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Adaptive memory systems for remembering the salient and the seemingly mundane

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Abstract: In an adaptive memory system, events should be prioritized in memory based on their own significance as well as the significance of preceding or following events. Here we argue that tag-and-capture models complement the GANE model by describing a mechanism that supports the transfer of memory benefits from one event to the next.

Imagine you are enjoying a brisk hike through the forest. You round a bend and stop dead in your tracks—a large bear is on the trail ahead, staring directly at you. Your attention is entirely focused on this unexpected and potential threat. You remain unharmed, but you will remember this moment for years to come. The GANE model provides a compelling account of how arousal at the moment of experience leads to selective memory for prioritized information-- for instance, the bear. In the aftermath of emotional events, however, we often remember other details that seemed inconsequential at first but were experienced in connection to the emotional event. For example, you might also remember seeing a fresh animal print in the mud earlier in your hike. These memories are adaptive,

as you do not want to wander unprepared into bear territory again. How we selectively remember information that occurred minutes to hours before an emotional experience is outside of the scope of the GANE model, but is well explained by a tag-and-capture model of memory consolidation.

Tag-and-capture refers to a model by which memory traces that are tagged during learning can benefit from periods of enhanced plasticity prior to or after learning, by capturing the plasticity-related products (PRPs) necessary for long-term consolidation (Redondo & Morris, 2011; Viola, Ballarini, Martínez, & Moncada, 2014). A key feature of this model is that weakly encoded memories stand the most to gain from this form of modulation, in that they are insufficient to drive long-term consolidation on their own. Moreover, the tag and capture phases need not occur simultaneously, but can be separated by minutes to hours as long as they affect the same neural targets. Although tag-and-capture models were initially applied to electrophysiological studies of long-term potentiation (Frey & Morris, 1997, 1998), it has since been shown that salient or arousing experiences, such as novelty exposure, can rescue weak memories (Moncada & Viola, 2007; Wang, Redondo, & Morris, 2010) that overlap with the salient event (Ballarini, Moncada, Martinez, Alen, & Viola, 2009).

A critical distinction between the GANE and tag-and-capture models is the timescales on which they are expected to operate. The GANE model proposes simultaneous engagement of noradrenaline and glutamate systems to enhance memory. Because this model necessitates coincidence detection across these neurotransmitter systems, the timeframe by which arousal can facilitate learning is limited to the duration of salient memoranda (i.e., the source of glutamate). In contrast, studies of behavioral tagging show that a salient experience can strengthen weak memories encoded up to 2 hours prior to the salient experience. In fact, behavioral tagging of some forms of hippocampal-dependent learning is more effective if the salient experience is introduced about an hour before or after weak learning, compared to if the salient experience occurs close in time (on the order of minutes) to the weakly-learned event (de Carvalho Myskiw, Furini, Benetti, & Izquierdo, 2014). In this way, tag-and-capture models are better able to

explain extended effects of salience, including arousal, on memory for relatively remote events.

The GANE and tag-and-capture models also make different predictions with respect to which kinds of information are selected for consolidation. The GANE model proposes a combination of enhanced plasticity for prioritized information and suppression of non-prioritized information, with priority determined by intrinsic salience or attentional selection at the time of learning. In contrast, tag-and-capture models rely on the presence of an encoding tag at the site of enhanced plasticity. This allows the tag-and-capture mechanism to prioritize information after the time of learning, depending on which information turns out to be most relevant to the salient event (Ballarini et al., 2009; Dunsmoor, Murty, Davachi, & Phelps, 2015). Thus, whereas the GANE model predicts memory improvements for prioritized information that coincides with an arousing event, tag-and-capture models predict memory improvements for information that acquires significance by virtue of its overlap with a separate arousing event. It is worth noting that both sets of mechanisms can, in theory, be deployed at any site of plasticity, offering flexibility in terms of which learning systems can benefit from arousal.

The relative temporal flexibility of tag-and-capture results from mechanisms that are distinct from GANE, including dopaminergic neuromodulation (Redondo & Morris, 2011). Critically, the dopaminergic system has properties that allow it to support consolidation at extended timescales. First, dopamine release in response to arousal is characterized by tonic, as opposed to phasic, activation (Grace, Floresco, Goto, & Lodge, 2007), such that a single arousing event could result in prolonged increases in dopaminergic tone and facilitated learning (Shohamy & Adcock, 2010). Second, dopamine acts on relatively late stages of memory consolidation, allowing for salient events and encoding to be disparate in time. That is, dopamine affects protein synthesis-dependent long-term potentiation-- a process necessary for consolidation-- as opposed to memory encoding via early long-term potentiation (Lisman, Grace, & Duzel, 2011). Because dopamine-mediated synthesis of PRPs can occur independently from encoding, it may be particularly relevant for the consolidation of weakly encoded events, relative to

strongly encoded events that are able to initiate PRP synthesis on their own through mechanisms like those described in GANE. It is worth noting that there is some evidence that, like dopamine, noradrenergic responses can be long-lasting (McIntyre, Hatfield, & McGaugh, 2002) and involved in tag-and-capture effects (Moncada, Ballarini, Martinez, Frey, & Viola, 2011). However, additional research is needed to understand to what extent these neurotransmitter systems support memory consolidation at different timescales and for different kinds of information.

To conclude, the GANE and tag-and-capture models are complementary in that they can explain a range of memory phenomena occurring at and around the time of an arousing event. The GANE model makes novel predictions for what separates what we remember from what we forget, whereas tag-and-capture models are better suited to explaining why we often remember information from a window of minutes to hours around an emotionally salient event. Thus, the brain's ability to select information for consolidation into long-term memory is not determined only by the cognitive and neurobiological mechanisms operating at the moment of encoding. Rather, an adaptive memory system prioritizes the salient, but also allows the seemingly mundane to take on significance following new meaningful experiences.

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