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Research report

Dissociating effects of acute photic stress on spatial, episodic-like and working memory in the rat

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HIGHLIGHTS

- We compare acute photic stress effects on three memory dependent tasks.
- Focus on the normalization phase of the stress response.
- Spatial memory performance was detrimentally affected in a spatial water maze task.
- Object-location deficits but no temporal-object impairments were observed in an episodic-like memory task.
- Rats' performance was unaffected in an operant delayed matching-to-sample task.

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ABSTRACT

Adaptively responding to acute stress has been of great importance for human and animal survival. However, for our species, stress-related disorders are putting an ever-increasing burden on healthcare systems. It is thus crucial to understand the basic processes and cognitive changes associated with acute stress. Here, we examined the effects of acute stress exposure on spatial (water maze) and memory (delayed match to sample and episodic-memory-like tasks) performance. We found striking performance deficits in stressed animals navigating in the water maze. We also found, in an episodic-like memory task, striking object-location deficits, but not in temporal-object association learning in stressed animals. Finally, no differences were apparent for any delay periods (up to 30 s) in a delayed match to sample task. Taken together, these results show a strong differential effect of acute stress on differing memory processes.

1. Introduction

The physiological response to acute stressors – the acute stress response – serves a variety of adaptive responses. However, a sustained stress response may cause a variety of deleterious effects. Estimates for the US alone suggest work-related stress costs relate to $150 billion p.a. in lost productivity, absenteeism, poor decision-making, stress-related mental illness, and substance abuse [34]. Many studies have shown deleterious effects of stress, especially of an acute nature on cognition in humans and rodents alike (for review see [1–4]). Here we examine the effects of acute stress on a variety of cognitive processes, in order to better understand how stress may differentially affect differing functions. We focus in particular on the normalization phase of the acute stress response, where the brain is thought to recover from the acute stress exposure (for review, see [1]). Our aim was to characterize in detail the behavioral changes associated with this phase by introducing a 30 min break after the stress exposure, and before testing animals in the various memory tasks.

Stressors applied before learning impair spatial memory performance (24 h post-training) in the water maze (MWM) and the radial arm water maze (RAWM) [5–7]. In all three studies the duration of the stressor was between 30 min and 1 h but for both Diamond et al. [5] and Park et al. [7] training trials started immediately after the stress ceased, whereas in Kims' study there was a delay of 4–5.5 h. Similarly, a mild elevated platform stress (30 min), in very young rats (3–4 weeks old), showed retrieval impairments 30 min after training [8]. Interestingly, the same study reported no effects with a short (15 s) foot-shock protocol. A 2 min predator exposure did

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not show memory deficits when learning started 30 min after the stress resulted however in a large memory enhancement when immediately introduced prior to the learning trials [9].

Testing episodic-like memory in rodents is more challenging than spatial memory [10]. Based on results presented in [11] we adapted their protocol to test episodic-like memory. The protocol is based on a combination of an object-recognition task and a temporal memory task to introduce episodic-like events where the animal is tested for object recency and object–place associations. The concept behind this protocol is that the rats' spontaneous exploration behavior favors novelty [11–13]. Kart-Teke et al. [11] have shown that rats demonstrate "what, where, and when" memory based on object preference exploration patterns. In their experiments rats recognized previously explored objects and remembered their order of appearance. For example rats spent more time exploring an "old familiar" object relative to a "recent familiar" object. This led to the conclusion that the animals recognized previously explored objects and remembered their order of first appearance. Further, rats preferred a displaced "recent familiar" object, compared to a stationary "recent familiar" object, while the exact opposite was observed for the displaced and stationary "old familiar" objects suggesting an integrated memory for objects, place and time. In an additional set of experiments they applied a mild injection stress 30 min before training during the sample trials, which abolished any differences in object exploration. Thus this task provides us with the opportunity to extend our understanding of higher-order memory processes with a strong spatial component.

Delayed matching (or non-matching)-to-sample tests have been extensively used to assess working memory in rodents [14–17]. Animals are generally presented with a sample stimulus during the sample phase and after a certain retention interval have to remember the matching (DMTS) or the non-matching (DNMTS) stimulus of the sample trial. Although, several publications have reported prominent working memory performances in humans under high stress conditions (e.g. [18,19]) there is to the best of our knowledge no report of acute extrinsic stress effects on rodents involving working memory tasks such as the DMTS.

Here we systematically compare performance on these spatial, episodic-like and short-term memory tasks. We predict that there will be differential patterns of sensitivity to the recovery phase after exposure to an acute stressor.

2. Materials and methods

2.1. Animals

A total of 76 male Hanover Wistar rats (B&K, United Kingdom), weighing between 420 and 465 g at the start of the experiment, were used for the study. Rats were housed in pairs in a temperature-controlled laminar airflow unit and maintained on a 12:12 light–dark cycle (08:00–20:00 h). All tests were carried out between 12:00 and 16:00 o'clock. Rats received food and water ad libitum. Experiments were carried out in accordance with regulations laid out by LAST Ireland and were compliant with the European Union directives on animal experimentation (European Community Council Directive 86/609/EEC).

2.2. Stress protocol

For all behavioral experiments rats were randomly assigned to either the stress group(s) or the control group. Rats assigned to the stress group(s) underwent a 30 min light stress exposure. This mild stress consisted of 30 min of exposure to bright light (~120 CD) in a small round bucket. After 30 min of bright light exposure, rats were allowed another 30 min of rest before training or testing in the respective experiments was started. The use of photic stress was based on earlier work in the lab [20] which demonstrated that this technique reliably induced a stress response. This mild-to-moderate stressor was chosen over more extreme stressors as being more naturalistic (as compared to electric shock for example). A settling period of 30 min was introduced so the normalization phase in respect of the stress response timeline would have been initiated [21].

2.3. Water maze task

Before training in the water maze commenced, rats ($n = 16$) were habituated for three days to the experimenter for 10 min per animal per day. The black tank for the water maze, which was 1.5 m in diameter, 40 cm in height, was filled with water (30 cm, ~22 °C). A black curtain (with two big white cues) around the water tank was used to separate the recording environment from the rest of the room and room lights were dimmed to allow continuous and noise-free tracking of the animals. Rat movements were tracked with EthoVision 3.0 software (Noldus, NL) via a camera mounted above the tank.

The main training protocol consisted of five days of learning trials with semi-random starting position and a fixed hidden platform submerged about 1.5 cm below the water surface in the southwest quadrant of the tank. A trial consisted of 60 s where the animal was allowed to search for the platform (if the animal did not find the platform it was guided to the target platform), a 15 s period where the animal was allowed to remain on the platform and finally 30 s in a holding box near the tank before the next trial started. Rats were introduced into the tank always facing the wall and allowed to slide into the water. After four trials per day, the rats were dried with a towel and kept in a heated environment for a short time before being placed back into their home cages.

The number and location of the start positions were chosen to ensure near equal length to the platform and that the animal was not memorizing specific routes but was orienting itself via the distal cues provided [22]. For the probe trial, the platform was removed from the tank and the animal was introduced once for 60 s, in the northeast quadrant, into the tank to search for the supposed location of the platform. To ensure any differences in performance were not due to visual deficits caused by the light stress in the stress group, a separate visual cue session was undertaken on the next day. For this session, the platform was reintroduced in the previous location (SW) in the tank with a white flag attached (~30 cm × 30 cm) and the animals were started four times in each of the four starting positions. After a one-day break, a three-day reversal training scheme was started. In short, the platform location was placed in the opposite quadrant (NE) and the starting positions were reversed accordingly (see Fig. 1B).

2.4. Episodic-like memory task

The open-field environment (90 cm × 90 cm × 35 cm, black painted wooden walls) was indirectly illuminated by four 60 W bulbs. A black curtain surrounding the experimental set-up prevented other visual cues present in the room being seen by the animals. Two distal visual cues were attached to the black curtain to allow reliable and consistent spatial orientation for the animals. A video camera mounted above the center of the environment was used for recording behavior; the samples were stored to allow offline analysis. Between each of the trials the objects, the arena as well as the floor, were cleaned thoroughly with an alcohol-based cleaning solution to extinguish any odors present from previous trials. Two distinct sets of objects were used for the task. One set of objects was identical white non-transparent bottles with a smooth surface and a plastic top. They were 20 cm in height with a base diameter of 10 cm. The other set was a stack of identical Duplo®