

Title: Putting memory in context: Dissociating memories by distinguishing the nature of context

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## Research Highlights:

- Adaptations of SOR tasks allow memory to be assessed by manipulating context.
- The term context is vaguely defined and broadly applied making comparisons difficult.
- Different neural systems process memory depending on the context being used.
- Different neural systems process context based memory depending on the question being asked.
- There is an urgent need to clearly define how context is experimentally manipulated.

## Keywords:

Contextual cues; Rats; Humans; Memory; Episodic memory; Object recognition

## Abstract:

In recent years, spontaneous recognition tasks have become commonplace methods of assessing memory in animals. Adaptations of these tasks allow us to look at the role of objects, contexts and spatial locations in memory. Recent findings have highlighted that not all types of contexts in these tasks rely on the same neural systems. Similarly, asking different questions about the same types of context can allow the dissociation of neural systems underlying these memories. Here we review the current position in how context is used in such tasks, and we consider the fundamental importance of clearly defining both the nature of the context being used, and the questions asked of it in order to fully appreciate the neural and cognitive mechanisms being studied in such tasks.

## Introduction

In recent years, spontaneous tasks of recognition memory in rodents have become a widely used tool for understanding the neural basis of memory. These tasks build on the work of Berlyne[1], in the 1950s who showed that rats preferred to explore novel objects with reduced exploration of the objects on subsequent exposures, reflecting a degree of habituation or familiarisation with the objects. Later work by Ennaceur and Delacour [2], utilised this finding to develop an easy to administer task of memory that does not require animals to learn specific performance rules in order to complete the task. In this spontaneous object recognition (SOR) task, the animals are first exposed to two copies of the same object in a sample phase. They are given time to explore these objects and familiarise themselves to them. Then, after some variable delay period, a test is administered in which they are presented, in the same environment, to another copy of the previously seen item alongside a completely novel object. If the animals are able to remember the previous sample event then they will be able to identify the previously seen object as familiar, and hence will have a preference for exploring the novel object. This preference is measured through exploration time of the objects, with the most common measure of performance being a discrimination ratio that accounts for individual variations in an animal's overall levels of exploration  $[(\text{time exploring novel item} - \text{time exploring familiar item}) / (\text{time exploring novel} + \text{familiar items})]$ .

The SOR task has become increasingly popular in recent years because alternative tasks of recognition memory (such as delayed match to sample) require a rule to be

learnt prior to the task, and for that rule to be applied to demonstrate memory. As such, any impairments might not be in recognition memory per se, but in either the learning or application of such rules. However, whilst the SOR task does not suffer from this problem there are other issues (such as stress induced by multiple instances of handling) that can influence behaviour on the task (such issues, for example, may result in a degree of neophobia). The result of these influences on a spontaneous task is large amounts of variance in the data; animals typically run one trial (sample and test) a day and the behaviour of individuals can be highly variable. Therefore, the task typically requires large numbers of animals to produce sufficient statistical power, and this can, at times, mask the effects of manipulations on memory (see Ennaceur [3], for a review). However, in recent years some of these issues have been overcome. Building on the work of Albasser et al. [4], we have developed a new continual trials apparatus [5] that allows the animals to complete the SOR task without any within-session handling. Rather than taking animals in and out of the arena between sample and test (inducing stress, and therefore affecting spontaneous behaviour), the animals are trained to return to an external starting point themselves at the end of the exploratory period. This not only allows a single trial to be run without handling, but actually allows the animal to run multiple trials within a single day's session. Reduced handling and increased number of trials combined together means that SOR tasks run in the continual trials apparatus have greater reliability, and can show the same level of statistical power with a near 50% reduction in animal numbers [5].

The SOR task can also be adapted to understand more than just recognition memory for objects. Standard variations of the task can include testing memory for

locations (two copies of an object at sample, one of which is found in a novel location at test) [6,7]. In addition, memory can be tested for combinations of features. For example, object-location memory can be tested by having two different objects (e.g. A and B) in two locations (e.g. left and right) at sample, and then two copies of one of those objects (e.g. A) in both the locations at test. Here the novelty is defined not by novelty of the object or the novelty of the filled location but by the novelty that a particular object has not been seen in that particular location before. The memory is once again displayed through spontaneous preference for exploring the novel combination of object and location [8].

Like the simple object recognition task, this task can also be used in the continual trials apparatus [5] to improve reliability. Similarly, memory for the combination of object and context can be tested [7]. In this task (see Fig. 1), two copies of a single object (e.g. A) are presented in an arena with particular visual and tactile features (e.g. Context X) in one sample event. In a second sample, two copies of a different object (e.g. Object B) are presented in an arena with different visual and tactile features forming a different context (e.g. Context Y). At test the animal returns to one of the contexts (e.g. Context X) with one copy of each of the previously seen objects (A and B). In this situation, object A has been seen in this context previously, whilst object B has not. The combination of object B in context X is novel, and recognition of this is expressed by the animal through preferential exploration of object B in this context. Once again, this type of recognition memory can be tested in the continual trials apparatus [5].

Memory for combinations of features can be taken one step further by asking animals to show their memory for combinations of three features, object, location and context together [9]. In this task (see lower panel in Fig. 1), the first sample event has two objects (e.g. A and B) placed in two locations (e.g. left and right) in a context (e.g. context X) defined by visual and tactile features. After exploring this sample event, the animal is given a brief delay outside of the apparatus before being returned to another context (context Y). Now the same objects (A and B) are presented again, but in opposite locations (i.e. if A was on the left in X, it is on the right in Y). Once again the animals explore this sample event. Following a variable delay, animals are then returned at test to one of these contexts (e.g. context X) and now there are two copies of one of the previously seen objects (e.g. A) in each of the previously filled locations. Now the only novelty present is the combination (in this particular example) of object A on the right in context X. Object A has been seen in context X before, and has been seen on the right before, but never on the right in context X. This task is of particular interest as the combination of object, location and context has been argued to be an operationalisation of episodic memory, with animals showing memory for what (object) happened, where (location) on which occasion (context) [10].

### The nature of context

The ability to manipulate context in SOR tasks highlights its potential importance. By defining context as part of a memory, for example, we are able to explore episodic memory within animals (reviewed in [10]). However, in order to fully understand the

processes involved in such memory tasks, we need to be clear about the nature of the features of the memory being used. In this case, clearly understanding the nature of the stimulus being defined as the context is required. From an associative learning perspective, con-textual representations can be described as the binding together and integration of various elements of sensory information [11]. However, contexts are not merely a gathering of sensory information; pre-exposure to each individual element of a context is not enough to create contextual conditioning. Exposure to a whole context is required to form a representation [12] suggesting that contexts are an integrated representation of various components of available sensory information.

#### Use of context in human experiments

In human memory research, the term context is a broadly applied and vaguely defined concept. In the broadest sense, context can refer to all residual incidental information encoded when an item is taken into memory. This contextual, or other, information may or may not be useful during retrieval. Manipulating context experimentally can mean a variety of things: the physical, spatial–temporal, environmental, physiological or emotional state in which an item was encoded into memory [13]. Godden and Baddeley [14], showed that items on a word list were better remembered when tested in the same context that learning took place in. In this experiment, context referred to the physical environment: on land or underwater. In associative learning terms, context has been described as a strengthening operator when items on a word list are recalled in similar circumstances to how they were learned. Here, context refers to the level of semantic processing required



during encoding: deep verses shallow [15]. Context can also refer to a variety of sensory processes occurring at the time of encoding. Context can refer to: auditory stimuli (background music, see [16,17]; a specific voice, [18]; olfaction (incidental odour-context cues in tests of free-recall, see [19]), vision (background scenes, see [20,21]); complex picture discriminations [22]; colour, [18] or even mood [23] and mental state [24]. Context can also refer to processing spatial information [25], or the social context in which items are encoded [26].

In both the human and the animal literature, manipulating context can refer to concrete aspects of the physical and visual environment. Equally, context can refer to more abstract components, including altering task demands or sensory information such as odour or auditory cues. Whether or not context contributes to animal memory analogous to contextual contributions to human memory is difficult to determine. What is known is that context contributes to memory, specifically episodic memory (for discussion, see [27,28]).

The distinction between these multiple types of context is critical in understanding the neural basis of the memories being tested in the rodent SOR tasks described earlier. For example, as well as the episodic what-where-which (WWWhich; object-location-context) task described above [9], other groups have used an alternative SOR task to assess episodic memory in rodents, namely what-where-when (WWWhen; object-location-time) [29,30]. Here, then, are two different episodic tasks in rodents, both utilising the spontaneous recognition paradigm by combining features to assess an animal's memory of a unique and individually experienced event. In both cases, events are differentiated by contextual information, but the

nature of this information is different in each case. In the WWWhich task, the context defining an occasion is described by visual and tactile elements of an arena in which the event happens. In the WWWhen task, the context is defined as a temporal context (i.e. the event happened first or second, earlier or more recently, etc.). Although these contextual cues are very clearly different between the two tasks, one might expect them both to utilise episodic memory, and therefore rely on the same neural systems. Indeed, both the WWWhich task [9,31] and the WWWhen task [29,30] are similarly dependent upon the hippocampal system.

Three decades after Tulving (1983) redefined the concept of episodic memory, subjective experience, a critical component of episodic processes in humans, has remained a contentious point when drawing comparisons between rodent and human research findings. However, as outlined above, the neural basis of memory has been widely and effectively studied in rodents by examining the components of episodic memory in such tasks as WWWhich and WWWhen, where the focus is on the content (rather than the experience) of the memory. However, it appears that the neural systems for these two episodic tasks can be dissociated. In mice with an age-dependent pathology modelling Alzheimer's disease, the WWWhich task is impaired at the age of 6 months when pathology is confined to the medial temporal lobe, whilst the WWWhen task remains unimpaired at 12 months, even when the pathology has spread beyond this region [32]. This dissociation is not unique to rodent SOR tasks. When humans were asked questions similar to those presented in rodent versions of the tasks, it was possible to address the participants' phenomenological experience by asking them to attribute their response to the process of either recollection or familiarity whilst also quantifying participants'

accuracy. The WWWhich task could only be solved by recollection (implying it is a task of episodic memory) whilst the WWWhen task could also be solved by familiarity-based mechanisms, suggesting it does not require episodic memory for accurate performance [33]. These results show that tasks ostensibly measuring the same cognitive process (episodic memory) can differ in terms of both cognitive and neural mechanism when the difference between them is the way in which a unique occasion is identified, either contextually in WWWhich or by how recently it was experienced in WWWhen. Another apparent distinction in the way in which types of con-text influence the neural mechanisms involved in memory can be seen in studies of the role of acetylcholine in memory using contextual information. Despite the fact that lesions to the hippocampus severely impair the episodic WWWhich task in rats [9,34] when immunotoxic lesions of the cholinergic input to the hippocampus are made, rats show no impairment at all on the task [35]. Thus, whilst this task is clearly dependent upon the hippocampus [9], it is not dependent upon the cholinergic input to the hippocampus. However, the WWWhich task in rats is closely related to another task of episodic memory, this time one that has been used with monkeys. By combining various objects, locations and unique backgrounds, Gaffan [36] created scenes which he argued make up integrated 'snapshots' that represent episodic memory. In this experiment, the monkeys learned a two-choice visual discrimination (i.e. which of two objects presented in a problem is rewarded), but these objects were in problem-unique fixed locations against problem-unique backgrounds integrated to create a contextual backdrop for the memory, i.e. every time a visual discrimination problem was seen, the same objects were in the same location against the same background. Good performance in this task in monkeys is also reliant on the hippocampal system [36], but in contrast to the WWWhich task in rats,

it is also dependent on the cholinergic input to the hippocampus and temporal cortex [37]. Here, then, there are two similar tasks, one requiring rats to explore and recognise objects in fixed locations and where features of the environment define the occasion being remembered, and one where monkeys scan a 'snapshot' scene and learn the reward contingencies of objects in particular locations on those backgrounds. Both these tasks rely on the hippocampus, but the involvement of cholinergic inputs to the hippocampus differentiates them. These seemingly discrete differences highlight the process-dependent nature of episodic memory. When the task components remain the same (objects in particular locations, nested in a specific occasion), but the task demands are altered (e.g. exploration of object for rats, scanning scenes in monkeys), the reliance on cholinergic projections to the hippocampus varies despite both tasks addressing WWWhich questions.

Taken together, these results suggest that the process of episodic memory is an integrative one requiring the component parts of the what-where-which task to form a unified memory of a single event. Where WWWhen tasks have been seen to be unimpaired in AD mice, whilst WWWhich is impaired [32] and where WWWhen has been seen to be solvable through familiarity-based mechanisms [33], it has been proposed that this is a result of not having a unified memory of the event. Rather, it was proposed [33] that a familiarity based (non-episodic) solution was available through (for example) having a sense of familiarity over what happened and where, and combining that with a relative sense of memory strength to judge how recently it had occurred. This combined What-Where and When memory is distinct from a single, unified WWWhen representation. However, it remains true that although the WWWhen tasks in these studies did not require episodic memory, episodic memory

was, nonetheless, available. One question that remains unanswered is why, if episodic memory is available, it isn't used to solve these non-episodic tasks. Episodic memory can be used, after all, in even the simplest object recognition task [e.g. 33]. Addressing this question explains precisely why SOR tasks are so effective in the study of episodic memory. When presented with an SOR task, learning is entirely incidental and capitalises on the animals' natural curiosity. There is no food reward to drive the learning of a strategy to solve the task. As a result, the ability to flexibly apply the incidentally learned information (whether it be contextual, sensory, visual, tactile, etc), to recollect an event is what makes a task episodic.

Whilst lesion studies can help differentiate the relative involvement of various medial temporal lobe structures in behavioural tasks with differing contextual cues [32] and behavioural demands [9 versus 38; 35], dissociations of representations of different types of context can also be seen in single-cell recording studies. By integrating spatial information, place cells in the hippocampus are thought to build an internal map of an environment [39]. It is supposed that these representations are mediated by the environmental context, with place fields of an individual neuron remapping when moving from one environmental context to another [40–42]. The control of this remapping by the environmental context is relatively well understood, but recent work suggests once again that the nature of the contextual stimuli is important. Spiers et al. [43] recorded place fields from hippocampal cells whilst animals explored a maze with multiple rooms leading from a common corridor. When extra-maze cues were removed and the visual and tactile properties of the different rooms were kept identical, the place fields of some cells within the hippocampus failed to remap when the animal moved from one room to another. However, when one of the

rooms was identified not only by its position along the corridor, but also by a visually and tactilely distinctive context, the place fields remapped when the animal entered this room, whilst continuing to represent the other rooms in an identical manner. This is a surprising finding as it seems unlikely that identical rooms along a corridor disorientate the animals so much that they cannot distinguish one from another. Rather than the visual and tactile contextual cues, other contextual cues will help animals to differentiate where they are in such an environment, such as entry point along the corridor, or sounds from the room, or smells in the environment, or locomotor activity over the time in the apparatus. However, these contextual cues seem influence the firing rate of place cells in a very different way to more 'traditional' contextual cues. The location of the place field appears to be strongly influenced by the typical visual and tactile contextual cues, but less so by these less clearly identifiable contextual cues. It cannot be claimed that no remapping of place fields occurs within these cells when the rooms are identical as it remains a possibility that there is, for example, rate remapping or that the network remaps whilst some individual place fields do not. Nonetheless the effect of different types of contextual information on the activity of place cells seems clear.

#### Differential use of the same context

To this point we have discussed how the use of different types of context can clearly differentiate both the cognitive and neural mechanisms at play in memory involving those contexts. However, it also appears true that different neural mechanisms underlie memory using the same type of context when the question being asked

about that contextual information is different. The clearest example of this can be seen in a series of studies by Eacott and Norman [9,38]. In these studies, a range of SOR tasks were used, including two that utilised context in the form of visual and tactile environments in which objects were presented. These tasks were either object-context (What-Which) or object-location-context (WWWhich; episodic memory). Both tasks required the animals to experience two sample events and a test, and each required animals to explore objects within particular contexts (see Fig. 1). However, the effect of lesions to the fornix or postrhinal cortex on these tasks could be doubly dissociated [38]. Lesions to the postrhinal cortex led to significantly impaired performance on the What-Which task [38], but spared performance on the WWWhich task [9]. In contrast, lesions to the fornix severely impaired WWWhich performance, whilst What-Which performance was relatively intact.

What is surprising about the results of Eacott and Norman [9,38], is that the postrhinal cortex is considered to be the anatomical route to the hippocampus for contextual information [see 44 for review]. It is not, therefore, surprising that the postrhinal-lesioned animals are impaired at the object-context task [38], but it is surprising that the same animals are unimpaired at the WWWhich task [9]. For the WWWhich task, animals must still access information about the context of an event. This information must enter the hippocampus as animals with lesions of the fornix are impaired at this task [9], a finding confirmed when selective bilateral hippocampal lesions produced a similar pattern of impairments [31]. However, it seems that the route of this contextual information into the hippocampus is independent of the postrhinal cortex. There are numerous possible explanations for this, such as cross-over of information between post-rhinal and perirhinal cortex [44] and different neural

systems in cortex and hippocampus for processing context [45,46]. However, neither of these possibilities can explain the double dissociation of function between perirhinal cortex and hippocampus in these SOR tasks. In both cases the context is the same: an arena with visual and tactile information present. If the information could be processed via perirhinal cortex for the WWhich task, then why can it not be processed in that way for the object-context task? Similarly, if it is that the context used is tapping into either the hippocampal context system or the cortical context system, then why are different tasks using the same type of context impaired differently by lesions to these two systems?

An alternative possibility was discussed by Eacott and Gaffan [47]. In this explanation, it is not the nature of the context that should differentiate the neural system on which each task relies, but rather the nature of the question being asked. The WWhich task is designed as an episodic task, based around Clayton and Dickinson's operationalisation of episodic memory (as what happened, where and when, [48]) and substituting which occasion for when something happened. In the object-context task, the animal is recognising a novel combination of object and context (where each is a separate and dissociable component of the memory) [9,10,38]. However, for the WWhich task (as with episodic memory in humans) the memory is not the sum of the memory for the three components. Rather, the memory is a unitary memory of a single event [49,50]. Because of this difference, the WWhich is an episodic task, and the object-context task is not. As a result, the WWhich task is expected to rely on recollection (as does episodic memory) whilst the non-episodic object-context task could be solved using familiarity-based memory processes [32,33]. It is this difference in process that determines the neural



substrates of memory. Although both tasks ask animals to remember information within the same type of contexts the WWWhich task requires recollection, and is dependent upon the hippocampus. In contrast, the context information processed in the post-rhinal cortex is sufficient to support familiarity-based memory, but not recollection-based memory [47].

Even within the hippocampus there are dissociations between tasks using the same type of contextual information. Animals with depletion of the cholinergic input to the hippocampus are unimpaired on the WWWhich task, but the same animals are impaired at a location-context (Where-Which) task [51]. Once again, in each case, the contexts being used are the same (visually and tactily distinct walls and floors in an open arena), but the effect of lesions is different depending on the nature of the question being asked. This supports the view that even though different types of context may themselves rely on different neural systems when being used to ask the same question (consider WWWhich and WWWhen [32,33], discussed above), it is also true that the same type of context is processed by different neural systems when being used in different types of behavioural tasks when different questions are asked of the animal.

## Conclusions

The evidence supports the literature from human studies that there are many and varied types of context in animal memory. Defining such a ubiquitous term as context

is difficult, although many have tried. One clear definition comes from a review by Rudy [12] in which he considers context to have two well defined properties: 'stability' (they must be independent of the observer, i.e. in the absence of the observer, the relationship between features, and their meaning, remains the same) and be subject to 'component variation' (i.e. the component features of the context must be able to be rearranged in relation to one another to create new contexts). However, we would propose that even such clear definitions such as these are unhelpful in understanding what part context plays within encoding and retrieving a memory. The data discussed here shows clearly that what context is, how it is used and what systems it relies on, depends on a variety of issues. However, in relating these tasks to human memory, there are a number of additional issues to be addressed. As discussed earlier, context in tasks of memory in humans is often equally poorly described, but in addition to the issues discussed above, we also have to consider semantic associations. For example, in Rudy's [12] examples of well-defined context, he describes how component variation might include the movement or replacement of items in an office, and that with numerous such replacements, a new context is established (although, as he points out, the point at which these substitutions are dealt with as a new context itself needs to be the subject of empirical study). However, we also have many semantic associations with contexts around us, and these can be independent of the relationships of features within those contexts (e.g. my office is always 'my office' whether or not my chair is in its usual location, or a novel one). These semantic associations with context are complex, can develop over a lifetime and are complicated by additional associations brought by language use. It is worth establishing that in the SOR tasks described here, the tasks are always carried out in highly familiar contexts (i.e. contexts to

which the animals have been habituated over many days). Indeed, it is possible that some of the complexities of context in human memory can be more fully understood in animals, where the lifetime experience of the animal can be carefully controlled, and therefore the familiarity with, and associations made, to the context in which the tasks are run can be differentiated.

Nonetheless, for work in animals and humans we make the case that there is an urgent need to carefully define the contexts being used. This goes beyond merely defining what a context may or may not be, but rather extends to being clear both the nature of the context and how it is being used much in the way any other procedural demands of a task would be empirically reported. Both these issues can clearly determine the neural basis of the memory being studied, and need to be explicitly considered when interpreting the literature.

## References

- [1] Berlyne DE. Novelty and curiosity as determinants of exploratory behaviour. *JPsychol Gen Sect* 1950;41:68–80.
- [2] Ennaceur A, Delacour J. A new one-trial test for neurobiological studies of memory in rats. 1: Behavioral data. *Behav Brain Res* 1988;31:47–59.
- [3] Ennaceur A. One-trial object recognition in rats and mice: Methodological and theoretical issues. *Behav Brain Res* 2010;215:244–54.
- [4] Albasser MM, Chapman RJ, Amin E, Iordanova MD, Vann SD, Aggleton JP. New behavioral protocols to extend our knowledge of rodent object recognition memory. *Learn Mem* 2010;17:407–19.
- [5] Ameen-Ali KE, Eacott MJ, Easton A. A new behavioural apparatus to reduce animal numbers in multiple types of spontaneous object recognition paradigms in rats. *J Neurosci Methods* 2012;211:66–76.
- [6] Ennaceur A, Neave N, Aggleton JP. Spontaneous object recognition and object location memory in rats: the effects of lesions in the cingulate cortices, the medial prefrontal cortex, the cingulum bundle and the fornix. *Exp Brain Res* 1997;113:509–19.
- [7] Dix S, Aggleton JP. Extending the spontaneous preference test of recognition: evidence of object-location and object-context recognition. *Behav Brain Res* 1999;99:191–200.
- [8] Ennaceur A, Meliani K. A new one-trial test for neurobiological studies of memory in rats. III. Spatial vs. non-spatial working memory. *Behav Brain Res* 1992;51:83–92.

[9] Eacott MJ, Norman G. Integrated memory for object, place, and context in rats: a possible model of episodic-like memory. *J Neurosci* 2004;24:1948–53.

[10] Easton A, Eacott MJ. Cholinergic mechanisms of episodic memory: what specific behavioural tasks can tell us about specific neural mechanisms. *Brain Res Bull* 2013;92:21–8.

[11] Pickens CL, Holland PC. Conditioning and cognition. *Neurosci Biobehav Rev* 2004;28:651–61.

[12] Rudy JW, O'Reilly RC. Contextual fear conditioning, conjunctive representations, pattern completion, and the hippocampus. *Behav Neurosci* 1999;113:867–80.

[13] Murnane KMK, Phelps MP. Context-dependent recognition memory: the ICE theory. *J Exp Psychol - Gen* 1999;128:403–15.

[14] Godden DRBAD. Context-dependent memory in two natural environments: on land and underwater. *Br J Psychol* 1975;66:325–31.

[15] Malmberg KJ, Shiffrin RM. The one-shot hypothesis for context storage. *J Exp Psychol Learn Mem Cogn* 2005;31:322–36.

[16] Balch WR, Lewis BS. Music-dependent memory: the roles of tempo change and mood mediation. *J Exp Psychol Learn Mem Cogn* 1996;22:1354–63.

[17] Mead KML, Ball LJ. Music tonality and context-dependent recall: The influence of key change and mood mediation. *Eur J Cogn Psychol* 2007;19:59–79.

- [18] Souchay C, Guillery-Girard B, Pauly-Takacs K, Zofia Wojcik D, Eustache F. Subjective experience of episodic memory and metacognition: a neurodevelopmental approach. *Front Behav Neurosci* 2013;7.
- [19] Isarida T, Sakai T, Kubota T, Koga M, Katayama Y, Isarida TK. Odor-context effects in free recall after a short retention interval: a new methodology for controlling adaptation. *Mem Cogn* 2014;42:421–33.
- [20] Wang W-C, Yonelinas A, Ranganath C. Dissociable neural correlates of item and context retrieval in the medial temporal lobes. *Behav Brain Res* 2013;254:102–7.
- [21] Fenske MJ, Aminoff E, Gronau N, Bar M. Top-down facilitation of visual object recognition: object-based and context-based contributions. In: Tse M-CMMA, editor. *Progress in Brain Research*: Elsevier; 2006. p. 3–21.
- [22] Rugg MD, Vilberg KL, Mattson JT, Yu SS, Johnson JD, Suzuki M. Item memory, context memory and the hippocampus: fMRI evidence. *Neuropsychologia* 2012;50:3070–9.
- [23] Isarida T, Isarida TK. Effects of simple- and complex-place contexts in the multiple-context paradigm. *Quart J Exp Psychol* 2010;63:2399–412.
- [24] Smith SM. Mood is a component of mental context. *J Exp Psychol Gen* 1995:124.
- [25] Hoscheidt SM, Nadel L, Payne J, Ryan L. Hippocampal activation during retrieval of spatial context from episodic and semantic memory. *Behav Brain Res* 2010;212:121–32.

[26] Olf M, Frijling JL, Kubzansky LD, Bradley B, Ellenbogen MA, Cardoso C, et al. The role of oxytocin in social bonding, stress regulation and mental health: An update on the moderating effects of context and interindividual differences. *Psychoneuroendocrinology* 2013;38:1883–94.

[27] Smith DM, Bulkin DA. The form and function of hippocampal context representations. *Neurosci Biobehav Rev* 2014;40:52–61.

[28] Smith DM. The Hippocampus, context processing and episodic memory. In: Dere E, Easton A, Nadel L, Huston JP, editors. *Handbook of Episodic Memory*. Elsevier; 2008. p. 465.

[29] Good MA, Barnes P, Staal V, McGregor A, Honey RC. Context- but not familiarity-dependent forms of object recognition are impaired following excitotoxic hippocampal lesions in rats. *Behav Neurosci* 2007;121:218–23.

[30] Dere E, Huston JP, De Souza Silva MA. Episodic-like memory in mice: simultaneous assessment of object, place and temporal order memory. *Brain Res Protoc* 2005;16:10–9.

[31] Langston R, Wood ER. Exploring the circumstances under which the hippocampus is required for spontaneous object-location recognition. *SFN abstracts* 2006;66:12.

[32] Davis KE, Eacott MJ, Easton A, Gigg J. Episodic-like memory is sensitive to both Alzheimer's-like pathological accumulation and normal ageing processes in mice. *Behav Brain Res* 2013;254:73–82.

[33] Easton A, Webster LAD, Eacott MJ. The episodic nature of episodic-like memories. *Learn Mem* 2012;19:146–50.

[34] Langston R, Wood E. Associative recognition and the hippocampus: Differential effects of hippocampal lesions on object-place, object-context and object-place-context memory. *Hippocampus* 2010;20:1139–53.

[35] Easton A, Fitchett A, Eacott MJ, Baxter MG. Medial Septal cholinergic neurons are necessary for context-place memory but not episodic-like memory. *Hippocampus* 2011;21:1021–7.

[36] Gaffan D. Scene-specific memory for objects: a model of episodic memory impairment in monkeys with fornix transection. *J Cogn Neurosci* 1994;6:305–20.

[37] Easton A, Ridley RM, Baker HF, Gaffan D. Lesions of the cholinergic basal forebrain and fornix in one hemisphere and inferior temporal cortex in the opposite hemisphere produce severe learning impairments in rhesus monkeys. *Cerebral Cortex* 2002;12:729–36.

[38] Norman G, Eacott MJ. Dissociable effects of lesions to the perirhinal cortex and the postrhinal cortex on memory for context and objects in rats. *Behav Neurosci* 2005;119:557–66.

[39] O'Keefe J, Nadel L. *The hippocampus as a cognitive map*. Oxford: Oxford University Press; 1978.

[40] Muller RU, Kubie JL. The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. *J Neurosci* 1987;7:1951–68.

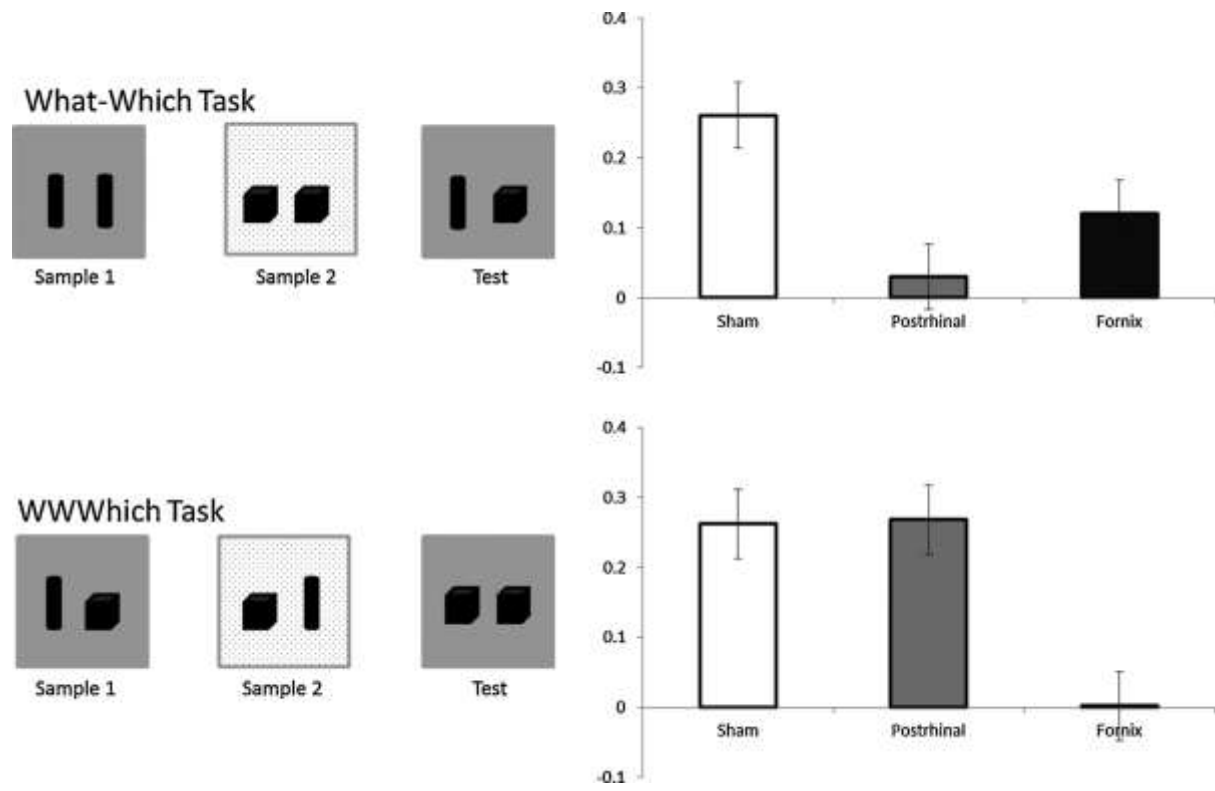
[41] Leutgeb S, Leutgeb JK, Treves A, Moser MB, Moser EI. Distinct ensemble codes in hippocampal areas CA3 and CA1. *Science* 2004;305:1295–8.



- [42] Anderson MI, Jeffery KJ. Heterogeneous modulation of place cell firing by changes in context. *J Neurosci* 2003;23:8827–35.
- [43] Spiers HJ, Hayman RM, Jovalekic A, Marozzi E, Jeffery KJ. Place field repetition and purely local remapping in a multi-compartment environment. *Cereb Cortex* 2013.
- [44] Aggleton JP, Brown MW. Interleaving brain systems for episodic and recognition memory. *Trends Cogn Sci* 2006;10:455–63.
- [45] Rudy JW. Context representations, context functions, and the parahippocampal-hippocampal system. *Learn Mem* 2009;16:573–85.
- [46] Nadel L. The hippocampus and context revisited. In: Mizumori SJ, editor. *Hippocampal place fields: relevance to learning and memory*. Oxford University Press; 2008.
- [47] Eacott MJ, Gaffan EA. The roles of perirhinal cortex, postrhinal cortex, and the fornix in memory for objects, contexts, and events in the rat. *Quart J Exp Psychol B* 2005;58:202–17.
- [48] Clayton NS, Dickinson A. Episodic-like memory during cache recovery by scrubjays. *Nature* 1998;395:272–4.
- [49] Clayton NS, Bussey TJ, Dickinson A. Can animals recall the past and plan for the future. *Nature Rev Neurosci* 2003;4:685–91.
- [50] Easton A, Eacott MJ. A new working definition of episodic memory: replacing ‘when’ with ‘which’. In: Dere E, Easton A, Nadel L, Huston JP, editors. *Handbook of episodic memory*. Amsterdam: Elsevier; 2008. p. 185–96.

[51] Easton A, Fitchett A, Baxter MG, Eacott MJ. Cholinergic lesions of the medial septum impair where-which memory but not episodic memory in the rat. European Brain and Behavior Society: EBBS; 2009.

FIGURE 1



## Figure Legends:

### Figure 1

Two spontaneous object recognition tasks used to double dissociate the effects of lesions to the fornix or postrhinal cortex. Upper panel: Performance on a what-which (object-context) task was impaired by postrhinal lesions but not lesions to the fornix (Norman and Eacott, 2005). Lower panel: Performance on a what-where-which (wwwhich; episodic memory) task was impaired by fornix lesions but not postrhinal lesions (Eacott and Norman, 2004).