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How do we keep information 'on-line'?

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Abstract

New magnetoencephalography results indicate that a putative marker of conscious processes, namely, the global broadcasting of information across large-scale cortical networks, can also operate during the maintenance of non-conscious input. I discuss the implications for the theoretical linkage between conscious awareness and working memory functions.

Main text

A fundamental problem in psychology and neuroscience is to understand how the contents of the mind develop on a moment-to-moment basis. Intuitively, awareness seems a prerequisite to keep relevant information on-line and guide behavior. Accordingly, influential neural models propose that information is selected and kept available for conscious inspection and higher-order cognitive processes by virtue of sustained activity in parietofrontal networks (cf. global neuronal workspace theory) and recurrent neural feedback loops [1]. It is often implied that non-conscious input may only trigger feed-forward neural responses that typically fail to support high-order cognitive processes that require on-line maintenance of information.

King and colleagues [2] put these models to a test by applying machine learning techniques to magnetoencephalography (MEG) data recorded while human participants were tasked to remember the orientation of a brief and masked stimulus during a short maintenance period (see Figure 1A). Even when observers reported no experience of seeing the stimulus, memory performance was significantly above chance (Figure 1B), in keeping with the view that non-conscious processes may pervade executive control and higher-order mnemonic functions [3, 4]. Using MEG data from single trials, a decoder was trained to predict features of the memory target (i.e. the physical absence vs. presence of the item, its contrast, orientation). Even when observers reported no experience of the stimulus, its presence/absence could be decoded during the maintenance period. Most notably, a decoder trained to discriminate stimulus presence/absence on the early stages of maintenance generalized across later processing stages equally well in both conscious and non-conscious trials (Figure 1C). These temporal generalization results also showed that the later maintenance stages are increasingly metastable and encode the presence of the target for much longer durations than the early stages. This is consonant with a neural architecture in which non-conscious memoranda spreads and feeds back across multiple processing stages in a similar way to their conscious counterparts.

A 'threshold' model of consciousness would posit that non-conscious processes are a reflection of conscious counterparts but mainly differing in magnitude (e.g. similar neural processing substrates/hierarchies but attenuated activity in non-conscious states). In keeping with this 'threshold' view, decoding of the presence/absence of the memory target during maintenance was greater with higher visibility ratings (Figure 1D). Also, the temporal generalization results were suggestive of similar processing architectures for non-conscious and conscious maintenance, however the generalization of the decoder trained on the later stages of maintenance was lower and of shorter duration on non-conscious trials (see Figure 1C). This begs the fundamental question of whether or not distinct neural coding schemes support non-conscious and conscious maintenance. An intriguing result was that decoding of the relevant memory feature (i.e. orientation) on non-conscious trials was highly reliable following the stimulus, but far weaker during the maintenance period, yet, it recurred again with the onset of the test (see Figure 1C, bottom-right). Obviously the orientation of the non-conscious item was somehow retained in the brain as participants used this information to support above chance performance in the delayed discrimination test. However, and contrary to the conscious trials, there was little evidence that non-conscious trials were characterized by a sustained neural response that coded the relevant orientation feature (although the error in decoding was biased towards the orientation of the target during the maintenance phase). One possibility is that activity-silent neural coding schemes [5] (e.g. via modulation of synaptic weights in the absence of persistent neuronal firing) are most characteristic of information maintenance processes that are decoupled from conscious awareness. That decoding of the relevant orientation feature tended to wax and wane during non-conscious maintenance in King et al study may not therefore be due to low signal-to-noise, but could relate to a distinct neural coding scheme relative to conscious maintenance. This result also argues against the view that 'non-conscious' maintenance is mediated by observers making a conscious guess of the non-conscious stimulus and then keep it on-line [6], as then orientation decoding should have been greater than chance level during the maintenance phase.

Relevant clues to disassociate non-conscious vs. conscious maintenance mechanisms could come from brain localization analyses of the MEG signals, which in King et al. study involved a network of visual areas following the stimulus, extending to parietal cortex during maintenance and frontal substrates during decision making; however, given the known difficulties in localizing brain sources in MEG, defining the anatomy of conscious and non-conscious maintenance awaits further investigation. Future work could exploit recent developments in merging neural representation similarity analyses in MEG and functional MRI data [7]. Assessing the neural representational spaces of conscious and non-conscious contents across longer maintenance

periods than those used by King et al. would help define the spatio-temporal neural dynamics of maintenance across states of un(awareness).

It is also important not to underestimate the multiplicity of contexts that are relevant to study the interplay between working memory and conscious awareness. Memory paradigms using visible items demonstrated how memoranda may adopt different states of access for goal-directed behavior depending on attention [8]. An outstanding issue is whether this is extensible to the case of non-conscious maintenance and how this is modulated by the observer's attention state during the encoding of the relevant information or the withdrawal of attention during the maintenance period, since the single memory item in King et al. study always appeared at an attended location. Also, the limits and scope of brain maintenance mechanisms remain to be tested when observers have objectively null sensitivity of the presence/identity of the information [9]. More broadly, additional experimentation is needed to pinpoint the domain-generality/specificity of the underlying mechanisms, for instance, testing non-conscious neural maintenance across visual and verbal domains of increasing complexity and assessing whether the maintained information can be further manipulated in a goal-directed manner. The approach of King et al. certainly paves the way to track moment-to-moment changes in mental representations across states of (un)awareness, yet tackling the above issues in future work will boost the ramifications of this approach for understanding the bases of working memory and associated higher-order mnemonic functions [10] and their role in guiding behavior.

Acknowledgements

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Figure Legends

Figure 1. Illustration of the experimental protocol and results. (A) Example of a trial in the task. On target present trials, oriented gratings (the memory target) appeared for 17 ms, masked, and followed by a test grating 800 ms later. Participants had to report whether the test was oriented clock- or anti-clockwise relative to the memory target, and report the visibility of the masked stimulus on each trial ('0' means no experience of stimulus). (B) Behavioral results. The bar graph shows the proportion of correct responses as function of visibility. (C) Results from the temporal generalization analyses in which a decoder of the presence/absence of the target is fitted from MEG data at a given timeframe and tested in another timeframes. Classification performance is measured by the AUC (area under the ROC curve). (D) Decoding estimates of target presence (top) and orientation (bottom) across each time period of the trial and visibility ratings, with significant levels marked by *.

Figure