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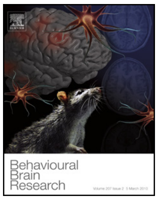

Research report

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

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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.

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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.

1. 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 [(time exploring novel item − time exploring familiar item)/(time exploring novel + 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

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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].

2. 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, contextual 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.

3. 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]).