Neuroscience and Biobehavioral Reviews 167 (2024) 105934

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Context in memory is reconstructed, not encoded

Alexander Easton[a,*], Aidan J. Horner[b,c], Simon J. James[d], Jeremy Kendal[e], John Sutton[f,g], James A. Ainge[h]

[a] Department of Psychology, Durham University, UK
[b] Department of Psychology, University of York, UK
[c] York Biomedical Research Institute, University of York, UK
[d] Department of English Studies, Durham University, UK
[e] Department of Anthropology, Durham University, UK
[f] Department of Philosophy, University of Stirling, UK
[g] Centre for the Sciences of Place and Memory, University of Stirling, UK
[h] School of Psychology & Neuroscience, University of St Andrews, UK

ARTICLE INFO

Keywords:
Context
Episodic memory
Hippocampus

ABSTRACT

Context has long been regarded as an important element of long-term memory, and episodic memory in particular. The ability to remember not only the object or focus of a memory but also contextual details allow us to reconstruct integrated representations of events. However, despite its prevalence in the memory literature, context remains difficult to define and identify, with different studies using context to refer to different sets of stimuli or concepts. These varying definitions of context have not prevented it from being a key element of many models of memory. Within these models, context is usually explicitly encoded as an element of an event and processed through different neural pathways to other elements of the event, such as objects. Here we challenge the notion that context in memory is encoded. We offer an alternative where context in memory takes a variety of forms depending on the question being asked. We propose events are simply encoded, but the focus of retrieval (object) and context are not defined until recall.

"For me, context is the key – from that comes the understanding of everything" Kenneth Noland.

For many years, it's been clear that context has a critical role in long-term memory and many studies have explicitly examined the role of context in memory processes. Retrieval of memory is greater when the context at the point of encoding matches the context at the point of retrieval, whether that's a physical (e.g. on land or underwater) context (e.g. Godden and Baddeley, 1975) or a physiological state (e.g. Goodwin et al., 1969). Fear is strongly associated with context, with fear inducing stimuli having a particular effect within a context in which the fear has been experienced (e.g. Maren, 2001). When considering episodic memory, one might discuss the ability to retrieve incidental contextual information (e.g. Yim et al., 2013). In all these cases, context is a central part of either the memory itself or the retrieval of that memory.

Despite its clear role in memory, the task of defining a context is challenging. What distinguishes contexts from what we might call objects within the same memory? For episodic memory where an event is being remembered, is context merely the background, irrelevant material, and if so how do we know what's irrelevant until we need to retrieve the memory? Is it a particular type of input? For example, whilst spatial information has been argued to be a critical element of context within a memory (e.g. Burgess et al., 2001), it can clearly also be a non-contextual part of the memory, i.e. spatial information can also be the object or focus that we are remembering. Definitions of context are not confined to one domain, such as spatial information. Temporal information is often also considered a contextual cue (e.g. Bouton, 1993), alongside emotion (e.g. Kim et al., 2013) and many other individual features of an event or experience. It might be thought that there are even equivalents to perceptual mechanisms when defining context. In visual perception our visual system uses environmental and perceptual cues to differentiate object from background. Might similar mechanisms be at play in memory? It seems unlikely. Such figure/background distinctions in visual processing give rise to distinct visual illusions, such as the face or vases illusion. In this case either faces or vases can be seen at any one moment, but not both at once. One is background, one is object. There are, to our knowledge, no similar examples in memory for

---

* Correspondence to: Department of Psychology, Durham University, Durham DH1 3LE, UK.
E-mail address: alexander.easton@durham.ac.uk (A. Easton).

https://doi.org/10.1016/j.neubiorev.2024.105934
Received 25 July 2024; Received in revised form 14 October 2024; Accepted 26 October 2024

mnemonic illusions that would occur from similar processes.

Various attempts have been made to operationalise contexts (e.g. Stark et al., 2018) but there are always exceptions to such generalisations. There have also been attempts to define different systems for different types of context (e.g. Rudy, 2009), sometimes within specific species or for specific tasks (such as fear conditioning). It is important, then, to consider the form 'context' has taken across the memory literature. The reference to a vague, poorly defined, singular 'context' in the literature assumes that all contexts used in different tasks are the same, and all use the same cognitive mechanisms. However, if these contexts can take so many different forms, we can reasonably ask what they are contexts for. What is the putative stable focus of memory to which contexts attach?

Here we argue that context is confusing and difficult to define because it is typically considered something identifiable at the point of encoding. In contrast, we propose that 'context', like other elements of long-term memory, is reconstructed as part of recollection. Indeed, context makes no sense until the point of recall. Once the focus of a memory has been determined, then the associated contextual information can be identified; but not until this point.

1. Context and place cells

Let us begin with one area in which contextual control of memory is well studied; place cells in rodents. There is much evidence that place cells within the hippocampus show different activity patterns in different contexts (e.g. Anderson and Jeffery, 2003; Hayman et al., 2003; Leutgeb et al., 2005; Smith and Mizumori, 2006a; Ventura et al., 2024). In its most straightforward operationalisation, context is defined in these studies as different shaped chambers that are experienced by the animal in the same physical location (i.e. the chamber is in the same position in the room but the context is changed by inserting new walls and floors). Walls and floors of the chambers are changed or manipulated to create different shaped contexts within the same spatial location. In these studies, populations of place cells can combine to represent a map of the context, which re-maps to the other context. This remapping can take various forms but the population of cells can encode that the context of the environment has changed. As both 'contexts' are in the same physical location in the room, the assumption is that the only difference between them is the shape of the environment, meaning that this difference is the contextual cue controlling the place cell's activity.

Even within the place cell literature in rodents, however, this straightforward environmental shape is not the only context known to control place cell representations. Others, for example, have used a combination of colour, texture, and spatial location to define context (e.g. Komorowski et al., 2009). Place cells remain able to use these non-shape based differences to encode items within each context differently. Place cells are also able to encode items within different contexts when those contexts are defined by the temporal sequence of events (Manns et al., 2007), or even when the contexts are defined by the task demands, such as the location of a reward within the environment (Smith and Mizumori, 2006b, Ainge et al., 2007a, Ainge et al., 2012).

In each of these cases, place cells' activity is reported as being mediated by context, but the nature of each context is very different. In comparing the place cell activity across these studies, an implicit assumption is made that in each case 'context' is equivalent, i.e. the notion of context generalises across these studies, and is assumed to have the same effects on memory, and on the neural processes at study. It is possible, however, that whilst each has a superficially similar effect on behaviour, the real nature of context is different between these studies.

Whatever the right, or wrong, of this generalisation, it has a significant impact on our ability to define and operationalise what it is that we mean by 'context'. It also suggests that if all these types of context are equivalent (in that they have the same impact on the mediation of memory) then context is a broad and difficult to define concept, made up both of specific sensory (Wood et al., 1999) and spatial inputs (Muller and Kubie, 1987), but also controlled by task demands (Wood et al., 2000, Ainge et al., 2007b, Dupret et al., 2010), emotion (Moita et al., 2003), temporal changes (Mankin et al., 2012; Mau et al., 2018) and other more difficult to elucidate changes to the environment (Alvernhe et al., 2008, Vandrey et al., 2021).

1.1. *The complexity of context*

This complexity of context is dealt with in part by influential context drift models such as the Temporal Context Model (TCM; Howard and Kahana, 2002, Estes, 1950) or the Contextual Binding Theory (Yonelinas et al., 2019) which propose context to be an ever-changing group of inputs with variation in the specifics of the context across time. Context might then be constituted of temporal information, physiological and emotional states, spatial environment, lighting, etc. The context for a given memory will be the combination of all these smaller elements, some of which will be similar across memories, some of which will be much more unstable. For each episodic memory, however, the combination of these component elements will be unique and provide a specific and unique context for that memory.

Although these models deal with the complexity of elements that might sum to form a specific context, there are challenges that remain. Let's once again consider the place cell literature in rodents. In the simplest form of context manipulation, where the environment's shape is changed, it mediates the place field of the cell. A study by Wills et al. (2005) examined how two different shaped environments determined contextual control of the place field. With one square and one circular environment, they observed the typical finding that the place field in the square was stable, and the one in the circle was stable, but that they differed from each other. By adding additional shapes (e.g. an octagonal box) which shared properties with both the circular and square environments, they showed that place fields switched abruptly from square to circular representations (and vice versa) and did not slowly adjust as the arena shape morphed between these two extremes. In essence, the cell's activity was as if there were only two environment shapes (context). When an ambiguous environment shape was presented, the cell categorised it as one or other context, and not as some new and distinctive context; an effect also seen in humans (Steemers et al., 2016).

Some other studies (e.g. Leutgeb et al., 2005) have shown that place cells can represent the ambiguous 'morphed' environment shapes. In humans too, fMRI studies reveal environment specific codes in the hippocampus (e.g. Kyle et al., 2015), and differences in hippocampal subregions when defining distinct but highly similar environments (Stokes et al., 2015). There is clear evidence, then, that there is nuanced control of memory by the shape of the environment, and yet in some subregions and in some experimental cases it remains that the control of memory by these environments is more categorical r. Existing models of contextual control of memory (such as context drift models) are poor at being able to explain how environmental stimuli can be both differentiated and generalised. To a significant extent the problem can be explained by needing to encode context in both this nuanced and categorical way. What, however, if context did not need to be encoded at all?

1.2. *Does context need to be encoded at all?*

Think about the use of context in our own everyday episodic memories. Consider a memory from summer 2022. You might now recall that memory as 'just before Queen Elizabeth II died'. That provides a temporal context for the memory. However, at the moment of the event being remembered you did not encode the memory as being 'just before Queen Elizabeth II died' as you didn't know when she would die. That is a semantic label applied to the context after the point of encoding, and yet it becomes a consistent and useful context for the memory. Whilst there may be complexities in this example that reflect human experience, the key point is that for this example, context is not determined at the point of encoding. This key point can be true of non-human species too. A rat might recall the last time it was placed in a circular box, without at that event knowing it would be the last occasion. If we consider context to be a way of allowing us to separate events from one another in our memory (e.g. Gaffan, 1994), then this can sometimes be in ways we only understand after the event.

Of course, elements such as perceptual, emotional, social and even mnemonic factors will be encoded at this time, and will to a great extent interact (different people will encode similar events around the Queen's death differently depending on whether or not they had a particular relationship with her). However, none of these elements of the event need to be explicitly encoded as the context of the memory. Sometimes these individual elements might be extremely salient. Someone particularly close to the Queen may have an overwhelming sense of sadness at her passing, and we might think this sadness is encoded as an emotional context to the memory. But we should be careful not to endow certain elements of the memory (such as sadness) with special properties (such as contextual control of memory) when salience will suffice. Highly salient information will be recalled easily with the memory, and certain types of information (like sadness to a death) will be unlikely to be the focus of the question, meaning they often appear as context (ever present and never the object of a memory). That does not, however, mean we should automatically consider them to be an encoded context without good evidence.

Our claim that context is not encoded at the moment of the event may appear controversial given prevailing assumptions. Yet there are other reasons to suggest context in episodic memory is established when the event is being remembered. Temporal information has long been regarded as key to episodic memory (see Tulving, 1983, 2002), yet what form does that temporal information take? We know that episodic memories are not 'time stamped' in the brain (Friedman, 2007), but rather where knowledge of an exact time occurs it often is generated through semantic cues (e.g. it was summer 2022 because it was just before Queen Elizabeth died). In contrast, other forms of temporal information in episodic memory include temporal order and relative recency (e.g. Fouquet et al., 2010; Roberts et al., 2008; Kuruvilla et al., 2020). For relative recency we are often able to consider how long ago something occurred through a judgement of memory trace strength, i.e. the more vivid and strong a memory appears the more likely it is to have happened recently. Such metacognitive assessments may be vital at retrieval in assigning certain features of an event representation as 'context' (Mahr et al., 2023; Perrin et al., 2020; Perrin and Sant'Anna, 2022).

We are once again faced with a context (in this case a temporal context for an episodic memory) that can only be understood at the point of recall, not at the point of encoding. How long ago something happened cannot be encoded with the memory as there is no way of knowing when recall will occur. Instead, it can only be assessed at the point of recall. There is some doubt about whether how long ago something happened behaves in the same way as other (visuo-tactile) contexts in episodic memory recall (e.g. Davis et al., 2013; Easton et al., 2012; Roberts et al., 2008; Kuruvilla et al., 2020), but there is little doubt that in everyday episodic memory this judgment of how long ago a memory occurred is a frequent element of the context of an event.

1.3. Contexts and objects within event memory

To fully understand the nature of context in this way, as something that is not encoded, we need to understand what a context is within an event. Imagine an event where you go to the cinema after work, with a friend. You sit in the middle row on an aisle, and your friend sits next to you. During the film they spill some of their drink on you. One challenge of understanding the nature of context in this episodic memory is that most elements of this memory can be the focus or object of the memory, and most elements can be part of the context. If you were to be asked 'when was the last time someone spilt a drink on you?' you would be able to recall this event. However, the precise cinema, the film etc. would be part of the event being remembered, but not the focus of the question being asked. In contrast if you were to be asked 'what was the last film you saw at that particular cinema?' you would be able to answer with the name of the film, but who you were with, and that a drink was spilt are now not directly relevant to the target of retrieval. Critically, the context differs depending on the question being asked, and therefore only at recall can the context for the memory be defined (i.e. only once the question has been asked can one determine the background, or contextual, information). One might ask, then, whether in an event which is rich in detail and where you recall the event for a specific purpose, is the context of the event simply the remaining detail within the event? Even physiological responses such as heart rate, which are often considered elements of context (as per the contextual binding theory of episodic memory) can become the focus of the question 'when was the last time your heart raced?', perhaps with the answer it was when you had a cold drink poured over you unexpectedly.

From this perspective, there is little within the detail encoded of an event that cannot be a focus of the memory, in which case is it even sensible to ask what the context is within the memory? In discussing context of a memory are we simply referring to elements of the event which are not directly relevant to the reason for recall? Does this help us to understand why contexts are not helpful to be defined at the time of encoding? We don't know what question will be asked of the memory later; indeed, this flexibility has been suggested to be a critical element of episodic memory (Clayton et al., 2001).

Nonetheless, some highly influential models of memory do consider context to be identified at the point of encoding and treated differently within the processing of a memory, for example, the Binding of Item and Context (BIC) model (Diana et al., 2007). This BIC model explicitly considers context something that should be encoded, and retrieved, by the parahippocampal cortex, whilst the hippocampus plays a specific role in associating context and item information to support recollection. Models like this, then, require context to be identified when the event occurs, encoded in the parahippocampal cortex and kept distinct from item information in the perirhinal cortex, meaning items and context are defined as such at encoding. Such models require there to be a focus of the event, which is encoded as an item, and (inline with the drifting context models; Howard and Kahana, 2002; Yonelinas et al., 2019) other ever-changing elements of the event (internal and external to the individual) are encoded as context. Yet these ever changing elements of the event that are encoded as context must also generalise to ensure whole events have a single context. For example, heart rate might change slightly during a conversation, but this is generalised to allow the conversation to be seen as one event. One might be able to argue that retrieval of the memory from different cues (when did you last go to the cinema, or when did you last get a drink poured over you) can be created from the association between this event's context and the items within it, but we once again face the dilemma of defining what makes something a context, and what makes something an item.

A series of studies in rodents also challenges that concept that context is encoded separately from other elements of an event memory. Eacott and Norman (Eacott and Norman, 2004a; Norman and Eacott, 2004, 2005) ran a series of studies in which rats were assessed for their memory of combinations of features. They were tested either on their recognition of an object (in a single context), their recognition of an object within a particular context, their memory for an object in a particular location, or their memory for a particular object in a particular location within a particular context. In these studies, context was defined as the interior walls and floors of an arena, which are known to offer contextual control of place cells (e.g. Anderson and Jeffery, 2003). Eacott & Norman demonstrated that lesions of the perirhinal cortex impaired recognition of objects, whilst lesions of postrhinal cortex (the rodent analogue of parahippocampal cortex) impaired recognition of objects in particular contexts (Norman and Eacott, 2005), all supportive of the proposal that context and items/objects are processed through distinct processes and regions. However, the critical finding was that lesions of the postrhinal cortex did not impair recognition of objects in particular locations within particular contexts, although disruption of the hippocampus through fornix lesion did (Eacott and Gaffan, 2005; Eacott and Norman, 2004b). Critically, then, whilst postrhinal cortex appears to be critical for the recognition of context in one task (object-context), it is not critical for a similar, more complex task (object-place-context task). This difference in postrhinal involvement is despite context being a critical element of both memory tasks. If context really is encoded as a distinct part of the memory, and processed through this postrhinal pathway separately to other information, how is it that only some memories using context rely on this system?

This is not an isolated incident in the literature with many studies finding roles for different parts of the memory network in processing context. As well as postrhinal cortex (Gastelum et al., 2012; Bucci et al., 2021), other studies have reported that perirhinal cortex (Barker and Warburton, 2020), lateral entorhinal cortex (Wilson et al., 2013a,b; Vandrey et al., 2020; Persson et al., 2021), medial entorhinal cortex (Hunsaker et al., 2013) and the hippocampus (Mumby et al., 2002; 2010) are all critically important for context-dependent memory. This argues against context as a singular concept that is assigned at encoding and is much more consistent with context being any number of cues that best disambiguate a memory from other similar memories at retrieval, perhaps requiring the interaction of multiple brain regions to generate it. The diversity of brain regions suggested to process context would likely result from the wide range of stimuli and concepts suggested to make up context. Different brain regions will receive different inputs that define the type of information they process and so the choice of context definition will then affect which brain area/network supports that context specific task.

To this end, perhaps the most valuable step the field can take is to more clearly define the conditions of experiments. Rather than using terms like ‘context’ to refer to any background element of the memory which is not the focus of the task, clarity and comparability between studies would be greatly improved by careful description of the experimental condition and all likely salient elements of stimuli.

1.4. Implications and Future Directions

All the evidence supports the view that context is not a single feature of an event that can be separated from the object or spatial information and encoded and processed separately (at least at the point of encoding). Perhaps critical to a new understanding of context in memory is the realisation, as in the cinema example above, that context makes sense only at the point of recollection. We don’t know it was our most recent trip to the cinema until the question is asked and we can appraise that temporal context. We don’t know something happened just before the drink was spilled on us until after the drink was spilled on us. However, once the question is asked then the nature of the context becomes obvious. In Eacott and Norman’s rat studies too it seems the nature of the question asked (the task) determines the way in which context is processed. We don’t know what is important for a future memory at the time of encoding, so how can we be sure what aspects of the event will be incidental context? In these cases, context only makes sense at the point of retrieval. The action of recall has a directed purpose; to answer a question, to drive a behavioural choice, to select an appropriate action etc. This act of recall, then, is the moment at which the object of the memory and the contextual elements of the memory are decided.

In models of memory, such as BIC (Diana et al., 2007) object/item elements of a memory are associated with context. This is the basis by which context controls retrieval. The association of an item with its context means that in retrieving the memory in the same context as it was encoded then the retrieval of the item is made easier by its association with the context that is present. However, what if all elements of a memory were instead encoded merely as elements of a memory; undifferentiated? The implications of context being a feature of retrieval rather than encoding can be understood in considering the impact on existing knowledge. In Godden & Baddeley’s famous diving experiment (Godden and Baddeley, 1975), participants were better able to recall a word list learned on land when tested on land, and one learned under water when tested under water. In our proposal, participants wouldn’t need to encode ‘underwater’ as a context. Instead, the word list being remembered is encoded, as is being underwater, as is the change in heart rate, temperature, breathing style and so on that comes with being underwater rather than on land. Here, rather than using these constant changes in elements of the environment to monitor changes in context (as in context drift models), they are instead merely each encoded as a separate and contingent element of the ongoing experience of the event. No one element is determined as the focus for future memory (unless we are aiming to specifically memorise something for recall in the future). At retrieval, then, each individual element of the event can act as a retrieval cue, giving improved retrieval of memory. The greater the match of the current environment to the environment when the event happened, the more precise each retrieval cue will be, generating greater success in the retrieval process. In this way, retrieval in the same context as one encoded generates better memory but not through any need for a separate representation of context at encoding. Instead, the context is the elements of the memory defined as incidental by the question. Our proposal offers other insights into this classic approach to context dependent memory. Would divers have been able to better discriminate two underwater events separated by the presence or absence of word list learning? We expect they would, given that no element of the event is itself a context, so the context-dependent memory benefit should be able to be provided by any similarities between conditions. Nonetheless, undoubtably there will be some cues or features of an event which accrue more strength and control of memory than others. Is attention critical to such modulation, or salience? It seems worthy to investigate the way in which attention at encoding might influence the nature of context at retrieval. We would predict that shifting attentional focus at encoding will have no discernable effect on the nature of context at retrieval although it may change the salience of different elements of the environment when asked about as the object of a memory.

If we instead turn our focus to work in animals and humans on differential activity in distinct brain regions for the processing of context, what happens if our methods shift towards asking about the same event in different ways, such as in our example of the drink being spilled in the cinema. Would different brain regions always respond to the context, whatever the context is, or would we begin to see differentiation in these regions for types of stimulus whether they are the object or the incidental background of a memory? Such findings would then allow us to question whether such differences are apparent at retrieval as well as, or instead of, encoding.

Our proposal might at first seem at odds with the well-established Event Boundary Theory (e.g. Radvansky, 2012, Zacks and Swallow, 2007). Here the segmenting of everyday life into distinctly encoded parts is aided by shifts in context (such as walking through a doorway). This may seem to imply that context and context changes have to play a part at encoding. However, our proposal here does not deny or challenge that things change over time. Our perspective, our internal feelings and thoughts, our position, or social environment etc all change constantly through the day. In our model these remain encoded, and therefore changes in the environment can allow events to be parsed from continual experience. In our cinema example, events might be bounded by the action of spilling the drink. The continuous experience has now been parsed as before and after the drink was spilt. That does not require the spilling of the drink to be ‘labelled’ as a context of the event at the time of encoding. Instead it might be simply that these boundaries provide convenient structure to the retrieval of memory, and can bound working memory processes, but do not need to be encoded as a context. After all, event boundaries can also be flexible. I might recall an event as being at the cinema, or as the lead up to the drink being spilt, or even that time with my friend at the cinema and the rest of the evening.

Boundaries seem, then, able to be flexible just like context, and to some extent the bounding of the event at recall might be structured around context determined by the question, rather than by perceptual, emotional, social or other changes in the environment at the point of encoding.

In essence, we propose that the context, like other elements of long-term memory, is defined and reconstructed at retrieval. There is no need for a precise representation of all elements of the encoding episode. Over time elements of certain contexts will form relatively fixed relationships that generalise across events. Diving underwater will always be related to wearing your scuba gear, temperature changes, breathing changes etc. Only changes from these expected values need to be noted. Retrieval of previous experiences during an event updates our knowledge of these relationships, and it is likely to be this updated knowledge that forms the context at retrieval later. Our knowledge of an event before the Queen dies is updated when the Queen dies and in future retrieval we now have a context that can be represented as ‘the time before the Queen died’ when such a context for memory made no sense at the point of encoding.

Acknowledgements

This paper is the result of work from the interdisciplinary Representing Memory project supported by Durham University’s Institute of Advanced Study (IAS). We also acknowledge the support of the Durham University IAS in awarding Fellowships to JA, AH & JS.

Data availability

No data was used for the research described in the article.

References

Ainge, J.A., van der Meer, M.A., Langston, R.F., Wood, E.R., 2007a. Exploring the role of context-dependent hippocampal activity in spatial alternation behavior. Hippocampus 17 (10), 988–1002. https://doi.org/10.1002/hipo.20301.

Ainge, J.A., Tamosiunaite, M., Woergoetter, F., Dudchenko, P.A., 2007b. Hippocampal CA1 place cells encode intended destination on a maze with multiple choice points. J. Neurosci. 27, 9769–9779. https://doi.org/10.1523/JNEUROSCI.2011-07.2007.

Ainge, J.A., Tamosiunaite, M., Wörgötter, F., Dudchenko, P.A., 2012. Hippocampal place cells encode intended destination, and not a discriminative stimulus, in a conditional T-maze task. Hippocampus 22, 534–543. https://doi.org/10.1002/hipo.20919.

Alvernhe, A., Van Cauter, T., Save, E., Poucet, B., 2008. Different CA1 and CA3 representations of novel routes in a shortcut situation. J. Neurosci. 28 (29), 7324–7333. https://doi.org/10.1523/JNEUROSCI.1909-08.2008.

Anderson, M.I., Jeffery, K.J., 2003. Heterogeneous modulation of place cell firing by changes in context. J. Neurosci. 23, 8827–8835.

Barker, G.R.I., Warburton, E.C., 2020. Putting objects in context: a prefrontal-hippocampal-perirhinal cortex network. Brain Neurosci. Adv. 4, 2398212820937621. https://doi.org/10.1177/2398212820937621.

Bouton, M.E., 1993. Context, time, and memory retrieval in the interference paradigms of Pavlovian learning. Psychol. Bull. 114 (1), 80–99. https://doi.org/10.1037/0033-2909.114.1.80.

Bucci, D.J., Phillips, R.G., Burwell, R.D., 2021. Contributions of postrhinal and perirhinal cortex to contextual information processing. Behav. Neurosci. 135 (3), 313–325. https://doi.org/10.1037/bne0000436.

Burgess, N., Becker, S., King, J.A., O’Keefe, J., 2001. Memory for events and their spatial context: models and experiments. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 356 (1413), 1493–1503. https://doi.org/10.1098/rstb.2001.0948.

Clayton, N.S., Griffiths, D.P., Emory, N.J., Dickinson, A., 2001. Elements of episodic-like memory in animals. Philos. Trans. R. Soc. Lond. B 356, 1483–1491.

Davis, K.E., Easton, A., Eacott, M.J., Gigg, J., 2013. Episodic-like memory for what-where-which occasion is selectively impaired in the 3xTgAD mouse model of Alzheimer’s disease. J. Alzheimer’S. Dis. 33 (3). https://doi.org/10.3233/JAD-2012-121543.

Diana, R.A., Yonelinas, A.P., Ranganath, C., 2007. Imaging recollection and familiarity in the medial temporal lobe: a three-component model. Trends Cogn. Sci. 11 (9), 379–386. https://doi.org/10.1016/j.tics.2007.08.001.

Dupret, D., O’Neill, J., Pleydell-Bouverie, B., Csicsvari, J., 2010. The reorganization and reactivation of hippocampal maps predict spatial memory performance. Nat. Neurosci. 13 (8), 995–1002. https://doi.org/10.1038/nn.2599.

Eacott, M.J., Gaffan, E.A., 2005. The roles of perirhinal cortex, postrhinal cortex, and the fornix in memory for objects, contexts, and events in the rat. Q. J. Exp. Psychol. B 58, 202–217.

Eacott, M.J., Norman, G., 2004a. Integrated memory for object, place, and context in rats: a possible model of episodic-like memory? J. Neurosci. 24 (8), 1948–1953.

Eacott, M.J., Norman, G., 2004b. Integrated memory for object, place and context in rats: a possible model of episodic-like memory. J. Neurosci. 24 (8), 1948–1953. https://doi.org/10.1523/JNEUROSCI.2975-03.2004.

Easton, A., Webster, L.A.D., Eacott, M.J., 2012. The episodic nature of episodic-like memories. Learn. Mem. 19 (4), 146–150. https://doi.org/10.1101/lm.025676.112.

Estes, 1950. Towards a statistical theory of learning. Psychol. Rev. 57 (2), 94–107.

Fouquet, C., Tobin, C., Rondi-Reig, L., 2010. A new approach for modeling episodic memory from rodents to humans: the temporal order memory. Behav. Brain Res. 215 (2), 172–179. https://doi.org/10.1016/j.bbr.2010.05.054.

Friedman, W.J., 2007. The meaning of “time” in episodic memory and mental time travel. Behav. Brain Sci. 30, 323.

Gaffan, D., 1994. Scene-specific memory for objects: a model of episodic memory impairment in monkeys with fornix transection. J. Cogn. Neurosci. 6, 305–320.

Gastelum, E.D., Guilhardi, P., Burwell, R.D., 2012. The effects of combined perirhinal and postrhinal damage on complex discrimination tasks. Hippocampus 22 (10), 2059–2067. https://doi.org/10.1002/hipo.22063.

Godden, D.R., Baddeley, A.D., 1975. Context-dependent memory in two natural environments: on land and underwater. Br. J. Psychol. 66 (3), 325–331.

Goodwin, D.W., Powell, B., Bremer, D., Hoine, H., Stern, J., 1969. Alcohol and recall: state-dependent effects in man. Science 163 (3873), 1358–1360.

Hayman, R.M.A., Chakraborty, S., Anderson, M.I., Jeffery, K.J., 2003. Context-specific acquisition of location discrimination by hippocampal place cells. Eur. J. Neurosci. 18 (10), 2825–2834. https://doi.org/10.1046/j.1460-9568.2003.03035.x.

Howard, M.W., Kahana, M.J., 2002. A distributed representation of temporal context. J. Math. Psychol. 46 (3), 269–299. https://doi.org/10.1006/jmps.2001.1388.

Hunsaker, M.R., Chen, V., Tran, G.T., Kesner, R.P., 2013. The medial and lateral entorhinal cortex both contribute to contextual and item recognition memory: a test of the binding of items and context model. Hippocampus 23 (5), 380–391. https://doi.org/10.1002/hipo.22097.

Kim, J.S.-C., Vossel, G., Gamer, M., 2013. Effects of emotional context on memory for details: the role of attention. PLoS ONE 8 (10), e77405. https://doi.org/10.1371/journal.pone.0077405.

Komorowski, R.W., Manns, J.R., Eichenbaum, H., 2009. Robust conjunctive item–place coding by hippocampal neurons parallels learning what happens where. J. Neurosci. 29 (31), 9918–9929. https://doi.org/10.1523/JNEUROSCI.1378-09.2009.

Kuruvilla, M.V., O’Connor, A.R., Ainge, J.A., 2020. Distance- rather than location-based temporal judgements are more accurate during episodic recall in a real-world task. Memory 28 (6), 783–794. https://doi.org/10.1080/09658211.2020.1783319.

Kyle, C.T., Stokes, J.D., Lieberman, J.S., Hassan, A.S., Ekstrom, A.D., 2015 Nov 27. Successful retrieval of competing spatial environments in humans involves hippocampal pattern separation mechanisms. Elife 4, e10499. https://doi.org/10.7554/eLife.10499.

Langston, R.F., Wood, E.R., 2010. Associative recognition and the hippocampus: differential effects of hippocampal lesions on object-place, object-context and object-place-context memory. Hippocampus 20 (10), 1139–1153. https://doi.org/10.1002/hipo.20714.

Leutgeb, S., Leutgeb, J.K., Barnes, C.A., Moser, E.I., McNaughton, B.L., Moser, M.B., 2005. Independent codes for spatial and episodic memory in hippocampal neuronal ensembles. Science 309 (5734), 619–623. https://doi.org/10.1126/science.1114037.

Mahr, J.B., van Bergen, P., Sutton, J., Schacter, D.L., Heyes, C., 2023. Mnemicity: a cognitive gadget? Perspect. Psychol. Sci. 18 (5), 1160–1177. https://doi.org/10.1177/17456916221141352.

Mankin, E.A., Sparks, F.T., Slayyeh, B., Sutherland, R.J., Leutgeb, S., Leutgeb, J.K., 2012. Neuronal code for extended time in the hippocampus. Proc. Natl. Acad. Sci. 109 (47), 19462–19467. https://doi.org/10.1073/pnas.1214107109.

Manns, J.R., Howard, M.W., Eichenbaum, H., 2007. Gradual changes in hippocampal activity support remembering the order of events. Neuron 56 (3), 530–540. https://doi.org/10.1016/j.neuron.2007.08.017.

Maren, S., 2001. Neurobiology of Pavlovian fear conditioning. Annu. Rev. Neurosci. 897–931.

Mau, W., Sullivan, D.W., Kinsky, N.R., Hasselmo, M.E., Howard, M.W., Eichenbaum, H., 2018. The same hippocampal CA1 population simultaneously codes temporal information over multiple timescales. Curr. Biol. 28 (10), 1499–1508.e4. https://doi.org/10.1016/j.cub.2018.03.051.

Moita, M.A., Rosis, S., Zhou, Y., LeDoux, J.E., Blair, H.T., 2003. Hippocampal place cells acquire location-specific responses to the conditioned stimulus during auditory fear conditioning. Neuron 37 (3), 485–497. https://doi.org/10.1016/s0896-6273(03)00033-3.

Muller, R.U., Kubie, J.L., 1987. The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. J. Neurosci. 7 (7), 1951–1968. https://doi.org/10.1523/JNEUROSCI.07-07-01951.1987.

Mumby, D.G., Gaskin, S., Glenn, M.J., Schramek, T.E., Lehmann, H., 2002. Hippocampal damage and exploratory preferences in rats: memory for objects, places, and contexts. Learn Mem. 9 (2), 49–57. https://doi.org/10.1101/lm.41302.

Norman, G., Eacott, M.J., 2004. Impaired object recognition with increasing levels of feature ambiguity in rats with perirhinal cortex lesions. Behav. Brain Res. 148, 79–91.

Norman, G., Eacott, M.J., 2005. Dissociable effects of lesions to the perirhinal cortex and the postrhinal cortex on memory for context and objects in rats. Behav. Neurosci. 119 (2), 557–566. https://doi.org/10.1037/0735-7044.119.2.557.

Perrin, D., Michaelian, K., Sant’Anna, A., 2020. The phenomenology of remembering is an epistemic feeling. Front Psychol. 11, 1531. https://doi.org/10.3389/fpsyg.2020.01531.

Perrin, Denis, Sant'Anna, André, 2022. Episodic memory and the feeling of pastness: from intentionalism to metacognition. Synthese 200. https://doi.org/10.1007/s11229-022-03567-4.

Persson, B.M., Ambrozova, V., Duncan, S., Wood, E.R., O'Connor, A.R., Ainge, J.A., 2021. Lateral entorhinal cortex lesions impair odor-context associative memory in male rats. J. Neurosci. Res. 100, 1030–1046. https://doi.org/10.1002/jnr.25027.

Piterkin, P., Cole, E., Cossette, M.P., Gaskin, S., Mumby, D.G., 2008. A limited role for the hippocampus in the modulation of novel-object preference by contextual cues. Learn Mem. 15 (10), 785–791. https://doi.org/10.1101/lm.1035508.

Radvansky, G.A., 2012. Across the event horizon. Curr. Dir. Psychol. Sci. 21 (4), 269–272.

Roberts, W.A., Feeney, M.C., MacPherson, K., Petter, M., McMillan, N., Musolino, E., 2008. Episodic-like memory in rats: is it based on when or how long ago? Science 320 (5872), 113–115. https://doi.org/10.1126/science.1152709.

Rudy, J.W., 2009. Context representations, context functions, and the parahippocampal-hippocampal system. Sep 30 Learn Mem. 16 (10), 573–585. https://doi.org/10.1101/lm.1494409. PMID: 19794181; PMCID: PMC2769166.

Smith, D.M., Mizumori, S.J., 2006a. Hippocampal place cells, context, and episodic memory. Hippocampus 16, 716–729.

Smith, D.M., Mizumori, S.J.Y., 2006b. Learning-related development of context-specific neuronal responses to places and events: the hippocampal role in context processing. J. Neurosci. 26 (12), 3154–3163. https://doi.org/10.1523/JNEUROSCI.3234-05.2006.

Stark, S.M., Reagh, Z.M., Yassa, M.A., Stark, C.E.L., 2018. What's in a context? Cautions, limitations, and potential paths forward. Neurosci. Lett. 680, 77–87. https://doi.org/10.1016/j.neulet.2017.05.022.

Steemers, B., Vicente-Grabovestsky, A., Barry, C., Smulders, P., Schröder, T., Burgess, N., Doeller, C.F., 2016. Hippocampal attractor dynamics predict memory-based decision making. Curr. Biol. 26, 1750–1757. https://doi.org/10.1016/j.cub.2016.04.063.

Stokes, J., Kyle, C., Ekstrom, A.D., 2015. Complementary roles of human hippocampal subfields in differentiation and integreation of spatial context. J. Cog. Neurosci. 27, 546–559. https://doi.org/10.1162/jocn_a_00736.

Tulving, E., 1983. Elements of episodic memory. Oxford University Press.

Tulving, E., 2002. Episodic memory: from mind to brain. Annu. Rev. Psychol. 53, 1–25.

Vandrey, B., Duncan, S., Ainge, J.A., 2021. Object and object-memory representations across the proximodistal axis of CA1. Hippocampus 31 (8), 881–896. https://doi.org/10.1002/hipo.23331.

Vandrey, B., Garden, D.L.F., Ambrozova, V., McClure, C., Nolan, M.F., Ainge, J.A., 2020. Fan cells in layer 2 of the lateral entorhinal cortex are critical for episodic-like memory. Curr. Biol. 30 (1), 169–175.e5. https://doi.org/10.1016/j.cub.2019.11.027.

Ventura, S., Duncan, S., Ainge, J.A., 2024. Increased flexibility of CA3 memory representations following environmental enrichment. Curr. Biol. 34 (9), 2011–2019. e7. https://doi.org/10.1016/j.cub.2024.03.054.

Wills, T.J., Lever, C., Cacucci, F., Burgess, N., O'Keefe, J., 2005. Attractor dynamics in the hippocampal representation of the local environment. Science 308 (5723), 873–876, 10.1126/science.1108905.

Wilson, D.I., Langston, R.F., Schlesiger, M.I., Wagner, M., Watanabe, S., Ainge, J.A., 2013b. Lateral entorhinal cortex is critical for novel object-context recognition. Hippocampus 23 (5), 352–366. https://doi.org/10.1002/hipo.22095.

Wilson, D.I., Watanabe, S., Milner, H., Ainge, J.A., 2013a. Lateral entorhinal cortex is necessary for associative but not nonassociative recognition memory. Hippocampus 23 (12), 1280–1290. https://doi.org/10.1002/hipo.22165.

Wood, E.R., Dudchenko, P.A., Eichenbaum, H., 1999. The global record of memory in hippocampal neuronal activity. Nature 397 (6720), 613–616. https://doi.org/10.1038/17605. PMID: 10050854.

Wood, E.R., Dudchenko, P.A., Robitsek, R.J., Eichenbaum, H., 2000. Hippocampal neurons encode information about different types of memory episodes occurring in the same location. Neuron 27 (3), 623–633. https://doi.org/10.1016/s0896-6273(00)00071-4.

Yim, H., Dennis, S.J., Sloutsky, V.M., 2013. The development of episodic memory: items, contexts, and relations. Psychol. Sci. 2163–2172.

Yonelinas, A.P., Ranganath, C., Ekstrom, A.D., Wiltgen, B.J., 2019. A contextual binding theory of episodic memory: systems consolidation reconsidered. Nat. Rev. Neurosci. 20 (6), 364–375. https://doi.org/10.1038/s41583-019-0150-4.

Zacks, J.M., Swallow, K.M., 2007. Event segmentation. Curr. Dir. Psychol. Sci. 16 (2), 80–84. https://doi.org/10.1111/j.1467-8721.2007.00480.x.