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Prefrontal cortex and sensory cortices during working memory: quantity and quality

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The activity in sensory cortices and the prefrontal cortex (PFC) throughout the delay interval of working memory (WM) tasks reflect two aspects of WM—quality and quantity, respectively. The delay activity in sensory cortices is fine-tuned to sensory information and forms the neural basis of the precision of WM storage, while the delay activity in the PFC appears to represent behavioral goals and filters out irrelevant distractions, forming the neural basis of the quantity of task-relevant information in WM. The PFC and sensory cortices interact through different frequency bands of neuronal oscillation (theta, alpha, and gamma) to fulfill goal-directed behaviors.

Keywords: working memory; prefrontal cortex; capacity limit; memory precision; neuronal oscillations

Introduction

Working memory (WM) refers to the cognitive processes of maintaining and storing information in the short term (usually seconds) for subsequent goal-directed action^[1-3]. Persistent activity in both sensory cortices and association areas (especially the prefrontal cortex, PFC) throughout the delay interval of a WM task after sensory stimulus presentation (sample) are usually considered to be critical for WM maintenance, and to bridge the temporal gap between the sample and the subsequent contingent response (see reviews ^[4,5]). However, with regard to WM the role of the delay activity in sensory cortices has been thought to differ from that of the PFC. The former has been thought to represent and store selective sensory information and the latter has been considered to exert attentional bias and cognitive control over the former (see reviews ^[6,7]).

Despite the vast storage in human long-term memory, WM has been demonstrated to have a capacity limited by the number of items^[8,9] and this is strongly correlated with general cognitive ability^[10,11]. Recent advances in studying visual WM have shown a precision limit of representations in WM besides the capacity limit^[12-16].

Combined with the above findings, we propose that delay activity in the sensory cortices and PFC reflect the quality and quantity of representations in WM, respectively. Specifically, in this review, quantity refers to how many items/slots are stored in working memory, and quality refers to how precisely the features of each item/slot are represented in WM.

Sensory Cortices and the Quality of Working Memory

Neurons in the PFC have been shown to respond to sensory stimuli in WM tasks^[17,18]. Compared with those PFC neurons, neurons in sensory cortices appear to be more selectively tuned to stimulus features in WM tasks and consequently to maintain high-fidelity representations of stimulus information in the service of WM^[19].

Some human imaging as well as neurophysiological studies in non-human primates have indicated an absence of persistent activity in early sensory regions^[20-24]. However, other primate studies have revealed persistent modulation of neuronal activity in the primary visual cortex during the delay period of a WM task, which additionally correlates with the monkeys' memory performance^[25]. Furthermore, Zhou and Fuster found that single units in monkey primary somatosensory cortex (SI) show sustained firing during the retention period of a tactile WM task^[26] (Fig. 1A).

Recent advances in neuroimaging have shown the possibility of accurately decoding the representations of minds (see reviews ^[27,28]). Multivariate pattern analysis (MVPA) has been applied to the analysis of neural activity patterns in visual regions, and has revealed content-specific representations during WM^[29,30]. Harrison and Tong have shown that even if the overall delay activity is low in human visual cortices, orientations held in WM can still be clearly decoded from the activity patterns^[29]. This coincides with the neurophysiological data from monkey SI cortex during the delay period of a tactile WM task noted above^[26]. Furthermore, recent neuroimaging studies have shown that trial-specific stimulus information can be decoded from sensory cortices but not from the PFC^[31-33].

Not only do sensory cortices represent fine-tuned modality-specific sensory information during WM, but they can also be tuned to other sensory modalities (crossmodality) after associative training. Zhou and Fuster have shown that the sustained delay activity of SI neurons in monkeys is selective for visual stimuli in a visual-tactile cross-modal WM task^[34] (Fig. 1B). Applying to humans a paradigm similar to that used in monkeys, Ku and colleagues have found that the source of delay activity localized in human SI is modulated by cross-modal associations at the early stage of the delay (100-200 ms after the onset of sample stimuli) and the modulation exhibits a bottom-up pattern^[35]. Our recent transcranial magnetic stimulation (TMS) study has further shown that SI plays a causal role in performance in tactile-visual cross-modal WM^[36] (Fig. 1C). Interestingly, using MVPA, Christophel and Haynes have decoded motion patterns not only from visual areas, but also from SI, even if the task is a pure visual WM task and the visual-spatial pattern is without any association with touch^[37]. They have suggested that the tactile cross-modal representations are specific to complex dynamic stimuli^[37].

As the contents of WM can be decoded from sensory cortices but not the PFC^[31-33], we propose here that, compared with the PFC, sensory cortices represent more precise information about the memorandum, and in this way serve as quality assurance in WM.

Prefrontal Cortex and WM Quantity

Compared with relatively few studies on sustained delay activity in sensory cortices in WM tasks, the elevated delay activity in the PFC has long been recognized^[38]. At first, this PFC activity was interpreted as encoding the sensory features of WM items^[3]. However, growing evidence places more emphasis on is role in providing top-down control over the more posterior regions where information is primarily stored^[39,40].

In psychological studies, the quantity limit of WM for human has long been characterized as approximately 7 verbal items^[8] or 4 visual items^[9]. This limit has been attributed to activity in parietal areas^[41-43]. However, further studies have shown that high-capacity individuals are more efficient at filtering out irrelevant items, while low-capacity individuals cannot efficiently filter out such distractions^[44]. This filtering ability seems to be particularly critical since the high- and low-capacity groups tend to have similar capacity limits counting the number of both targets and distractors^[44]. The PFC has been shown to control accesses to WM^[45,46] and can then guarantee the quantity of task-relevant items in WM.

A similar quantity limitation has also been revealed in monkey neurophysiological studies^[46,47]. In addition, studies have shown that neurons in the PFC of numerically naive monkeys tune to a preferred numerosity^[48], independent of sensory modality^[49]. These neurons may potentially subserve the neuronal mechanisms underlying WM quantity.

The persistent delay activity in the PFC during WM has been demonstrated to be critical for maintaining behavioral goals and the means to achieve those goals (see review ^[6]). The number of goals simultaneously maintained, considering a goal/rule as an item/slot, can be regarded as the other aspect of WM quantity, the capacity of the central executive. This format of quantity is even more



Fig. 1. (A) A primary somatosensory (SI) unit is activated differentially by touch and retention of the vertical edges (the sample stimulus). The receptive field of the unit is indicated in a diagram of the monkey's hand, and the location of the unit is marked by a triangle in a brain section diagram. In the study, the tactile stimuli used in a delayed matching-to-sample task are a pair of objects that differ in the direction of edges (vertical *versus* horizontal) on their surface (modified from ^[20]). (B) An SI unit favors the horizontal visual cue in the cue period as well as the horizontal ridges in the tactile choice. A pair of icons is used as visual cues in a visual-tactile cross-modal working memory (WM) task; they are black-and-white patterns of parallel stripes, vertical in one icon and horizontal in the other (modified from ^[25]). (C) A possible model of cross-modal WM proposed in a transcranial magnetic stimulation study. The early storage of tactile information is processed and briefly maintained in the contralateral SI, and the information is later transferred to the posterior parietal cortex and PFC^[36]. (D) Schematic showing the representation of sensory input in sensory cortices reflects the quality aspect of WM, and the prefrontal top-down control activity reflects the quantity aspect of WM. The sensory cortices are synchronized in gamma cycles, and interact with the PFC to fulfill the needs of goal-directed behavior. Theta and alpha oscillations serve the interaction between sensory cortices and the PFC.

severely limited. Charron and Koechlin have proposed that the frontal lobes in the two hemispheres represent two concurrent goals^[50]. Similar hemispheric limitation has

also been proposed through neurophysiological data from non-human primates^[47]. Further, the frontal lobe in each hemisphere can be subdivided according to the abstraction of processed goals, which may result in different capacity limits for each hierarchy^[51]. Although the quantity of the capacity limitation for the central executive in WM is still not well-defined, as pointed out above, the quantity property of WM does exist in the PFC.

Neural Oscillations Serve the Interaction between PFC and Sensory Cortices

A complete WM function requires the combination of quantity and quality, which relies on the coordination of the PFC and sensory cortices. It has been suggested that oscillatory synchronization underlies inter-cortical communications^[52]. In this review, we mainly focus on three frequency bands that are important to WM performance in humans as well as non-human primates: theta (4-8 Hz), alpha (8–13 Hz), and gamma (>30 Hz).

Cortical theta rhythms are probably generated in hippocampal-cortical feedback loops^[53]. Frontal theta occurs during WM in both humans and non-human primates^[46,53-55]. The theta power increases during WM encoding, maintenance, and retrieval, compared with its baseline level^[56]. Theta power is modulated proportionally to the number of memoranda^[57,58], which represents the quantity of WM. Long-range theta coupling between the PFC and sensory cortices serves communication between these areas and can also influence behavior, as it has been shown that theta coupling between V4 (sensory association cortex) and the PFC predicts WM performance^[59].

Alpha oscillations have been known to be the most dominant rhythm in scalp electroencephalography since its discovery almost a century ago^[60]. The alpha rhythm was originally associated with an idling mental state, but has recently been found to play a functional inhibitory role in attention and WM (see review ^[61]). The cortical alpha rhythm is thought to be generated *via* thalamocortical and cortico-cortical loops^[62]. It has also been shown to increase with the number of items to be remembered in different sensory domains^[63,64], and might represent the quantity of WM. Jensen and colleagues have proposed a model that the magnitude of alpha oscillations actually determines how many representations are processed^[65]. However, the oscillations may mainly serve to protect the information of WM memoranda from distractions^[66,67], as alpha power also goes up when the number of distractors increases^[66]. A recent TMS study has shown that frontal-parietal alpha oscillations can be modulated by PFC activity^[69], which implies that alpha oscillations could also be a working band for communication between the PFC and sensory cortices during WM. Besides the above studies linking alpha oscillations with WM quantity, two new studies have indicated their role in WM precision^[70,71], so it cannot be ruled out that alpha oscillations are also correlated with WM quality. Future studies to disentangle the roles of alpha power and phase would help to answer this question, since it has been shown that the phase-locked and non-phase-locked parts of alpha oscillations are related to different processes during WM^[72].

Gamma synchronization was first found to subserve perceptual binding^[73,74]. Recently, this synchronization has been suggested to be critical to WM (see reviews^[75,76]). Although there is no direct evidence linking gamma oscillations to WM precision, their functional role in mentally representing objects^[77] and predicting successful memory encoding^[78] has led us to propose a role of gamma oscillations in WM quality. It should also be noted that a large number of studies link WM load to the amplitude of gamma oscillations^[79-82]. However, as the number of memoranda (WM load) increases, more feature information regarding the memoranda needs to be remembered to successfully perform WM tasks. In addition, gamma activity has been suggested to be more important in sensory binding or even in multisensory integration^[83]. It therefore seems that it is a more plausible assumption to connect gamma oscillations to their role in WM quality. Future studies to disentangle the contribution of the number of items/slots or features to the modulation of gamma oscillations will be of interest.

Taken together, these works suggest that WM quality is likely maintained in higher-frequency oscillations, as in the gamma cycle, or to some extent in the alpha band, and WM quantity is related to lower-frequency oscillations, such as theta and alpha. In a recent review, Roux and Uhlhaas have proposed that the cross-frequency coupling of theta-gamma or alpha-gamma codes for distinct WM information: sequentially verbal or visuo-spatial information, respectively^[84]. Therefore, gamma activity likely represents objects in certain phases of theta and alpha activity, in which the PFC and sensory cortices communicate with each other to accomplish WM performance.

Some Topics Not Completely Covered in This Review

Given space limitations, we could not cover every aspect of the topic of quality and quantity in WM. However, several important issues merit brief consideration.

The posterior parietal cortex (PPC) also plays an important role in WM and is critical for the capacity limit^[43]. Recent studies have suggested that inferior and superior portions of the PPC represent different types of WM information during the delay period, the inferior portion indicating the binding between spatial locations and memoranda, and the superior portion specifying the complexity of sample stimuli^[41,85,86]. Therefore, the PPC may be involved in both the quantity and quality aspects of WM.

Besides the roles of theta, alpha, and gamma oscillations in WM, beta oscillations (20–30 Hz) recorded at frontal sites have also been shown to be parametrically modulated in WM by sensory stimuli^[64,67,87-89]. Therefore, the beta rhythm might be another candidate for representing WM quality.

Drawn from a plethora of studies, we propose here that the WM quality is represented in sensory cortices and the WM quantity is represented in the PFC. However, the opposite cannot be ruled out. It is notable that the quality of representation decoded from sensory cortices declines with increasing quantity of memoranda^[32]. On the other hand, as suggested above, frontal beta oscillations represent parametric sensory information^[64,67,87-89]. Future work on the bi-directional influence between quality and quantity would be helpful to disentangle these intertwined factors.

Concluding Remarks

Here, we propose a framework with the fine-tuned sensory representation in sensory cortices, which reflects the quality aspect of WM and is carried on by higher-frequency neural oscillations (gamma, beta/alpha), and the prefrontal topdown control activity that reflects the quantity aspect of WM and is carried on by lower-frequency neural oscillations (theta/alpha). As quality and quantity are intertwined and essential parts of WM, activity in the sensory cortices and PFC during WM interacts to fulfill the requirements of goaldirected behavior, and higher- *versus* lower-frequency oscillations might serve as the communication frequency to synchronize both intra- and inter-area activities (Fig. 1D). Future work to assess neuronal activity simultaneously in both the PFC and sensory cortices in WM tasks will be of great interest.

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