross WL, Conant LL, Seidenberg MS. Concept representation reflects multimodal abstraction: a framework for embodied semantics. *Cereb Cortex*. 2016:26:2018–2034.

Gao Z, Bentin S, Shen M. Rehearsing biological motion in working memory: an EEG study. *J Cogn Neurosci*. 2015:27:198–209.

Grossman E, Donnelly M, Price R, Pickens D, Morgan V, Neighbor G, Blake R. Brain areas involved in perception of biological motion. *J Cogn Neurosci*. 2000:12:711–720.

Haatveit BC, Sundet K, Hugdahl K, Ueland T, Melle I, Andreassen OA. The validity of d prime as a working memory index: results from the "Bergen n-back task". *J Clin Exp Neuropsychol*. 2010:32:871–880.

Hafri A, Trueswell JC, Epstein RA. Neural representations of observed actions generalize across static and dynamic visual input. *J Neurosci*. 2017:37:3056–3071.

Hasan BAS, Valdes-Sosa M, Gross J, Belin P. "Hearing faces and seeing voices": Amodal coding of person identity in the human brain. *Sci Rep*. 2016:6:1–8.

Hasson U, Chen J, Honey CJ. Hierarchical process memory: memory as an integral component of information processing. *Trends Cogn Sci*. 2015:19:304–313.

Hsiao K, Noble C, Pitman W, Yadav N, Kumar S, Keele GR, Terceros A, Kanke M, Conniff T, Cheleuitte-Nieves C et al. A thalamic

orphan receptor drives variability in short-term memory. *Cell*. 2020:183:522, e519–536.

Hu Y, Geng F, Tao L, Hu N, Du F, Fu K, Chen F. Enhanced white matter tracts integrity in children with abacus training. *Hum Brain Mapp*. 2011:32:10–21.

Injoque-Ricle I, Burin DI. Working memory and planning in children: validation of the tower of London task. *Neuropsicología Latinoamericana*. 2011:3:31–38.

Kiefer M, Pulvermüller F. Conceptual representations in mind and brain: theoretical developments, current evidence and future directions. *Cortex*. 2012:48:805–825.

Lingnau A, Downing PE. The lateral occipitotemporal cortex in action. *Trends Cogn Sci*. 2015:19:268–277.

Liu LD, Pack CC. The contribution of area MT to visual motion perception depends on training. *Neuron*. 2017:95:436, e433–446.

Liu S, Poh JH, Koh HL, Ng KK, Loke YM, Lim JKW, Chong JSX, Zhou J. Carrying the past to the future: distinct brain networks underlie individual differences in human spatial working memory capacity. *NeuroImage*. 2018:176:1–10.

Lu X, Huang J, Yi Y, Shen M, Weng X, Gao Z. Holding biological motion in working memory: an fMRI study. *Front Hum Neurosci*. 2016:10:251.

Nachev P, Kennard C, Husain M. Functional role of the supplementary and pre-supplementary motor areas. *Nat Rev Neurosci*. 2008:9:856–869.

Nee DE, Brown JW. Rostral-caudal gradients of abstraction revealed by multi-variate pattern analysis of working memory. *NeuroImage*. 2012:63:1285–1294.

Nee DE, Brown JW. Dissociable frontal-striatal and frontal-parietal networks involved in updating hierarchical contexts in working memory. *Cereb Cortex*. 2013:23:2146–2158.

Nee DE, D'Esposito M. The hierarchical organization of the lateral prefrontal cortex. *Elife*. 2016:5.

Nettelbeck T, Burns NR. Processing speed, working memory and reasoning ability from childhood to old age. *Pers Individ Differ*. 2010:48:379–384.

Nilsson J, Lebedev AV, Rydström A, Lövdén M. Direct-current stimulation does little to improve the outcome of working memory training in older adults. *Psychol Sci*. 2017:28:907–920.

Owen AM, McMillan KM, Laird AR, Bullmore E. N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. *Hum Brain Mapp*. 2005:25:46–59.

Pitcher D, Ungerleider LG. Evidence for a third visual pathway specialized for social perception. *Trends Cogn Sci*. 2021:25:100–110.

Pourtois G, Sander D, Andres M, Grandjean D, Reveret L, Olivier E, Vuilleumier P. Dissociable roles of the human somatosensory and superior temporal cortices for processing social face signals. *Eur J Neurosci*. 2004:20:3507–3515.

Puckett AM, Bollmann S, Junday K, Barth M, Cunnington R. Bayesian population receptive field modeling in human somatosensory cortex. *NeuroImage*. 2020:208:116465.

Rasmussen C, Bisanz J. Representation and working memory in early arithmetic. *J Exp Child Psychol*. 2005:91:137–157.

Reinhart RMG, Nguyen JA. Working memory revived in older adults by synchronizing rhythmic brain circuits. *Nat Neurosci*. 2019:22:820–827.

Riggall AC, Postle BR. The relationship between working memory storage and elevated activity as measured with functional magnetic resonance imaging. *J Neurosci*. 2012:32:12990–12998.

Rosenke M, van Hoof R, van den Hurk J, Grill-Spector K and Goebel R. A Probabilistic Functional Atlas of Human Occipito-Temporal Visual Cortex. *Cereb Cortex*. 2021:31:603–619.

Rottschy C, Langner R, Dogan I, Reetz K, Laird AR, Schulz JB, Fox PT, Eickhoff SB. Modelling neural correlates of working memory: a coordinate-based meta-analysis. *NeuroImage*. 2012:60:830–846.

Schmidt TT, Y-h W, Blankenburg F. Content-specific codes of parametric vibrotactile working memory in humans. *J Neurosci*. 2017:37:9771–9777.

Shen M, Gao Z, Ding X, Zhou B, Huang X. Holding biological motion information in working memory. *J Exp Psychol Hum Percept Perform*. 2014:40:1332–1345.

Sloan NP, Byrne LK, Enticott PG, Lum JA. Non-invasive brain stimulation does not improve working memory in schizophrenia: a meta-analysis of randomised controlled trials. *Neuropsychol Rev*. 2020:1–24.

Sokolov AA, Zeidman P, Erb M, Ryvlin P, Friston KJ, Pavlova MA. Structural and effective brain connectivity underlying biological motion detection. *Proc Natl Acad Sci U S A*. 2018:115: E12034–E12042.

Sreenivasan KK, Curtis CE, D'Esposito M. Revisiting the role of persistent neural activity during working memory. *Trends Cogn Sci*. 2014:18:82–89.

Stilla R, Sathian K. Selective visuo-haptic processing of shape and texture. *Hum Brain Mapp*. 2008:29:1123–1138.

Vaina LM, Solomon J, Chowdhury S, Sinha P, Belliveau JW. Functional neuroanatomy of biological motion perception in humans. *Proc Natl Acad Sci*. 2001:98:11656–11661.

Wang S, Itthipuripat S, Ku Y. Electrical stimulation over human posterior parietal cortex selectively enhances the capacity of visual short-term memory. *J Neurosci*. 2019a:39:528–536.

Wang C, Xu T, Geng F, Hu Y, Wang Y, Liu H, Chen F. Training on abacus-based mental calculation enhances visuospatial working memory in children. *J Neurosci*. 2019b:39:6439–6448.

Wu F, Gu Q, Shi Z, Gao Z, Shen M. Striding over the "classical statistical inference trap"——application of Bayes factors in psychological studies. *Chin J Appl Psychol*. 2018:3:195–202.

Wurm MF, Lingnau A. Decoding actions at different levels of abstraction. *J Neurosci*. 2015:35:7727–7735.

Wurm MF, Ariani G, Greenlee MW, Lingnau A. Decoding concrete and abstract action representations during explicit and implicit conceptual processing. *Cereb Cortex*. 2016:26:3390–3401.

Yan CG, Wang XD, Zuo XN, Zang YF. DPABI: data processing & analysis for (resting-state) brain imaging. *Neuroinformatics*. 2016:14: 339–351.

Zhou H, Geng F, Wang Y, Wang C, Hu Y, Chen F. Transfer effects of abacus training on transient and sustained brain activation in the frontal–parietal network. *Neuroscience*. 2019:408:135–146.

Zurowski B, Gostomzyk J, Gron G, Weller R, Schirrmeister H, Neumeier B, Spitzer M, Reske SN, Walter H. Dissociating a common working memory network from different neural substrates of phonological and spatial stimulus processing. *NeuroImage*. 2002:15:45–57.