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On the Short-Lived Nature of Working Memory: Drift and Decay in a Population-coding model

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Review of Schneegans and Bays

The temporary storage and manipulation of information are known as working memory and are crucial to many cognitive abilities, including perception, problem-solving, and decision-making. Working memory research has a long and rich history, and a great deal of work has focused on characterizing and quantifying the critical limitations of the working memory system. This task has proven to be difficult; although working memory is described as both capacity-limited and short-lived, the specific nature of these constraints remains hotly debated (Lewandowsky et al., 2009; Luck and Vogel, 2013; Ma et al., 2014).

Data from behavioral experiments have been used to support various descriptions of working memory storage limitations, from suggestions of a fixed item limit of 7 ± 2 (Miller, 1956) to models positing the existence of 3 or 4 storage “slots” (Luck and Vogel, 1997; Cowan, 2001). Recently, visual working memory tasks requiring the report of a probed item from a continuous feature dimension have provided evidence that the precision

of item recall decreases as more items are stored (Wilken and Ma, 2004). These behavioral data can be described by models incorporating a fixed number of discrete item representations (Zhang and Luck, 2008) but are also accounted for by models where an unlimited number of representations can be maintained with variable precision (van den Berg et al., 2012).

The temporal limitations of working memory are also up for debate (Lewandowsky et al., 2009; Barrouillet et al., 2012). Despite the intuitive simplicity of representations that decay over time, controlling for various confounds during the delay period of memory tasks has proven difficult (Jonides et al., 2008). For example, some suggest that spontaneous decay of verbal information in working memory is counteracted via subvocal rehearsal of task stimuli (Baddeley et al., 1975) or by a refreshing process driven by internal attention (Barrouillet et al., 2004, 2012). To control for these hypothesized processes, some verbal working memory experiments involve a concurrent unrelated distractor task (e.g., repeating a nonsense phrase aloud or performing simple arithmetic), which typically reduces recall performance (Oberauer et al., 2016). While this effect may support the decay theories above, distractor processing itself may require representation in working memory and thus compromise otherwise robust

task representations through an interference process (Oberauer et al., 2012).

The impact of elapsed time on working memory for visual stimuli is also unclear. While some delayed recall studies (Zhang and Luck, 2009; Shipstead and Engle, 2012; Souza and Oberauer, 2015) and memory-guided saccade experiments (Funahashi et al., 1989; White et al., 1994; Starc et al., 2017) report decreased performance with longer delay periods, others report no effect (Vogel et al., 2001; Gorgoraptis et al., 2011). Although these experiments do not involve a distractor task, other forms of delay period interference have been proposed (Oberauer et al., 2016). For example, there is evidence that memory-guided saccadic responses are biased toward stimuli from previous trials, an effect that is known as proactive interference (Papadimitriou et al., 2015).

Due to differences in task design and equivocal results, the temporal limitations of working memory remain contentious. In addition, the impact of elapsed time is typically studied in isolation from storage limitations; a mechanistic account that addresses both of these limitations would therefore be a step forward for the field.

A framework recently introduced by Schneegans and Bays (2018) attempts to take such a step. The authors build on previous work proposing a population coding account of working memory storage (Bays, 2014). Their population coding (or

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“neural resource”) model suggests that features of items stored in working memory are represented by tuned populations of neurons, and that recall involves decoding the stored features. This model accounts for the impact of set size on recall precision by assuming that total population activity is normalized. As the number of representations within the population increases, the activity representing each stored feature decreases. The sampling and decoding of progressively noisier representations can thereby account for increased behavioral response variability.

The authors extend this framework to address the temporal limitations of working memory recall by comparing two hypotheses. The “decay” hypothesis posits that the rate of population activity representing an item continuously decreases over time (their Fig. 1A, top). Accordingly, the increased delay duration would have essentially the same impact as increased set size. Alternatively, the “drift” hypothesis posits that total population activity remains fixed, but drifts stochastically along a continuous feature dimension over time (their Fig. 1B, top). To test these hypotheses behaviorally, the authors took advantage of a less-studied feature of working memory performance: response time (RT).

In previous work, Schneegans and Bays (2016) reported that increasing set size in a spatial working memory task resulted in monotonic increases in RT and variability. Consistent with work describing working memory retrieval as a decision process (Pearson et al., 2014), they showed that the RT data could be fit by a model involving the accumulation of evidence toward a response threshold. In the current work, Schneegans and Bays (2018) suggest that evidence for a particular feature value takes the form of neural spiking activity. In this case, a greater number of spikes representing a feature would result in a faster accumulation of evidence to the response threshold and therefore a faster RT. Within this framework, population activity normalization explains the impact of set size on RT: at higher set sizes a probed feature would have fewer spikes representing it, so the accumulation of evidence to the response threshold would take longer.

The decay and drift hypotheses considered by Schneegans and Bays (2018) therefore make contrasting behavioral predictions about the impact of delay duration. Reduced population activity in the decay model predicts an increase in both response time and variability (their Fig.

1A, bottom), whereas normalized activity in the drift model predicts increased response variability without affecting RT (their Fig. 1B, bottom).

Behavioral data were collected from human participants performing a multiple-item variant of the classic oculomotor delayed-response task (Funahashi et al., 1989; Schneegans and Bays, 2018, their Fig. 2), where both set size (1, 2, or 4 colored items) and delay duration (0.5, 1, 2, or 4 s) were manipulated. Task performance replicated the significant increase in RT with set size shown previously (Schneegans and Bays, 2016), and the authors found no significant effect of delay duration on RT. This finding directly falsifies the decay hypothesis under the assumptions made here. Finally, the authors incorporated the two hypotheses into their population-coding model. Fits for all variants of the drift model were better able to capture the data than any version of the decay model. Together, these findings show that the decay model implemented here cannot account for imprecision in task performance, but they do not necessarily show that the drift hypothesis is the only mechanism able to account for their data.

As discussed above, the impact of time on working memory representations is controversial, and alternatives to temporal decay have often focused on the role of proactive interference (Papadimitriou et al., 2015). The latter posits that, when a long delay period is used, the temporal distance between a given trial and the previous trial is compressed, allowing information from the previous trial to interfere with the maintenance of stimuli during the current trial. Behavioral data from working memory experiments with both visual stimuli (Shipstead and Engle, 2012; Souza and Oberauer, 2015) and verbal stimuli (Oberauer and Lewandowsky, 2013) support this hypothesis, showing that decline in working memory recall performance with longer delay periods can be eliminated by fixing the ratio of intertrial to delay period duration. Schneegans and Bays (2018) suggest that such a process would be unlikely to account for their data, but they acknowledge that this hypothesis remains to be tested.

The population-coding model (Bays, 2014; Schneegans and Bays, 2018) is able to account for many aspects of behavior in working memory tasks but does not specify a neural mechanism for the maintenance of tuned activity over time. Persistent spiking activity during the delay period of working memory tasks is widely

regarded as a neural correlate of working memory maintenance (Zylberberg and Strowbridge, 2017), and was first observed in PFC (Fuster and Alexander, 1971; Kubota and Niki, 1971). Persistent spiking has since been identified in many cortical areas, including posterior parietal cortex (Gnadt and Andersen, 1988; Chafee and Goldman-Rakic, 1998) and sometimes visual cortex (Supér et al., 2001; Dotson et al., 2018). Cortical microcircuit models known as attractor networks suggest that this activity can be sustained via recurrent excitation due to the long decay time constant of NMDA receptors (Brunel, 2000; Compte et al., 2000). In combination with broad feedback inhibition, attractor networks form stable activity patterns given a tuned input. Critically, this tuned activity persists after the input is removed (Compte et al., 2000).

An alternative to persistent spiking activity posits that working memory instead relies on short-term activity-dependent changes in synaptic strength (Barak and Tsodyks, 2014; Mongillo et al., 2017). This mechanism is known as short-term synaptic facilitation and is typically associated with elevated levels of presynaptic Ca^{2+} , which allow repeated stimuli to elicit successively greater postsynaptic responses (Jackman and Regehr, 2017). Several computational models incorporating short-term synaptic facilitation suggest that activity patterns representing previously encoded information can be regenerated by subsequent network activation (Barak and Tsodyks, 2014). Recently, synaptic facilitation has also been proposed as a mechanism that could support proactive interference in the memory-guided saccade task (Kilpatrick, 2018).

Schneegans and Bays (2018) explicitly support a sustained activity account of working memory. They note that noise in a subclass of attractor networks sometimes referred to as “bump attractors” can cause feature-encoding activity to move stochastically along the represented feature dimension. Significant drift is not a general feature of bump attractor models, however (Standage and Paré, 2018), and has been shown to decrease with increasing network size (Compte et al., 2000). Thus, it is unclear whether drift occurs in the brain.

A recent attempt to identify a neural correlate of drift was made by Wimmer et al. (2014), who analyzed recordings from the PFC of monkeys performing a single-item oculomotor delayed-response task with a 3 s delay. They found that variabil-

ity in the tuned activity of PFC neurons correlated with saccade endpoint variability. This finding is consistent with the hypothesis that drift underlies behavioral imprecision, but evidence of a temporal correlation between tuning curve drift and behavioral imprecision is still lacking. The use of multiple delay durations and more than one memory item would allow for a more thorough investigation of the temporal dynamics proposed by Schneegans and Bays (2018).

While a causal link between the physiology of working memory and behavioral data must still be established, the updated population-coding model developed by Schneegans and Bays (2018) provides a framework that addresses two fundamental features of working memory storage. The authors formally implement both the temporal decay and stochastic drift of working memory representations within this framework, and find that temporal decay is unable to account for their experimental data. By making testable predictions for the impact of set size and delay duration on working memory representations, this research helps lay the groundwork for a more comprehensive understanding of the neural mechanisms underlying working memory.

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