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Precision, binding, and the hippocampus: Precisely what are we talking about?

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Running Title: Precision and the hippocampus

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Endel Tulving’s proposal that episodic memory is distinct from other memory systems like semantic memory remains an extremely influential idea in cognitive neuroscience research. As originally suggested by Tulving, episodic memory involves three key components that differentiate it from all other memory systems: spatiotemporal binding, mental time travel, and auto-noetic consciousness. Here, we focus on the idea of spatiotemporal binding in episodic memory and, in particular, how consideration of the precision of spatiotemporal context helps expand our understanding of episodic memory. Precision also helps shed light on another key issue in cognitive neuroscience, the role of the hippocampus outside of episodic memory in perception, attention, and working memory. By considering precision alongside item-context bindings, we attempt to shed new light on both the nature of how we represent context and what roles the hippocampus plays in episodic memory and beyond.

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4 When Endel Tulving first proposed the idea of episodic memory, he suggested that it
5 involved a fundamentally different memory system from semantic memory, one's memory for
6 facts about the world. Episodic memory, he argued, hinged on the idea that memories for
7 events share key components related to their embedding in time, thus changing the cognitive
8 process by which we can access and work with such memories (Tulving, 1985; 2002; 2005). In
9 particular, Tulving focused on three key components of such memories: their spatiotemporal
10 uniqueness, our ability to travel back and forth through these memories (which he termed
11 "mental time travel"), and the fact that we are aware of this process of moving through time
12 when we review memories (termed "autonoetic consciousness"). Subsequent work attempted
13 to connect Tulving's ideas of episodic memory with prefrontal cortex and hippocampus,
14 including HERA (Habib, Nyberg, & Tulving, 2003; Nyberg, Cabeza, & Tulving, 1996) and HIPER
15 models (Lepage, Habib, & Tulving, 1998; Lepage, McIntosh, & Tulving, 2001). While Tulving's
16 ideas about episodic memory as a distinct memory system have received wide support in the
17 literature and continues to influence how we conceive of the neural basis of episodic memory,
18 key questions remain in terms of understanding the neural processes and representations
19 underlying such memories.
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25 An important characteristic of episodic memories, according to Tulving, involved binding
26 an item-related signature with some kind of "source" from which the memory originated (also
27 termed "context"). For Tulving at least, context was what distinguished a specific occurrence of
28 an item, such as a word or picture, as unique from all the other occurrences of it (Wheeler,
29 Stuss, & Tulving, 1997). One example would be recollection of what one was thinking when
30 seeing the word "cat" in a list of words during encoding, such as "'cat' makes me think of Endel's
31 'cat' that got lost in Davis" or "'cat' makes me think of my friend's tabby." Retrieval of contextual
32 details was also critical to Tulving's ideas about episodic memory because it allowed recovery of
33 the unique encoding experiences associated with that word and thereby facilitated autonoetic
34 consciousness.
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38 Interestingly, temporal context, which has received considerably more interest and
39 attention since the work of Tulving, was considered largely a by-product of "executive"
40 functioning by the frontal lobe (Wheeler, et al., 1997). In this way, temporal context was not
41 something intrinsic or specific to context but emerged from other aspects of cognition.
42 Theoretical considerations of mental time travel as part of episodic memory similarly considered
43 time as important but did not explicitly define how it might be represented or interleaved with
44 such representations one might time travel through (Suddendorf & Corballis, 2007). We think
45 that considering the nature of "context," particularly its temporal nature, in significantly more
46 depth will help to advance our understanding of episodic memory by allowing us to link Tulving's
47 ideas about episodic memory to more recent work on context, binding, and precision.
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50 Like consideration of "context," another area that has seen significant development since
51 Tulving's work is in the neural basis of episodic memory. Intriguingly, Tulving pointed out,
52 somewhat presciently for our purposes here:
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55 "An operating component of a system [e.g., episodic memory] consists of a neural substrate and
56 its behavioral or cognitive correlates. Some components are shared by all systems, others are
57 shared only by some, and still others are unique to individual systems. Different learning and
58 memory situations involve different concatenations of components from one or more systems."
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5 We think that the point that “some components are shared by all / some memory systems” in
6 particular is important to help better understand what brain systems may be engaged and in
7 what manner during episodic memory encoding and retrieval. As we will argue here, “precision”
8 can be thought of as a more general property shared by nearly all memory systems, as more
9 precise representations generally will be of higher fidelity and usefulness in many domains (e.g.,
10 visual and auditory). We provide a more detailed definition of precision, which includes both
11 resolution and dimensionality (complexity), in a later section.
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14 Finally, we will also argue that the “binding” function of episodic memory – associating a
15 novel context with an item – is an operation on representations that may be partially or even
16 uniquely supported by the hippocampus. The idea of binding thus includes both the operation
17 of association and the idea that associated context must be high dimensional to be effective
18 (Cowell, Barense, & Sadil, 2019). Precision and binding help to shed light on some important
19 puzzles in memory research: in what ways does drifting context relate to episodic memory and
20 what role does the hippocampus play in cognitive processing outside of episodic memory, such
21 as perception and working memory?
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26 **Spatiotemporal context: Why is it important to episodic memory?**

27 To successfully retrieve an item or other information that was encoded in episodic
28 memory, one needs a cue specific to the encoding situation, which is often referred to as the
29 context or source under which an item was encoded. For example, recovering the thoughts that
30 we had when we encoded the word “cat” could provide sufficient information to cue recovery of
31 the word “cat,” like the image of a tabby or other cats that got lost in Davis. In this way, context
32 itself might not be unique, but could still be just good enough for recovering enough of a
33 memory to remember the word “cat.” In this case, though, we would not think of this form of
34 context as “episodic,” at least based on Tulving’s considerations, in that it does not necessarily
35 index a unique instance of “cat” that was encoded at a specific time point. Tulving also
36 acknowledged the importance of both space and time, and time in particular, in that time
37 provides a unique code for potentially recovering a memory. As we will discuss shortly in more
38 detail, it follows that space and time must be of sufficiently high precision to serve as a unique
39 cue to retrieve the item paired with context.
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44 In practice, remembering an item based on encoding it 3.4 seconds compared to 3.5
45 seconds seems unlikely as candidate for how we cue items that we encoded (Friedman, 1993,
46 2007). Although Tulving did not explicitly define how time might be stored as part of *mental time*
47 *travel*, subsequent considerations suggested that recency effects and changes in events (such
48 as temporal boundaries, an issue we will explore more shortly) could provide a means of doing
49 this (Suddendorf & Corballis, 2007). In contrast, we think that a “drifting” representation of
50 temporal context may be particularly important to how we represent time. In this way, “drifting”
51 refers to the type of gradual change typical of time. Changes in spatial context or event
52 boundaries, in contrast, provide a “shift” that can result in more dramatic dimensional changes
53 in context. Shifting context in this way would be a more rapid type of change that results when
54 you move from one location to another. Drifting and shifting context provide a means by which
55 context is sufficiently different, and possibly unique, from all the other contexts that have been
56 associated with an item and neighboring items.
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4 To serve as an effective cue during retrieval, a context representation must be
5 associated with an item during encoding, a process often referred to as *binding, or*
6 *spatiotemporal binding*. Binding of items to a unique spatiotemporal context allows an episodic
7 memory to be differentiated from the myriad of others we experienced in an experiment and/or
8 in a day. We can think of binding “demands” increasing as a function of the dimensionality of
9 the stimuli themselves, with context an example of a particular complex type of stimulus with
10 multidimensional features (Yonelinas, 2013). As we have noted earlier, however, episodic
11 memory, at least for veridical retrieval of the encoded stimulus content, should contain at least
12 some unique temporal tags that relate to the encoded context (Polyn, Norman, & Kahana,
13 2009). It is important to think in more detail, then, about exactly what is context and why, to
14 serve as an effective retrieval aid, must it be high-dimensional and unique? In other words,
15 exactly what is being bound to the item representation in terms of context that allows recovery
16 of spatiotemporal details?
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18 One possible definition is that context is whatever the item is not. While this could
19 include a coarse (low dimension, low resolution) representation of drifting time, this is not
20 something one would directly perceive, and without some definition of time, such a definition
21 does not provide much traction with Tulving’s conception of episodic memory. Another
22 definition often used of context relates to how we represent space (Nadel & Willner, 1980).
23 While space undoubtedly is a powerful cue for encoding and retrieving episodic memories
24 (Hupbach, Gomez, Hardt, & Nadel, 2007; Robin, Wynn, & Moscovitch, 2016), the extent to
25 which space alone allows us to distinguish one item from another, particularly if we are in the
26 same location during an experiment, is somewhat doubtful. Space also suffers, unfortunately,
27 from some degree of circularity in terms of how we think about it. As we have argued
28 elsewhere, space is often defined as whatever a brain structure like the hippocampus does
29 (Ekstrom & Ranganath, 2017) or how we imagine space to be when we remember locations
30 (Ekstrom, Harootonian, & Huffman, in press). Although we provide a stricter definition of space
31 later in this paper related to 2-D/3-D topological axes, space itself might be expected not to
32 change significantly over repeated exposures. Thus, while space could provide the types of
33 “shifts” important to context change, it would not provide a unique code necessarily for episodic
34 memory.
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36 Here, we think it is instead useful to adopt a more holistic definition of context that can
37 include both internal and external events that drift *and* shift over time (Howard & Kahana, 2002;
38 Polyn, et al., 2009; Watrous & Ekstrom, 2014; Yonelinas, Ranganath, Ekstrom, & Wiltgen,
39 2019). According to this definition, context changes gradually over time based on the properties
40 of diffusion drift (Howard & Kahana, 2002; Long, Danoff, & Kahana, 2015; Polyn, et al., 2009),
41 with external input, such as changing spatial location providing input that shifts the contextual
42 representation. In this way, context can vary considerably during a period of even 45 minutes of
43 an experiment involving encoding a list of words. Critically, the resolution and dimensionality,
44 and its uniqueness in terms of temporal drift, will help to determine how well it can serve as a
45 cue during retrieval. By binding each item on a list to this slowly drifting and changing context,
46 then, unique associations form the basis for potentially recovering words or objects that were
47 encoded. In this way, item-context bindings provide unique signatures for differentiating
48 encoded information, with the challenge being the extent to which such bindings provide
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4 sufficiently different representations for them to be retrieved from all of the other bindings that
5 occurred during that list learning episode.
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7 8 **Precision and context**

9 Given the importance of a relatively unique contextual representations to allow
10 differentiation from other memories, it seems reasonable to consider in more depth what one
11 might mean with regard to “unique.” This is an instance in which we think considering the
12 precision of contextual representations becomes particularly important. To differentiate an item
13 on a list from all other occurrences of that item, there needs to be sufficient information
14 embedded in the contextual representation to serve as an identifier for that item. This is where
15 the idea of precision first becomes apparent when we consider episodic memories. We will later
16 consider the importance of precision with regard to the hippocampus in a later section.
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18 Precision is important in many different ways to context, although the extent to which
19 context is differentiable from other aspects of drifting context does not necessarily have to relate
20 to its precision. We can think of precision as involving both resolution and dimensionality
21 (complexity), which are helpful to think about through two cases. A precise representation of
22 context could involve a high-resolution and high-dimensional representation which drifts over
23 time (Figures 1). A higher precision representation would have more elements (the matrix
24 representing context has more elements), meaning that the resolution of itself, much like a
25 picture of 512x512 vs. 1024 vs. 1024 pixels, would be higher. Additionally, such elements could
26 be higher dimensionality (complexity) such that a decomposition of the elements that make up
27 the matrix would reveal a higher number of linear-independent basis functions (Figure 1). This
28 would be an instance, which we think would be relatively common for well-encoded and
29 retrieved memories, in which resolution and dimensionality are correlated. Importantly, higher
30 precision (resolution + dimensionality) would allow for a greater number of items to potentially
31 be different, any of which could be usefully exploited for binding to an item.
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33 We could also imagine a situation in which a relatively low-precision contextual
34 representation could nonetheless serve well in memory. For example, if we get up and move to
35 a different place, the low precision vector would shift significantly, thereby providing
36 differentiable representations at the times of the shift. Such significant changes in context likely
37 relate to boundary effects in which either the narrative structure or high-order aspects of an
38 experience change sufficiently to induce a sense of “shift” (Ben-Yakov & Henson, 2018; Zacks &
39 Swallow, 2007). Under typical situations in which significant changes do not happen during the
40 experiment, though, a high-dimensional, precise contextual representation would be most
41 advantageous for encoding and retrieving memories. Therefore, under situations of extensive
42 shift, a lower dimensional representation would suffice but when in the same spatial context
43 (e.g., experiment room), a higher resolution representation is optimal.
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45 Note that the critical component here is the extent to which individual elements of the
46 matrix that make up context change over time, which can happen for a variety of different
47 reasons. According to the original conceptualization of context in the temporal coding model,
48 context itself steadily drifts in a time varying fashion based on diffusion drift properties such that
49 more distant time steps result in less similar random drifts (Howard & Kahana, 2002; Long, et
50 al., 2015; Polyn, et al., 2009). In the instances in which almost everything else stays the same
51 in an experiment (e.g., minimal changes in internal and external states) each word in a list we
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4 are trying to learn becomes associated with a slightly different context vector in which only a
5 small subset of elements change over time. Such drifting in temporal context helps explain
6 primacy and recency effects in free recall as temporal context is different from the beginning
7 and endpoints of the experiment, with overall less memory for words in the middle of the list due
8 to the only slight changes in drifting context. In contrast, if the participant gets up and moves to
9 a new room in the middle of the list, this will induce shifts in multiple differentiable elements (the
10 dimensionality) of the context matrix, resulting in greater memory for the middle parts of the list
11 (Polyn, et al., 2009).
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14 Another interesting example to consider here is the method of loci, well known to serve
15 as a mnemonic aid. Let's consider a situation in which we have a particularly precise
16 representation of locations of objects in our home, for example, we can readily point accurately
17 to the locations of objects within our house. While such a representation would not change
18 much once we have learned it well and can be thought of as primarily semantic, it is useful to
19 think how such a representation could nonetheless serve as an aid for episodic memory.
20 Specifically, with the method of loci, we typically imagine placing words in spatial locations as
21 each word is read to us in the list (Bower, 1972; Yates, 1966). If we imagine our apartment in
22 color, this would refer to a high-resolution type of representation as there are many elements,
23 like couches and chairs that are brown and beige. If we think of our apartment as involving
24 unique dimensions, like the positions and orientations of the furniture, the color of the walls, and
25 smells from the kitchen, then this would involve higher dimensionality (complexity). Then, if we
26 use our kitchen as a scaffold on which to remember items a list of words, a more precise
27 representation will in turn be more useful for encoding and retrieving words because we have
28 increased the number of dimensions over which we are binding with an object we are trying to
29 remember. In this case, interestingly, it is the mental movement within our house that provides
30 for binding with context, and the richer the context, the more the dimensionality and the more
31 effective the binding.
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34 We can also consider the precision of temporal representations and the role that
35 precision would play. The degree to which we can better differentiate a given moment in time
36 from another could be useful for binding to a specific item. For example, we recently
37 demonstrated that a precise representation of one's mental "lifeline" could serve comparably to
38 a spatial scaffold for anchoring episodic memories (Bouffard, Stokes, Kramer, & Ekstrom,
39 2017). What about representing time in the moment? While participants can readily judge
40 temporal durations, (e.g., was the item on the screen for 4 vs. 5 seconds (Ekstrom & Isham,
41 2017; Meck, Church, & Matell, 2013)), it is not clear that time drifts sufficiently within several
42 seconds to differentiate one item from another. While there is certainly evidence for neural
43 representations of time (Kraus, Robinson, White, Eichenbaum, & Hasselmo, 2013), with neural
44 representation of drifting temporal context contributing to episodic memory encoding and
45 retrieval (Manning, Polyn, Baltuch, Litt, & Kahana, 2011), it remains unclear whether we use
46 such precise representations of time to differentiate individual items on a list. In this way,
47 context "shifts" like event boundaries and changes in spatial context are likely to be more
48 effective in binding than changes in temporal context alone, which do not provide the same
49 degree of dimension change.
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59 **How does "precision" emerge from representation of context?**
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4 While we have considered the computational properties of temporal context to involve
5 diffusion drift (Howard & Kahana, 2002; Long, et al., 2015; Polyn, et al., 2009), we have not
6 defined the spatial aspects of *spatiotemoral* context. Past work considering spatial context has
7 argued that such representations should be *metric* (e.g., Bellmund, Gardenfors, Moser, &
8 Doeller, 2018). Like a piece of graph paper, such a representation contains an underlying
9 organization that follows Euclidean rules of geometry, for example, symmetry ($AB=BA$) and that
10 the angles of a triangle must equal 180° . With a metric representation, precision is a particularly
11 easy dimension to imagine, as it would simply relate to the scaling of the graph paper (finer =
12 higher resolution) or the noise of the representation (less noise = more unique elements =
13 higher dimensionality). In this way, there appear to be many commonalities between how we
14 might think about spatial navigation, contextual representation, episodic, and semantic memory
15 (Buzsáki & Llinás, 2017; Buzsaki & Moser, 2013). The issue here, however, is that storing a 4-
16 D representation of space time, particularly a high-resolution one, would require an enormous
17 amount of “disk” space. It is also not clear how internal changes, such as one’s mood, could be
18 mapped onto some kind of “metric.”

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23 Instead, we do not think it is necessary to assume any specific kind of metric or
24 underlying organization to spatial context, and instead, assume that this can also vary. There
25 may be instances in which a nearly metric representation of our kitchen could be useful for
26 encoding items. We think, however, that this aspect of context is often topological, in other
27 words, things relatively more similar/closer in space are stored nearby but lack any specific
28 metric on which they are encoded (Ekstrom, et al., in press; Ekstrom, Huffman, & Starrett, 2017;
29 Warren, 2019). This is shown in Figure 2 in which the exact spacing of objects in topological
30 spatial context do not matter as long as the *relative* positions are preserved. Notably, items
31 metrically or topologically spaced will have the similar precision and be of similar efficacy in
32 binding and representing items in memory. Importantly, topological space allows for the idea
33 that the scaffold itself may be of equal dimensionality and instead that what matters would be
34 the dimensionality of different elements (e.g., how many and what background features) we
35 store rather than their position in the context.

40 41 **Neural basis of contextual precision and binding within the hippocampus**

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43 Binding, or the process of associating a high-dimensional context with an item during
44 encoding, depends primarily on the hippocampus, consistent with arguments from amnesia,
45 neuroimaging, and other methodologies (Davachi, Mitchell, & Wagner, 2003; Davachi &
46 Wagner, 2002; Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath,
47 2007; Hamann & Squire, 1997; Insausti, Annese, Amaral, & Squire, 2013; Lee, Yip, & Jones-
48 Gotman, 2002; Lepage, et al., 1998; Milner, Corkin, & Teuber, 1968; Scoville & Milner, 1957;
49 Sherman, et al., 2011; Stark & Squire, 2000; Yonelinas, Kroll, Dobbins, Lazzara, & Knight,
50 1998). As argued above, we can think of binding as involving an association between the
51 context present during item encoding and the item itself, with context assumed to be sufficiently
52 precise and unique compared to other stored contexts to allow recovery during retrieval –
53 assuming sufficient cues can be recovered. Thus, for veridical recall of the item, we would
54 expect a relatively high-match between the retrieved and encoded context, similar to the idea
55 that encoding and retrieval involve a certain degree of match between neural activity during
56 encoding and retrieval (Gelbard-Sagiv, Mukamel, Harel, Malach, & Fried, 2008; Oedekoven,
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4 Keidel, Berens, & Bird, 2017). In this case, while precision will certainly be helpful in
5 distinguishing one context from another, it only needs to be sufficiently different from competing
6 contexts to allow completion to the correct trace. If context is imprecise, then the system will
7 enter an unstable attractor and potentially retrieve a different item or return no solution at all.
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9 Such considerations additionally highlight the importance of two computational
10 mechanisms to hippocampal-mediated item-context binding, *pattern completion and separation*.
11 These involve making two similar representations more different vs. making a different
12 representation more like a matching one (Cowell, et al., 2019; Levy, 1989; McNaughton &
13 Morris, 1987; Yassa & Stark, 2011). In particular, pattern separation should serve to reduce
14 interference between high resolution contextual representations to allow distinguishing of
15 competing contexts. This idea is also critical during encoding, as the item-context binding must
16 be sufficiently different from others such that the correct association is subsequently retrieved.
17 Pattern completion, in contrast, would be important during retrieval as it essentially serves to
18 match a retrieved trace to one during encoding. Note that if context involves low-precision
19 representations, pattern completion may occur to a different list or incorrect item, and thus the
20 importance of the precision of the context representation. Overall, such ideas fit with prior
21 proposals about episodic memory that have emphasized the importance of both high-
22 dimensional representations within the hippocampus as well as the importance of pattern
23 separation and completion to this process (Cowell, et al., 2019).
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30 **Contextual precision and episodic memory outside of the hippocampus**

31 The hippocampus is not the only brain area in which contextual processing and pattern
32 completion/separation occur (e.g., Cowell, et al., 2019). Consistent with this idea, recent work
33 has also highlighted the roles of areas outside of the hippocampus in episodic memory. In
34 support of this idea, both imaging and lesion evidence in humans suggest that posterior parietal
35 cortex, medial prefrontal cortex, precuneus / retrosplenial cortex, and other parts of the “core
36 recollection network” are also critical for episodic memory (Berryhill, Phuong, Picasso, Cabeza,
37 & Olson, 2007; Blumenfeld & Ranganath, 2007; Duarte, Ranganath, & Knight, 2005; Kim, 2011;
38 Rugg, Otten, & Henson, 2002; Thakral, Wang, & Rugg, 2016; Uncapher, Otten, & Rugg, 2006;
39 Wagner, Shannon, Kahn, & Buckner, 2005; Zeithamova, Dominick, & Preston, 2012) and their
40 interactions (Fornito, Harrison, Zalesky, & Simons, 2012; Geib, Stanley, Wing, Laurienti, &
41 Cabeza, 2015; King, de Chastelaine, Elward, Wang, & Rugg, 2015; Schedlbauer, Copara,
42 Watrous, & Ekstrom, 2014; Watrous, Tandon, Conner, Pieters, & Ekstrom, 2013). Most
43 compelling are findings that lesions to both prefrontal cortex and posterior parietal cortex, as
44 well as other areas like the mammillary bodies in the thalamus and retrosplenial cortex, produce
45 deficits in episodic memory, suggesting the necessity of these areas to episodic memory
46 function (Berryhill, et al., 2007; Duarte, et al., 2005; Gadian, et al., 2000; Newsome, et al., 2018;
47 Simons, Peers, Mazuz, Berryhill, & Olson, 2010; Valenstein, et al., 1987). The question
48 remaining, which we discuss only briefly here, is whether brain regions in the core recollection
49 network play specific roles in episodic memory that work in an additive manner or whether their
50 function can be better conceived as a non-additive.
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57 The additive perspective on the roles of brain regions within the core recollection
58 network suggests that each brain region contributes something “unique” to episodic memory.
59 Tulving, for example, favored the idea that prefrontal cortex provided “executive” control
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4 functions important to episodic memory and this idea has certainly been retained in other
5 formulations as part of source monitoring (Johnson, 2006; Van Petten, et al., 2004; Wheeler, et
6 al., 1997). According to an additive perspective on PFC function in episodic memory, PFC
7 performs monitoring and interference reduction functions but not the item-context bindings that
8 the hippocampus provides. Therefore, damage to the PFC should affect functions such as how
9 well a participant can hold a cue in memory and use this information to cue item-contextual
10 bindings within the hippocampus but does not contribute to the retrieval of the item-context
11 bindings themselves. Additive models are strongly consistent with double dissociations in which
12 damage to one brain area impacts performance on one task and not another, while the opposite
13 patterns occur for damage to a different brain area like the hippocampus (Baddeley, 2003).
14 Thus, areas like prefrontal cortex and posterior parietal cortex have specific, circumscribed roles
15 in episodic memory, and in this way, do not store a “trace” of item-context memory. Instead,
16 their function is “added” to that of the hippocampus (along with others), and together, the
17 emergent behavior is episodic memory.
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22 In contrast, non-additive models, which have gained increasing traction in graph theory,
23 suggest that “episodic memory,” as a cognitive construct, emerges from distributed interactions
24 between brain regions such as the core recollection network (Schedlbauer & Ekstrom, 2017;
25 Schedlbauer & Ekstrom, 2019). Consistent with the non-additive framework, cellular responses
26 to context are also present in brain areas outside of the hippocampus, such as place cells in the
27 rodent retrosplenial cortex (Mao, Kandler, McNaughton, & Bonin, 2017), visual cortex (Haggerty
28 & Ji, 2015; Ji & Wilson, 2007), prefrontal cortex (Fujisawa, Amarasingham, Harrison, & Buzsaki,
29 2008), claustrum (Jankowski & O'Mara, 2015) and even the human amygdala (see Figure 2C in
30 Miller, et al., 2013). The argument for non-additive coding, which we have made previously with
31 regard to both episodic memory and spatial navigation (Ekstrom, et al., 2017; Schedlbauer &
32 Ekstrom, 2017), posits that interactions across multiple brain hubs operate such that the role of
33 a hub cannot be distilled to a single function in cognition (Bassett & Gazzaniga, 2011; Finger,
34 Koehler, & Jagella, 2004). As such, binding depends on the interactions of multiple brain
35 regions, and cannot be distilled to a single region such as the hippocampus (Schedlbauer &
36 Ekstrom, 2017). To bring back our earlier example, this conceptualization would suggest that
37 both PFC and hippocampus play a role in both trace storage as well as episodic memory more
38 generally. This does not mean, however, that all regions within the core recollection network
39 contain identical neural architecture. PFC may be slightly biased neuroanatomically toward
40 executive-type functions and hippocampus to item-context bindings. While different brain
41 regions undoubtedly contain partially unique and partially overlapping neural patterns of
42 connectivity and computational capacities, the property of binding, according to the non-additive
43 framework, only emerges “normally” and collectively when these areas can interact.
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50 Currently, we do not think there is sufficient evidence to support either the additive or
51 non-additive perspective on the neural basis of episodic memory. While there is evidence that
52 areas of the core recollection network can be dissociated based on different dependent
53 measures (Bonnici, Cheke, Green, FitzGerald, & Simons, 2018; Richter, Cooper, Bays, &
54 Simons, 2016), we suspect that at least some of such effects could be task specific. Any form
55 of task-specific effects of activation patterns or perturbations within the core recollection network
56 would seem to relate better to a non-additive conceptualization, suggesting that different
57 episodic memory tasks may place different emphasis on components of the core recollection
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4 network. We also think the idea of interactions is a key and often overlooked aspect of models
5 of episodic memory, although more recent models do place an emphasis on such phenomenon
6 (Ranganath & Ritchey, 2012). Such intermediate versions of additive/non-additive network
7 models involve some segregation of function in anterior to posterior brain networks with
8 evidence for dynamic interactions between the two (Cooper & Ritchey, 2019). Future
9 experiments will be needed to address the extent to which item-context bindings, a key
10 component of memory, is additive or non-additive.
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13 14 **Precision, context, and hippocampal function**

15 To better understand context, we also need to consider how such an entity might take
16 shape in the first place. As we have discussed, many aspects of context are likely built on
17 semantic knowledge, what could be termed a scaffold or a script (Bartlett, 1932; Schank &
18 Abelson, 1977). One issue, however, as discussed above, is that the more static elements
19 present in a contextual representation the less effective it will be at distinguishing different
20 encoded items at retrieval. One way of producing different elements within this larger semantic
21 scaffold then could be based shifts in external input and drifting temporal context. For example,
22 using the method of loci will be facilitated by a more precise representation of the spatial
23 environment you employ as a scaffold and remembering what you had to eat at your favorite
24 restaurant will be facilitated by a more precise representation of the layout of the restaurant
25 (e.g., such that you could distinguish sitting in different places at different times). This process
26 will involve perception, attention, and working memory, all of which can happen at varying
27 degrees of precision.
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30 As we have described above in terms of computations, we can think of precision as
31 critical to the success of recall because it adds dimensionality and resolution to contextual
32 representations important to computational functions within the hippocampus like pattern
33 separation (Hindy, Ng, & Turk-Browne, 2016). As far as how precision manifests at the
34 representational/behavioral level, we can think of it in a manner consistent with that proposed in
35 the Precision and Binding Model (PBM) (Kolarik, Baer, Shahlaie, Yonelinas, & Ekstrom, 2017;
36 Yonelinas, 2013). Accordingly, precision can be thought of as a *continuous measure* of the
37 level of detail in a perceptual or memory representation (Aly, Ranganath, & Yonelinas, 2013;
38 Barense, et al., 2012; Kolarik, et al., 2016; Richter, et al., 2016; Yonelinas, 2013). This is
39 consistent with the idea that when we encode the color, orientation, or location of a stimulus, the
40 greater the resolution and dimensionality of attributes, the better differentiated from other
41 competing “source” information we have also encoded. In this way, precision is much like what
42 is often supposed in working memory and attention research as involving narrowly tuned
43 attributes directly related to encoding of that feature. With more features (orientation + color) to
44 be encoded, resource allocation results in increasingly noisy representations, decreasing
45 precision at the expense of greater memory for distinct stimulus features (Ma, Husain, & Bays,
46 2014).
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49 Given the importance of the hippocampus to episodic memory, and our proposal of the
50 additional importance of precision to perception, working memory, and attention, it may seem
51 surprising to suggest that the hippocampus plays a role beyond the widely agreed upon role in
52 item-context bindings. We think, however, that ample evidence now supports the idea that the
53 domain of the hippocampus extends beyond episodic memory alone. Even the original reports
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4 with patients H.M and E.P. noted some deficits in both perceptual and working memory
5 processes (Hamann & Squire, 1997; Insausti, et al., 2013; Milner, et al., 1968; Olson, Page,
6 Moore, Chatterjee, & Verfaellie, 2006; Scoville & Milner, 1957; Stark & Squire, 2000). These
7 findings, which typically have manifested in deficits in neuropsychological tests related to
8 working memory and perception, could potentially have origins in some of the patients'
9 heterogenous lesion locations. Additional evidence, however, from tests providing a more
10 detailed assay of working memory and perception suggests this is likely not the case and that
11 such deficits arise, in part, from effects related to hippocampal lesions.
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14 In one example, Aly et al. tested patients with medial temporal lobe lesions some of
15 which were largely circumscribed to the hippocampus, and healthy controls, on complex scene
16 images (Figure 3). Participants made perceptual judgments indicating whether two
17 simultaneously presented images were the same or different. Importantly, the perceptual
18 changes did not involve adding or removing specific objects in the scene but rather pinching or
19 expanding of the images such that there was only a slight mismatch between them. This was
20 important because this would have otherwise involved changes in discrete features that would
21 have readily helped participants identify perceptual differences. Strikingly, the patients exhibited
22 significantly reduced perceptual sensitivity on this task indicating that the hippocampus
23 contributed to perceptual discriminations when the task required the detection of very subtle
24 perceptual differences. For other examples of the importance of the hippocampus (and medial
25 temporal lobe more generally) to perception also see: (Barens, Gaffan, & Graham, 2007; Erez,
26 Lee, & Barens, 2013; Hindy, et al., 2016; Warren, Duff, Tranel & Cohen, 2011)
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29 The Aly et al. experiment, however, did not involve explicit manipulation of precision and
30 could best be considered a test case for whether the hippocampus plays a role in perception of
31 continuously changed features. To address this issue, Koen et al. tested patients and controls
32 who viewed a small set of colored objects and then after a 2 second delay were given a forced-
33 choice test for object-color (i.e., "which of the two colors was this object presented in?") or
34 object-location ("which of the two locations was this object presented in?"). This aspect of the
35 design has commonality with that used by Richter, et al. (2016) in the domain of episodic
36 memory. To explicitly manipulate precision, half of the test trials necessitated high precision
37 representations of color (e.g., one option was red and the other was a slightly different shade of
38 red) and half were low precision (e.g., one option was red and the other was yellow). Overall
39 difficulty was matched across high and low precision trials by varying set size. Importantly,
40 patients showed greater deficits relative to controls for more precise but not less precise
41 memory trials, which was true for both the location and color conditions. These findings suggest
42 the human hippocampus plays a necessary role in in working memory, and in particular, in the
43 resolution with which the items were stored and retrieved (Koen, Borders, Petzold, & Yonelinas,
44 2017).
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47 Another way to think of the manipulations in the Koen et al. study might instead be to
48 relate such representations to the precision of object-feature bindings. For example,
49 remembering the color and orientation of a stimulus could instead be thought of as involving
50 how this information is bound to the representation of the object. Overall, we think this idea
51 relates directly to the precision of information represented not only in the hippocampus but in
52 other structures as well, such as perirhinal cortex and other ventral stream structures. As we
53 noted earlier, however, precision is also important to contextual representations. There is also
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4 evidence in patients with hippocampal lesions to demonstrate that the hippocampus plays a
5 necessary role in precision for context. In this case, we will think of precision as important to the
6 issue of *spatial* context, but as our examples before demonstrated, precision is an important
7 consideration for many different forms of representation, including time, emotional valence, and
8 other relevant dimensions.
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10 To address precision related to spatial context, Kolarik et al. tested patients with lesions
11 to the medial temporal lobe, which included two patients with bilateral hippocampal lesions
12 (Kolarik, et al., 2017; Kolarik, et al., 2016). All participants navigated a large-virtual arena
13 (Figure 3) in virtual reality by searching for a hidden target. During acquisition, if the participant
14 did not find the target after 30 seconds, it was displayed on the screen, as is often done in
15 assays involving the virtual Morris Water to ensure that participants learn the hidden location
16 (Astur, Taylor, Mamelak, Philpott, & Sutherland, 2002). During probe trials (retrieval),
17 participants searched for the hidden target location, with no feedback provided. In this way, the
18 study assayed the precision of searches both during encoding (acquisition) and retrieval (probe
19 trials).
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23 To better understand the precision of the spatial searches, Kolarik et al. employed a
24 novel analysis involving squares to determine how much of the search occurred in the near or
25 far vicinity of the target area. Note that such information would be difficult to obtain with the
26 conventional quadrant measure used in many past studies of the Morris Water Maze. Similarly,
27 total distance and distance from target could obscure accurate searches that tended to be
28 slightly more distant from the hidden target or more meandering but still “on target.” Thus, the
29 dependent measure used in this study involved the percent of time spent in a 2-D area
30 surrounding the hidden target, with such “windows” at different distances from the target.
31 Patients spent significantly less time searching closest to the hidden target compared to
32 controls, but more time in the distant areas compared to the controls, a finding true for both
33 immediate and delayed testing. Together, these findings support the idea that hippocampal
34 lesions impair the precision of representations for context within the hippocampus, but that such
35 patients can still perform search strategies (allocentric) that are appropriate and partially
36 accurate for the task.
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41 These studies converge in showing the importance of considering precision when
42 examining the role of the hippocampus in episodic memory, working memory and perception.
43 We believe that many of the inconsistencies reported in prior studies regarding whether the
44 hippocampus is or is not involved in different long term, working memory, and perceptual tasks
45 can be explained by the extent to which the tasks requires high precision representations. The
46 results also highlight the fact that precision of both the item information and the context
47 information can be critical. For example, the navigation and the object-location working memory
48 results discussed above indicate that the hippocampus is particularly important in supporting
49 memory for precise contextual information, whereas the object-color working memory results
50 suggest that the hippocampus is important in supporting precise item information.
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56 **The neural basis of precision**

57 Somewhat unlike the operation of binding of item and context, precision refers to the
58 quality of a representation that would appear to be shared across many different brain networks
59 and regions (Cowell, et al., 2019). We can readily talk about the idea of precision, for example,
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4 in the sensory domain. When we perceive a scene, this necessitates some form of
5 representation within primary visual cortex. If we hear a sound and remember it, this requires
6 some form of representation within primary auditory cortex. Importantly, we would typically think
7 of such representations of varying precision, which will depend on factors like how well we
8 fixated the item on our retina or how the sound waves hit our cochlea, as well as attentional
9 factors related to encoding the stimulus. For example, a patient with a medial temporal lobe
10 lesion might still be expected to have a fairly precise representation of different pitches as part
11 of language provided by auditory cortex, even if their ability to effectively bind such information
12 in memory might be impaired.
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15 In fact, it is probably reasonable to think about precision as a phenomenon that would be
16 important to representation in many different brain areas. The extent to which we can recognize
17 a face likely depends on its resolution/dimensionality in brain areas central to this function.
18 Because we can think of the hippocampus as a convergence zone, it likely receives much of
19 this information through interactions and input from both primary sensory and secondary/tertiary
20 association areas. The question then is that given that the hippocampus would not appear
21 directly involved in perception of the stimulus, why would lesions to this area affect perception?
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24 As we have suggested, precision is likely a phenomenon supported by many different
25 brain regions, each of which may contribute certain dimensions (e.g., visual cortex) but together
26 which interact to produce what we think of as an aggregate on-line representation of the current
27 context/item. In this way, hippocampal activity, although a small part of a much larger sum,
28 contributes overall to the precision of the representation. In the case of space, this is relatively
29 easy to see at the neural level. Place cell activity, from which the location of an animal can be
30 partially decoded (Jensen & Lisman, 2000; Wilson & McNaughton, 1993), could contribute to
31 representations of spatial context. One example would be place cells changing with temporal
32 and other task related variables, thereby creating a dynamic form of contextual representation of
33 varying precision (Shapiro & Eichenbaum, 1999; Wood, Dudchenko, Robitsek, & Eichenbaum,
34 2000). In a similar vein, the distributed nature of time cells within the hippocampus (Kraus, et
35 al., 2013), which also exist in other brain structures (Buhusi & Meck, 2005), would likely
36 contribute to the overall resolution of a representation for time.
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39 How would hippocampal neural responses relate to the issue of item representation,
40 which might appear to be the case in the Koen et al study? Single neuron studies in the human
41 hippocampus have also identified item responses, like those to famous actors and animals
42 (Kreiman, Koch, & Fried, 2000; Quiroga, Reddy, Koch, & Fried, 2007; Quiroga, Reddy, Kreiman,
43 Koch, & Fried, 2005) and these would also be likely to contribute to the overall precision of any
44 representation for an item. Notably, such cells responded to concepts (Jennifer Aniston) rather
45 than specific instantiations of the concepts (such as a 90 degree or 180 degree oriented
46 Jennifer Aniston). The tasks themselves in these studies, however, did not involve detection of
47 such differences and rather questions related to whether the object was a house or not. Given
48 that other single neuron studies have suggested firing rate differences for different targets
49 (Wixted, et al., 2014) and conjunctive responses related to goals, landmarks, and locations
50 (Ekstrom, et al., 2003), it seems likely that tasks that require such “precise” types of neural
51 coding would also demonstrate such capacities in the human hippocampus.
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54 It seems surprising, however, to attribute a brain region like the hippocampus to a
55 function in perception, which is more often relegated to brain areas like primary visual cortex.
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4 As Tulving noted, though, some aspects of cognition are likely shared by many if not all brain
5 regions. In this way, we believe that the overall precision of a representation in perception and
6 memory emerges from the interactions of numerous areas across the brain. The critical role of
7 the hippocampus would be in linking the representation between other brain areas more directly
8 involved in perception, such as primary visual cortex, auditory cortex, and multimodal areas like
9 fusiform gyrus. In this way, simpler forms of representation would certainly be possible with a
10 lesioned hippocampus but would be impaired in terms of how well such representations were
11 overall integrated across domains.
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14 Why, however, would we need such representations across the brain? For one,
15 redundancy is almost certainly important to something as fundamental as perception and having
16 many processing modules that can contribute would overall increase one's ability to "max out"
17 on this important function. In addition, almost all brain regions would require some form of item
18 representation in order to perform more specific computations. Without a representation of a
19 face, there can be no memory for the face, and thus in the process of receiving the input for a
20 face, the hippocampus could also be contributing to the perception of it as well via distributed
21 interactions. Finally, as we argued above, the hippocampus, unlike parts of neocortex, would
22 be critical in linking these multimodal and disparate representations together via functional
23 interactions. For examples of such interactions between working memory and perception,
24 please see Teng and Kravitz (2019); for examples of such interactions between visual cortex
25 and the hippocampus, please see: Hindy, et al. (2016).
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29 We note that this conception of precision as a distributed phenomenon shared by many
30 different brain regions, with the hippocampus as one of many different "cogs" in this function yet
31 serving a linking function, goes against classic conceptions of hierarchical processing (Kravitz,
32 Saleem, Baker, Ungerleider, & Mishkin, 2013; Ungerleider & Mishkin, 1982). The idea of parallel
33 processing amongst brain regions, even those who appear to serve "deeper" visual functions,
34 however, is gaining increasing traction in the fields of perception and attention. For example,
35 visual perception, rather than preceding hierarchically behaviorally, shows several instances in
36 which some steps, like figure ground segregation, occur after object perception (Peterson, 1994;
37 Peterson & Gibson, 1994). Similarly, neural accounts of attention increasingly assume
38 distributed roles across multiple brain regions such that no one brain primarily modulates or
39 controls attention and instead, this emerges across interactions across many different "nodes"
40 (Shipp, 2004). Together, these ideas suggest that perception relies on the interactions of
41 multiple brain regions, many of which may share similar neural architecture involved in
42 representing aspects of context or items.
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45 46 47 48 **Novel explanatory and predictive power**

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50 We hope that our proposal here regarding episodic memory and hippocampal
51 involvement in memory and beyond will be helpful in generating new experiments.
52 Theoretically, we think the somewhat ubiquitous role of the hippocampus in areas outside of
53 memory has remained a bit of a puzzle, and classic theories of declarative memory do not have
54 a clear explanation of how this could be so (Squire, 1992; Squire, Stark, & Clark, 2004). Yet,
55 the evidence that hippocampal lesions impact perception, working memory, and even language
56 function, is considerable (Barensse, et al., 2007; Borders, Aly, Parks, & Yonelinas, 2017;
57 Graham, Barensse, & Lee, 2010; Konkel, Warren, Duff, Tranel, & Cohen, 2008; D. E. Warren,
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4 Duff, Jensen, Tranel, & Cohen, 2012; Warren, Duff, Tranel, & Cohen, 2010; D. E. Warren, et al.,
5 2011). This suggests that the hippocampus cannot be a module exclusively dedicated to
6 episodic memory. By casting hippocampus as contributing to representational precision as one
7 of many different players in the brain, and such on-line representation emerging through
8 dynamic interactions across many different brain regions, our model helps solve the puzzle of
9 how the hippocampus can play necessary, although perhaps more minor roles in areas outside
10 of episodic memory.
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13 Yet, the fundamental role of the hippocampus in episodic memory is undeniable and
14 bolstered by decades of work on the topic. By casting item-context binding as a primary role of
15 the hippocampus, with a few other areas (like the core recollection network) also contributing,
16 our model is consistent with this long tradition arguing for the centrality of medial temporal lobes
17 to amnesia. At the same time, by suggesting that areas of the core recollection network also
18 play necessary (and possibly non-additive roles) in episodic memory, our model helps solve
19 another potential puzzle regarding medial temporal lobe lesions. Past work in memory research
20 indicates that although damage to the hippocampus severely impairs episodic memory
21 encoding and retrieval (Corkin, 1984; Rempel-Clower, Zola, Squire, & Amaral, 1996; Scoville &
22 Milner, 1957; Yonelinas, et al., 1998), performance is rarely at chance in such patients,
23 suggesting some intact function (Gold, et al., 2006; Helmstaedter, Grunwald, Lehnertz,
24 Gleissner, & Elger, 1997; Zola-Morgan, Squire, & Ramus, 1994). While this could be due to
25 residual hippocampal tissue, we also think that compensation is another viable alternative that
26 our model provides for. According to this idea, assuming that other brain areas within the core
27 recollection network play important roles in binding, it could be that such regions can partially
28 compensate for lost function in the hippocampus, particularly if their computational role is
29 distributed and non-additive.
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32 Thus, our model provides for key yet untested predictions. Following hippocampal
33 lesions, we predict that level of impairment behaviorally should be a function of demands on
34 both item-context binding and representational precision. Thus, there may be cases in which
35 simple bindings are possible but precision is impaired, and vice versa, depending on the extent
36 to which the two must work in tandem (Yonelinas, 2013). In addition, we expect that, over time
37 following a lesion to the hippocampus, other brain areas within the core recollection network
38 may be able to compensate for lost binding function. As one example of this, a recent
39 manuscript by Froudust-Walsh, et al. (2018) found that hippocampal lesions in non-human
40 primates result in degradation amongst connected and interacting brain areas like precuneus
41 and parts of prefrontal cortex shortly after the lesion. Interestingly, however, over time these
42 same areas also increased connectivity with each other, suggesting changes that could relate to
43 neural compensation. Similarly, a recent study by Argyropoulos, et al. (2019) suggested that
44 functional connectivity patterns within areas of the core recollection network explain greater
45 variance in delayed memory performance in amnesiacs than gray matter loss within the
46 hippocampus. As one possible area of future investigation, the converse approach of what we
47 typically do with episodic memory and patients with medial temporal lobe damage could help
48 resolve some of the issues discussed in this manuscript. Specifically, identifying patients with
49 complete episodic memory loss and then determining their patterns of brain damage could help
50 resolve the extent to which binding functions are distributed across the core recollection network
51 and how such lesions also affect precision.
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5 **Conclusion**
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8 We have elucidated on the important concept of representational precision here to
9 attempt to explain both the role of the hippocampus in item-context bindings and its
10 contributions to representation more generally. The first area we explored, item-context binding,
11 is widely recognized as important to episodic memory in particular and involves associating a
12 unique context with an item representation. We suggest here that binding relies primarily on the
13 hippocampus, with other brain regions within the core recollection network also playing
14 necessary, but still unclear roles. Precision, in contrast, relates to both the resolution and
15 dimensionality of a representation and helps predict the extent to which a brain region like the
16 hippocampus will be necessary for cognition outside of episodic memory. Here, we conceive of
17 precision as important to both item and contextual representation and something that will tend to
18 be distributed across the brain. In this way, precision will emerge from interactions of shared
19 neural machinery across many different brain regions. Thus, lesions to almost any “cog” within
20 this larger machinery will impair the precision of such a representation, although lesions to the
21 recollection network would be needed to impair binding. By considering both binding (as an
22 operation) and precision (as related to the resolution and dimensionality of a representation),
23 these two aspects of can help better explain both lesion, behavioral, and fMRI findings related to
24 memory and perception.
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Figure 1: Precision in context representations

Four different possibilities for precision. Top left: high-resolution and high-dimensional representations, as shown both by the high-resolution image (matrix) representing the spatial environment and the principal components breakdown (inset), which indicates relatively high dimensionality (several components explaining significant variance). In contrast, as shown on the top right, the matrix is the same size (resolution) but is blurred and thus of lower dimensionality. On the bottom left, the same image but in black and white is of lower resolution but comparable dimensionality to the original image. Finally, a low-resolution, low dimension image involves a blurred version of the black and white image.

Figure 2: Comparison of metric and topological representations.

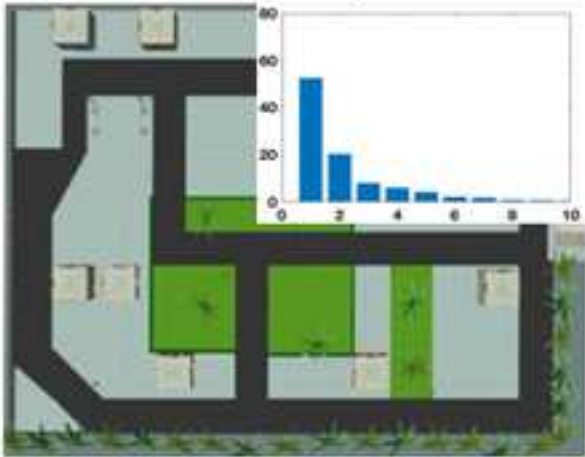
Top panel shows the original spatial context the participant learned. A metric representation involves the same physical arrangements of landmarks (A-G), preserving their spacing. A topological representation involves preserving the relative positions of the landmarks. Note that both metric and topological representations are similar dimensionality and resolution here although the topological representation would appear to involve less need for irrelevant information.

Figure 3: Empirical work supporting the role of the hippocampus in precision

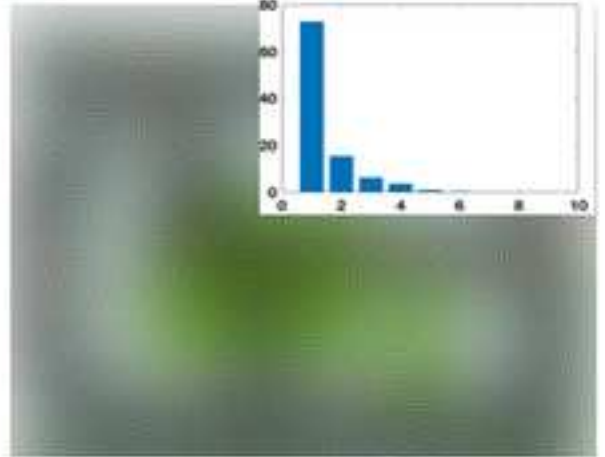
A. Aly et al. showed that hippocampal lesion patients, compared to controls, showed decrements in strength-based but not state-based perceptual judgments. Example image shows a strength-based difference between two scenes. B. Kolarik et al. showed that hippocampal lesion patients, compared to controls, showed decrements in the precision with which they searched for a hidden location in a virtual environment. Example VR image shows different precision windows surrounding a memorized hidden location. Asterisks indicate significant differences between patients and controls

Figure 1
[Click here to download high resolution image](#)

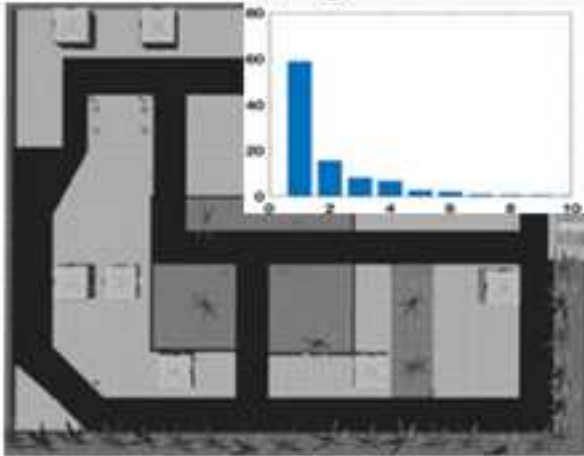
High-resolution, high-dimension



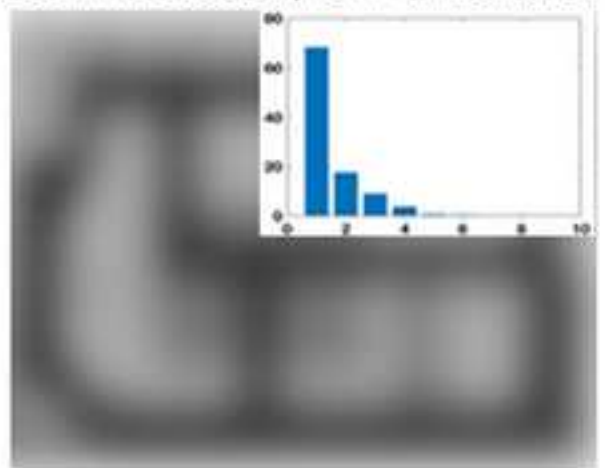
High-resolution, low-dimension



Low-resolution, high-dimension



Low-resolution, low-dimension



Original image



Figure 2
[Click here to download high resolution image](#)

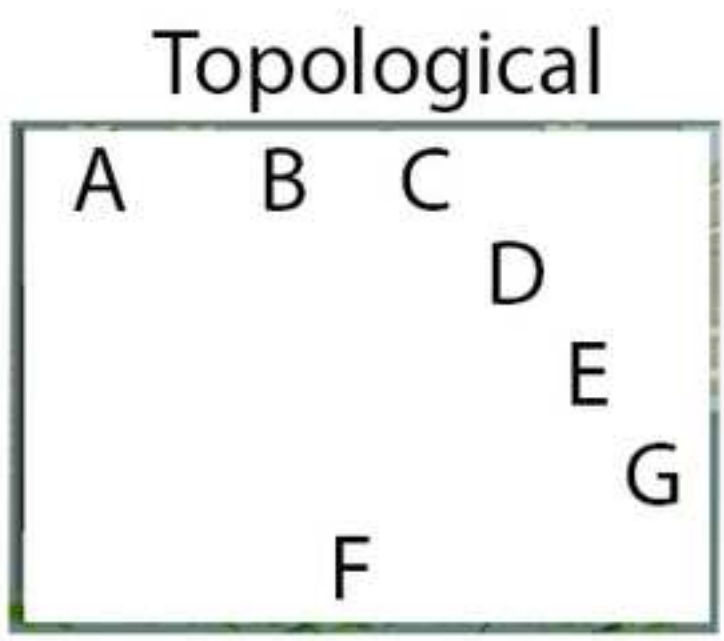
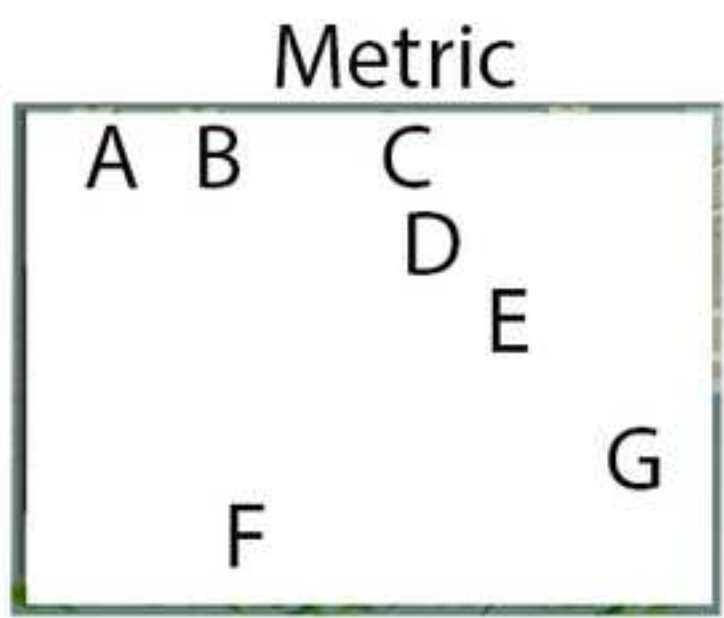
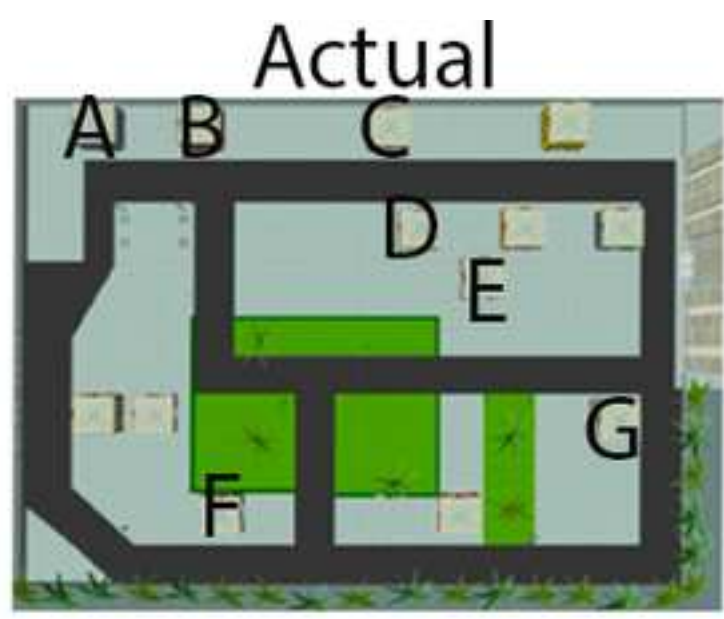


Figure 3

[Click here to download Figure: Figure3.pdf](#)



Are the images the same or different?

B.

