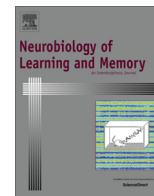




Contents lists available at ScienceDirect

Neurobiology of Learning and Memory

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

Short communication

Goldfish hippocampal pallium is essential to associate temporally discontinuous events

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ARTICLE INFO

Article history:

Received 2 June 2016

Revised 20 December 2016

Accepted 4 January 2017

Available online 6 January 2017

Keywords:

Teleost fish telencephalic pallium

Hippocampal pallium

Delay versus trace classical conditioning

Episodic-like memory

Vertebrate brain evolution

ABSTRACT

There is general agreement that the hippocampus of vertebrates, from fish to mammals, is involved in map-like spatial memory. However, in mammals the role of the hippocampus goes beyond the spatial domain as it is also involved in binding the temporally separate events that compose episodic memories. In this regard, the hippocampus of mammals is essential for trace classical conditioning, in which a stimulus-free time gap separates the conditioned stimulus (CS) and the unconditioned stimulus (US), but not for delay conditioning, in which both stimuli coincide in time. Although the involvement of the hippocampus in encoding relational memories based on a temporal frame-work has been extensively studied in mammals, there is scarce evidence about the possible contribution of the hippocampus of non-mammalian vertebrates to the temporal, non-spatial dimension of relational memories. The present work was aimed to determine if the ventral part of the lateral division of the area dorsalis telencephali (Dlv) of goldfish, proposed as homologous to the hippocampus of mammals, is also involved in trace classical conditioning. With this purpose, goldfish with lesions in Dlv, complete telencephalon ablation and sham operation, were trained in delay and trace heart rate classical conditioning. Dlv lesions severely impaired the acquisition of the conditioned response when a stimulus-free time gap was elapsed between the CS and the US (trace conditioning), but not when both stimuli overlapped in time (delay conditioning), revealing that this region, like the hippocampus of mammals, is essential to form the temporal associative memories required by trace conditioning. Present data suggest that the presence of a hippocampal pallium involved in relational, episodic-like memory that preserves both the spatial and the temporal dimensions of past events, could be a primitive feature of the vertebrate brain that has been conserved through evolution.

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1. Introduction

In mammals the hippocampus is essential for some particular forms of relational memory, such as map-like spatial memories, which allow allocentric or world-centered navigation and the flexible expression of the spatial knowledge (Burgess, Jeffery, & O'Keefe, 1999; Hampton, Hampstead, & Murray, 2004; Morris, 2006; O'Keefe & Nadel, 1978). A homologue of the hippocampus can be recognized also in all non-mammalian tetrapods (birds, reptiles and amphibians), located in a dorsomedial position in the telencephalon (Butler & Hodos, 2005; Jarvis, 2009; Nieuwenhuys, Ten Donkelaar, & Nicholson, 1998; Striedter, 2005). In every tetrapod species studied to date the hippocampus is involved in spatial memory (Coppola,

Spencer, Peterson, & Bingman, 2014; Morris, 2006; Rodríguez et al., 2002; Sherry & Duff, 1996) which suggests that this trait might be a primitive brain feature of the tetrapod lineage (Bingman, Rodríguez, & Salas, 2017; Salas, Broglio, & Rodríguez, 2003). Furthermore, developmental and neuroanatomical data provide evidence that a homologue of the hippocampus is present in ray-finned fishes as well, but occupying a dorsolateral position in the telencephalic hemispheres, as in this group of vertebrates the telencephalon undergoes a process of eversion instead of evagination during the embryonic development (Nieuwenhuys, 2011; Northcutt, 2006; Wullimann & Mueller, 2004). The fish hippocampal homologue, resembling the hippocampal function of mammals, is involved in map-like spatial memory and supports the flexible use of the acquired spatial information and the ability to use it inferentially in novel situations, for example to make shortcuts and detours (Broglio, Rodríguez, Gómez, Arias, & Salas, 2010; Durán, Ocaña, Broglio, Rodríguez, & Salas, 2010; Rodríguez et al., 2002; Uceda

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et al., 2015). The generalized involvement of the hippocampus in spatial cognition across vertebrates indicates that it may be a conserved feature in the vertebrate brain evolution.

However, in mammals the role of the hippocampus is not limited to the spatial domain as it is also involved in episodic or declarative memories based on a temporal frame-work. Thus, the hippocampus is essential for bridging temporal gaps in order to bind separate events that compose sequential memories (Kitamura, Macdonald, & Tonegawa, 2015; MacDonald, Lepage, Eden, & Eichenbaum, 2011; Meck, Church, & Olton, 1984; Staresina & Davachi, 2009). In this regard, the hippocampus of mammals is differentially involved in two variants of classical conditioning, trace and delay conditioning, which differ only in the temporal relationships between the conditioned stimulus (CS) and the unconditioned stimulus (US). Trace classical conditioning, which characterizes by a stimulus-free time interval between the CS and the US, requires declarative or relational memory and, therefore, is critically dependent on the functional integrity of the hippocampal system. In contrast, delay conditioning, where the CS and the US are contiguous in time, presents the automatic and reflexive features of procedural or non-declarative memory, and is readily acquired by hippocampus lesioned mammals (for review see, Christian & Thompson, 2003; Clark, 2011; Weiss & Disterhoft, 2015).

Although the implication of the hippocampus in trace classical conditioning has been extensively studied in mammals, there is scarce evidence about the possible involvement of the hippocampus of non-mammalian vertebrates beyond the spatial memory domain. This is an important question from an evolutionary perspective, because the lack of involvement of the non-mammalian hippocampus in trace conditioning would imply that the non-spatial, temporal associative memory functions of the hippocampus emerged with the mammalian lineage. Conversely, its presence would indicate that the temporal dimension of the hippocampal memory function could have appeared much earlier in phylogeny having been conserved through vertebrate evolution. In this context we evaluated in this experiment whether the teleost ventral part of the lateral division of the area dorsalis telencephali, proposed as the homologue of the hippocampus of amniotes, is also selectively involved in trace classical conditioning, a learning task that in humans require declarative memory and the awareness about the CS-US relationships (Clark & Squire, 1998; Knight, Nguyen, & Bandettini, 2006).

2. Methods and materials

2.1. Subjects

The experiment was carried out on 96 goldfish (*Carassius auratus*) of 12–14 cm in length obtained from an authorized supplier (GreenFish, Spain). Goldfish were housed in 200 L glass aquaria with aerated and filtered water at 19 ± 1 °C and subjected to a 14/10h light/dark cycle for two months before the experiment. Animals were fed twice a day with dry food for pond fish (Tetra-Pond, Germany). Goldfish were randomly assigned to one of the following surgery groups ($n = 24$, for each one): sham operated (Sh), telencephalon ablated (Tel), ventral part of the lateral division of the area dorsalis telencephali lesioned (Dlv), and pseudoconditioning unoperated (Pseudo). All animal procedures were performed under the guidelines of the European Community Directive 2010/63/UE and Spanish legislation (RD 53/2013).

2.2. Surgery

Animals were anesthetized by immersion in a solution 1:20,000 of tricaine methanesulfonate (MS222, Sigma) and then

immobilized in a surgical chamber with a constant flow of aerated water through the gills containing the same concentration of anesthesia. The lesions were performed by aspiration according to previously described methods (Durán et al., 2010; Martín, Gómez, Salas, Puerto, & Rodríguez, 2011). The location and extension of Dlv lesions were delimited according to Northcutt (2006). In the Tel group, both telencephalic lobes were aspirated carefully and the olfactory bulbs were spared. In Sh animals the nervous tissue was not damaged. Following surgery the fish were allowed to recover for a 4-days period before the beginning of training.

2.3. Apparatus

The apparatus and experimental setup used in this experiment was thoroughly described previously (Gómez, Durán, Salas, & Rodríguez, 2010; Martín et al., 2011). Briefly, the training was conducted in a conditioning chamber in which the animal remained immobilized between two curved plastic pads and partially covered with water. The CS consisted of a red light (illumination intensity = 200 lx) supplied by a transmitter photodiode (wavelength = 626 nm) placed at a distance of 1.5 cm from the left eye. The US consisted of a mild electric shock (train duration, 100 ms; width pulse, 10 ms; pulse rate, 50 Hz) provided by a stainless steel bipolar electrode (diameter = 100 μ m) subdermally implanted on the left side of the rostral extreme of the dorsal fin. The intensity of the US was adjusted for each animal to the lowest value (5.09 ± 0.1 mA; mean \pm SEM) required to elicit a reliable unconditioned response. The timing, duration and intensity of the CS and the US were provided by a digital stimulator (DS8000, World Precision Instruments, UK) controlled by MED-PC program (MED Associates, USA).

To monitor heart rate, bipolar silver cup electrodes were placed in the skin under the pectoral fins on both sides of the ventral thoracic cavity. The electrocardiographic (ECG) signal was amplified 50,000 \times and band-pass (0.1–50 Hz) filtered by a differential amplifier (NL905, Digitimer, UK), digitized at 500 Hz by an A/D converter and stored for offline analysis (Snapshot Storage Scope, HEM Data, USA). Data were acquired for 60 s in each trial, starting 20 s before CS presentation. Heart rate was assessed by detecting the frequency of occurrence of the R-peak from the ECG waveform. Trials with movement artifacts or arrhythmic heart rate during the baseline period were not included in any analysis.

2.4. Behavioral procedures

Before training, all animals were acclimated to the conditioning chamber for 60 min. During this time, animals were exposed to the experimental situation except the CS and the US. After this acclimation period, animals were trained in two consecutive phases: habituation and acquisition. Habituation phase consisted of 8 presentations of CS in order to ensure the habituation to the light. The acquisition phase in Sh, Tel and Dlv groups consisted of 54 paired presentations of CS and US and 6 CS-alone trials (test trials), which occurred once every 9 paired trials. Animals in Sh, Tel, Dlv and Pseudo groups ($n = 8$ for each one) were randomly assigned to one of three conditioning procedures: trace, short delay and long delay. The two different delay procedures were used to control for potential CS duration (short delay) and interstimulus interval (long delay) effects during acquisition. In the trace conditioning procedure a 13.9 s free-stimulus interval was introduced between a 1-s CS and the US (interstimulus interval, ISI = 14.9 s). In both delay conditioning procedures the CS and the US overlapped and coterminated. The short delay conditioning procedure (CS = 1 s, ISI = 0.9 s) matched to the trace conditioning with respect to CS duration and the long delay conditioning (CS = 15-s, ISI = 14.9 s) matched to the trace

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