

Journal Club

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Characterizing the Impact of Distracting Input on Visual Working Memory Representations

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Review of Lorenc et al.

Brains constantly receive a multiplicity of inputs from the environment, of which only a small part is relevant to achieve goals. The remainder constitutes a source of distraction and potential interference. To prevent the detrimental effect of distraction, the cognitive system uses executive attention, which directs cognitive resources to relevant input, along with inhibition, which suppresses distracting information (Myers et al., 2017; Noonan et al., 2018). However, these mechanisms sometimes fail; and consequently, distracting information impairs task performance. Behavioral evidence shows that these effects occur due to interference at both low (visual features of the stimuli; e.g., Rademaker et al., 2015) and higher (task rules; for a review, see Kiesel et al., 2010) levels, even for subliminal stimuli (e.g., Silvanto and Soto, 2012) or never-implemented task rules (e.g., Di Rosa et al., 2017).

Neural substrates of selective attention and mechanisms preventing attention failures have been widely investigated. Neuroimaging studies have identified var-

ious prefrontal and parietal areas involved in resolving interference (for a meta-analysis, see Deng et al., 2018) and orienting attention (see, e.g., Nee et al., 2013). Moreover, multivariate analysis of fMRI data has revealed neural representations of both relevant information (for a review, see Rissman and Wagner, 2012) and irrelevant input (Christophel et al., 2018). However, whether these representations interact and how distractors affect visual working memory (VWM) representations had not been unraveled.

Lorenc et al. (2018) aimed to identify brain regions encoding visual stimuli while they were maintained in working memory and to assess whether and how an intervening distractor affects stimulus representation. Hence, the authors had 12 healthy people perform a cognitive task while undergoing fMRI scanning. On each trial, participants had to memorize an oriented grating. Following a blank screen (delay 1), a distractor grating (or no distractor in one-third of the trials) was shown. After a second blank screen (delay 2), a test grating was displayed and participants had to adjust its orientation to match the memorized grating. Lorenc et al. (2018) applied an inverted encoding model (Brouwer and Heeger, 2009) to reconstruct orientation information from local patterns of brain activity related to stimulus presentation (during delay 1) in bilateral early visual cortex (regions V1–V3) and superior intraparietal sulcus

(IPS), an area involved in VWM information storage. To assess the effect of distractors on VWM representations, a further encoding model was trained on fMRI data from delay 1 and orientation representation was reconstructed using activity patterns from delay 2. Permutation tests were used to assess the quality of the reconstructions and possible changes in VWM representations due to distractors, and to compare reconstruction quality in different distractor conditions.

Results showed that reconstruction quality depended on both brain region and whether a distractor was present. Stimulus orientation could be reconstructed from activity patterns in bilateral early visual cortex and contralateral IPS during delay 1. After presentation of a distractor, stimulus orientation could be reconstructed from brain activity patterns in contralateral IPS but not in early visual areas. In contrast, when no distractor was shown, orientation reconstruction was reliable in contralateral early visual areas but not in IPS. In the presence of distractors, VWM representations in early visual areas were biased toward distractor orientation. The authors concluded that VWM representations in early visual areas are strictly dependent on visual stimulation, whereas IPS is recruited only in the presence of distractors to prevent their interference.

This pattern of results is in line with previous studies showing that, when a

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task is perceptually more difficult (as when distractors are present), accuracy of stimulus encoding decreases in visual areas but increases in parietal and frontal areas, compared to with easy tasks (e.g., Woolgar et al., 2011). Within the cognitive control framework, the flexible role of IPS in representing task-relevant information (Lorenc et al., 2018) fulfills the prediction of the adaptive coding hypothesis (Duncan, 2001) that information representation within the frontoparietal network adjusts dynamically, depending on task demands. Moreover, assuming adaptive coding of information, it is possible that IPS maintains stimulus representations only when this is needed to perform the task (e.g., when distractors are presented); in line with this hypothesis, Lorenc et al. (2018) could not reconstruct stimulus orientation in IPS when distractors were absent. Finally, the findings that stimulus representations are present in both sensory and higher-level cortices and that they show different characteristics are in keeping with sensory recruitment accounts of working memory, which posit that the same regions contribute to both sensory processing and information storage in VWM, although representations in different areas may serve distinct functions (Scimeca et al., 2018).

Recent studies investigating stimulus representation using retro-cues (i.e., cues presented during delay, before stimulus recall, to signal the target stimulus) may help to explain why presenting distractors had different effects on VWM representations in visual regions and IPS in Lorenc et al. (2018). Using an inverted coding model, Sprague et al. (2016) showed that representations of attended stimuli in visual regions and IPS decay over time but are recovered after presenting valid retro-cues. Importantly, only the cued stimulus (the attended one) could be reconstructed after valid retro-cue presentation. In a high-powered study and using a decoding approach, Christophel et al. (2018) further clarified that, whereas visual areas maintain only representations of attended stimuli, IPS retains also memories of unattended information after retro-cue presentation. Instead of attentional cues, Lorenc et al. (2018) used distractors and inverted coding models to assess how irrelevant information affects VWM representations in visual regions and IPS. They found that distractors bias representations in early visual areas, whereas information encoding in IPS is distractor-resistant. As visual

cortex implements processing of visual stimuli and maintains only representations of relevant information (Christophel et al., 2018), when irrelevant input (distractors) is presented after a stimulus representation is formed, it is possible that the processing of distracting information interferes with maintaining the current representation, thus impairing it, as Lorenc et al. (2018) found. Instead, as IPS can represent also irrelevant information (Christophel et al., 2018), distracting input in this region could be encoded as a separate representation, preventing incoming information from interfering with the maintained representation, which would thus be preserved, as shown in Lorenc et al. (2018). As the authors did not attempt to reconstruct distractor representation, further research is needed to test this hypothesis.

Adaptive recruitment of posterior regions to maintain VWM representation is implemented by frontal brain areas (e.g., D'Esposito and Postle, 2015). A further step in characterizing the ability to overcome distraction and reach goals would thus be to investigate the mechanisms by which top-down control signals from prefrontal areas prevent interference. One possibility is that these signals overcome interference by preventing irrelevant information from disrupting representations of relevant stimuli (as explained above) or, alternatively, by actively modifying working memory representations (e.g., by enhancing goal-relevant representations). Ferredoes et al. (2011) suggested that frontal regions exert top-down control over posterior regions representing relevant stimuli to protect maintenance of targets in the presence of distraction. The authors applied high-frequency transcranial magnetic stimulation to DLPFC during distractor presentation, producing higher activation only in regions encoding target information. This increase in brain activation was interpreted as reflecting enhancement of target representation. However, it is possible that both protection of target maintenance and suppression of distractor representation occur at the same time and are controlled by different prefrontal regions. Because Ferredoes et al. (2011) did not assess target and distractor representations directly, and only activity in DLPFC was perturbed, we cannot exclude this possibility. Unfortunately, Lorenc et al. (2018) did not examine distractor representations. Nor did they report results for target reconstruction in PFC regions. Therefore, their study can test neither whether suppression of distractor representation occurs nor how distractors af-

fect stimulus representations in frontal regions. Nonetheless, these are justifiable choices as identifying active representations of irrelevant items requires high experimental sensitivity (Christophel et al., 2018) and multivariate signal from frontal areas is harder to detect (Bhandari et al., 2018), and the study is likely underpowered (because of the small sample size) to perform these additional analyses.

In conclusion, Lorenc et al. (2018) extend previous research on the effect of attentional cues on VWM representations to distractors. By revealing the flexibility of these representations and supporting their different nature in distinct brain regions, the authors' findings prompt revision of some existing working memory models. In particular, theoretical accounts positing concurrent storage of rigid VWM representations among which the attentional system selects should allow for some degree of flexibility in representations. More flexible "resource models" (Ma et al., 2014) or theories advocating for the adaptive nature of information representations (Duncan, 2001; Scimeca et al., 2018) should be favored. Lorenc et al. (2018) provide initial insight into how distractors can alter neural representations of relevant information. Hopefully, this will stimulate research on how top-down input from prefrontal regions can counter distractor interference (e.g., by preventing distractors from disrupting memory representations), thus making representations resistant to conflicting input and enabling people to fulfill their goals despite variability in information coming from their environments.

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