

Research Note: Role of the hippocampus in spatial memory in Japanese quail

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ABSTRACT The Japanese quail is a powerful model to characterize behavioral, physiological, and neurobiological processes in Galliformes. Behavioral tests have already been adapted for quail to assess memory systems, but despite the pivotal role of the hippocampus in this cognitive process, its involvement in spatial memory has not been demonstrated in this species. In this study, lesions were created in the hippocampus of Japanese quail, and both lesioned and control quail were tested for spatial and cue-based

learning performances. These hippocampal lesions specifically impacted spatial learning performance, but spared learning performance when birds could solve the task using their cue-based memory. These findings, thus, highlight that the hippocampus plays a crucial role and is essential for spatial declarative memory. Future studies could aim to elucidate the cellular or molecular mechanisms involved in this form of memory.

Key words: spatial memory, cue-based memory, hippocampus, quail

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INTRODUCTION

The Japanese quail belongs to the order Galliformes and to the same family as chicken, Phasianidae. Japanese quail are small birds, easy to raise, with a rapid growth rate and a fast life cycle as they become sexually mature only 5 to 6 wk after hatching. These characteristics make Japanese quail a suitable animal model in many areas of avian biology (Mignon-gastreau and Minvielle, 2003; Huff et al., 2013; Beck et al., 2014; Molino et al., 2015; Knaga et al., 2018) and, more specifically, a powerful model for avian neurobiological studies. Quail have been extensively used to identify brain mechanisms responsible for seasonality, photoperiodism (Yoshimura, 2013), and for understanding the neurobiological bases of the reproductive activities of birds (Cornil et al., 2013; Qasimi et al., 2018). The fact that divergent lines of quail can be selected on behavioral patterns (Mills and Faure, 1991; Guzman et al., 2013) and, more recently, that transgenic quail can be produced (Seidl et al., 2013) are additional reasons why quail constitute a powerful model for research on bird neurobiology.

The brain mechanisms underlying the functioning of memory have been relatively well characterized in

mammals through investigations conducted on animal models, such as rats or mice, but those involved in birds are little known. Previous experiments have shown that birds are able to learn and memorize the location of a hidden reward using their spatial memory, a form of declarative memory based on forming a mental representation of the different positions of cues in the environment and requiring the hippocampus (Hampton and Shettleworth, 1996; Fremouw et al., 1997). Birds can also learn the location of a hidden reward using forms of non-declarative memory, as cue-based memory, which is considered to be relatively simple being based on a simple cue-response association. This form of non-declarative memory has been shown to be distinct from the spatial declarative memory because it is independent of the functioning of the hippocampus (Hampton and Shettleworth, 1996; Fremouw et al., 1997).

The present study aimed to demonstrate that the hippocampus was involved in spatial memory in quail to provide the basis for further neurobiological investigations in this species. Previous research indicates that quail should also be able to use both spatial and cue-based memories to solve a memory task (Ruploh et al., 2011; Lormant et al., 2018). To reach our objective, we first invalidated the hippocampus and then tested control and lesioned quail in 2 appropriate behavioral tests to study 2 forms of declarative and non-declarative memory, spatial and cue-based memory, respectively (Lormant et al., 2018).

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MATERIALS AND METHODS

Subjects

We used male Japanese quail bred and reared at the Pôle d'Expérimentation Avicole de Tours (UE PEAT, INRA, Nouzilly, France) unit where the experiment was performed. All birds were reared in individual cages in a battery (41 cm × 51 cm × 25 cm) under a 12:12 h light–dark schedule (light on: 06:00 h) at approximately 20 ± 2°C. Unless otherwise specified, food and water were provided *ad libitum*. Animal care and experimental treatments complied with the guidelines of the French Ministry of Agriculture for animal experimentation and European regulations on animal experimentation (86/609/EEC). They were performed in accordance with local animal experimentation regulations (authorized N°006352 of the French ministry of Agriculture in accordance with EEC directive) and with the ethics committee Val de Loire (agreement N°01833.01).

Surgery

Lesions of the hippocampus were performed when birds were between 4 to 5 wk old. A total of 11 birds with a lesion of the hippocampus and 9 sham-operated birds were submitted to the spatial task. A new cohort of 8 birds with a hippocampal lesion and of 11 sham-operated birds was used and tested in the dual spatial or cued task.

Quails were anesthetized (TEM Sega, France) with isoflurane 3% and placed in a stereotaxic instrument. Coordinates of holes and injection were 1.5 mm anterior to the parieto-occipital suture, 0.4 mm laterally to the sagittal midline and at a depth of 0.6 mm from the brain surface. A volume of 0.2 µL of N-Methyl-D-Aspartate (NMDA, Santa Cruz) solution (10 mg/mL; lesioned animals) or of saline solution (sham-operated animals) was injected in each hippocampus at the rate of 0.1 µL/min over a 2 min period through a Hamilton syringe fitted with a glass micropipette drawn to a fine tip. NMDA was chosen because it induces neuronal damage sparing fibers of passage (Zhang et al., 2004). The needle remained in place for 2 min after completion of the infusion before being withdrawn. The holes were sealed with a gelatin sponge, the skin was sutured and the bird was placed back in its home cage and left undisturbed for a period of 1 to 2 wk. Birds were only trained and tested after surgery, never before surgery.

The Spatial Learning Task

This test was previously used for quail by Lormant et al. (2018). Briefly, each bird was individually habituated to an octagonal arena (length of each side 50 cm) surrounded by walls and by a curtain. A total of 8 black visual cues were placed on the walls of the arena and on the curtain. A total of 8 cups were placed on the ground in the arena. About 1 h before each habituation session,

food was removed from the home cage. Once a day for 3 consecutive days, each quail was introduced into the center of the arena where each cup contained a mealworm. Birds were allowed to explore the arena and the cups freely until they found and ate all the mealworms or after a maximum time of 600 s. On each day, the number of worms eaten during the habituation session was recorded. For the eight following consecutive days, birds completed 3 spatial training trials per day with an inter-trial interval of 1 h. In each trial, the bird had to locate the 1 cup that contained 3 to 4 mealworms among the 8 identical cups placed in the arena. The location of the sole reward cup was constant throughout all the trials. The tested bird entered the area from 1 of 3 different starting points chosen randomly for each trial. The trial ended when the bird reached the reward cup and ate the mealworms or after a maximum of 300 s. The latency to reach the reward cup was measured for each trial and considered as a learning indicator (Lormant et al., 2018). The day following the last spatial training trial, animals underwent a probe test during which no food was deposited. Each bird entered the arena containing the 8 cups through a new entry and the latency to reach the target cup (the cup containing the reward during training) was scored.

The Dual Spatial or Cued Task

The arena used for the spatial or cued task, the habituation procedure and training were similar to those described above. This task was previously described in detail in Lormant et al. (2018). For the spatial or cued task, all the cups were black, except the reward cup that was white and contained 3 to 4 mealworms. The location of the sole white reward cup was the same for each trial. Thus, to solve the task and find the reward, birds could learn the “spatial” location of the reward cup (spatial memory) or simply learn that the white cup contained the reward (cue-based memory). In each trial, the latency to find the reward cup was recorded as a learning indicator. During the test performed the day following the last training trial, no cups contained any food and the white cup was relocated to another position. If the bird went back and visited the cup located in the same position as the reward cup during the training, it was categorized as a spatial learner. If the bird visited the relocated white cup, it was categorized as a cued learner.

Histology

About 6 to 8 wk after surgery, birds were sacrificed with an overdose of pentobarbital 6% (36 mg/100 g) and perfused transcardially with a saline solution followed by 300 mL of 4% paraformaldehyde. Brains were then removed from the skull, post-fixed overnight in paraformaldehyde, cryoprotected (sucrose solution 20%), and frozen in dry-ice. Brain were then sectioned in the coronal plane on a cryostat at −15°C at 50 µm.

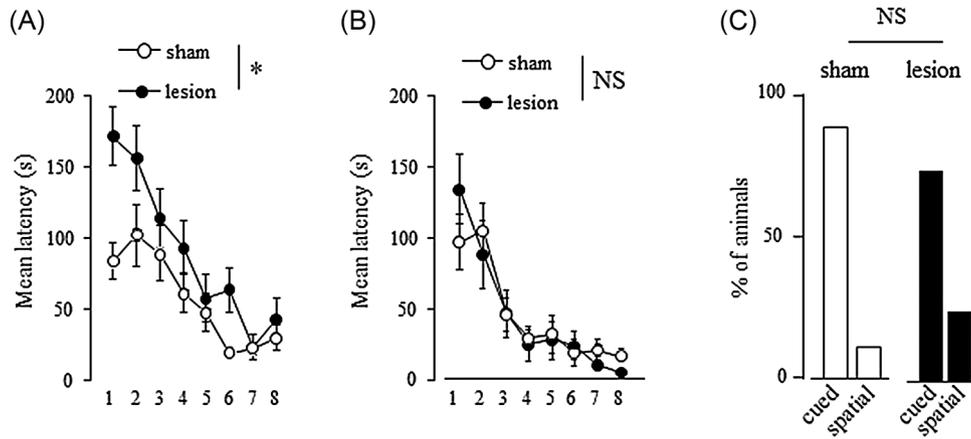


Figure 1. Learning and memory performances. **(A)** Mean latency (\pm SEM) to find the target cup over the consecutive days of the spatial training task (control operated $n = 9$; hippocampal lesioned quail, $n = 11$). **(B)** Mean latency (\pm SEM) to reach the target cups over the consecutive days of training of the dual spatial or cued task in control ($n = 11$) and hippocampal lesioned quail ($n = 8$). **(C)** Number of quail choosing the relocated white cup (cued) or the spatial location (spatial) during the probe test of the dual spatial or cued task. $*P < 0.05$

Sections were collected on Superfrost Plus microscope slides (Thermo Scientific). Every 6 sections were stained with Cresyl violet to determine the placement and extent of the lesion under a light microscope.

Statistical Analysis

Data from habituation (number of worms eaten) and training (latency to reach the target cup) were analyzed using parametric analyses of variance (ANOVA) with the groups as between-subject factors and with trials and days as within subject factors when required. For the test performed after spatial training, comparison of latency to reach the target cup between groups was analyzed using a *t*-test for independent groups. For the test conducted following the spatial or cued training, comparison of the number of animals choosing the spatial or the cued location between groups was analyzed using a Fisher's exact test. All statistical analyses were conducted using version 5.0 of the StatView statistical software (Abacus Concepts Inc., Berkeley, CA). Statistical significance was set at $P < 0.05$.

RESULTS

The Spatial Learning Task

Both quail with hippocampal lesion and sham-operated ones similarly habituated to the task because no difference was observed between both the groups in the increased number of mealworms eaten over days of habituation (effect of days: $F_{2,36} = 7.40$, $P = 0.002$; effect of group: $F_{1,18} = 0.51$, $P = 0.48$; interaction days \times groups: $F_{2,36} = 0.45$, $P = 0.64$; number of worms eaten, mean \pm sem—Day 1 sham: 5.22 ± 1.06 , NMDA: 5.27 ± 0.92 ; Day 2 sham: 7 ± 0.41 , NMDA: 6.09 ± 0.46 ; Day 3 sham: 7.56 ± 0.24 , NMDA: 6.91 ± 0.39).

During training, the latency to find the reward cup decreased over consecutive days of the experi-

ment in both the groups (effect of days: $F_{3,54} = 15.31$, $P < 0.001$; interaction days \times lesion: $F_{3,54} = 1.43$, $P = 0.24$; Figure 1A) but was higher in lesioned than in sham-operated birds (effect of lesion: $F_{1,18} = 5.11$, $P = 0.037$). During the test, the latency to find the target cup did not differ between the lesioned and sham-operated groups (mean \pm sem, sham: 25.11 ± 5.35 s; NMDA: 45.09 ± 12.85 s; $P = 0.20$).

The Dual Spatial or Cued Task

Both sham-operated and lesioned birds similarly habituated to the arena and the cups because no difference was observed between groups in the increased number of mealworms eaten over days of habituation (effect of days: $F_{2,34} = 25.00$, $P < 0.001$; group effect: $F_{1,17} = 0.06$, $P = 0.82$; interaction days \times groups: $F_{2,34} = 0.24$, $P = 0.79$; number of worms eaten, mean \pm sem—Day 1 sham: 1.73 ± 0.65 , NMDA: 1.88 ± 1.08 ; Day 2 sham: 4.73 ± 0.92 , NMDA: 4.50 ± 1.36 ; Day 3 sham: 6.46 ± 0.47 , NMDA: 5.75 ± 1.19).

During training, the latency to find the reward cup decreased over consecutive days of the experiment in both the groups (effect of days: $F_{3,51} = 21.85$, $P < 0.0001$; effect of lesion: $F_{1,17} = 2.25 \times 10^{-4}$, $P = 0.99$; interaction days \times lesion: $F_{3,51} = 0.25$, $P = 0.86$; Figure 1B). During the probe test (Figure 1C), 2 control birds choose neither the spatial location nor the white cup and were, thus, not included in the analysis. Indeed, independent of the lesion status ($P = 0.58$), birds preferentially chose the relocated white cup (8 out of 9 sham birds and 6 out of 8 lesioned birds).

Histological Evaluation of the Lesion

The location and extent of the lesion was relatively easy to determine due to the loss of cells within the lesioned area (Figure 2A). Typically, lesions were restricted to the dorsomedial part of the hippocampus

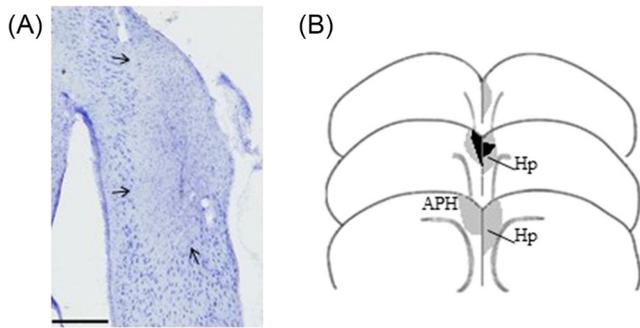


Figure 2. Illustration of an NMDA hippocampal lesion. (A) Cresyl violet staining of NMDA hippocampal lesioned quail. The arrows indicate the outline of the lesion. Scale bar: 200 μm . (B) Representation of the hippocampal lesion along the rostro-caudal axis of the quail hippocampus. The black and gray areas illustrate the smallest and largest lesions, respectively (Hp, hippocampus; APH, parahippocampal area).

located in the anterior hippocampus (Figure 2B) between the level of planes 5.0 to 6.0 of the quail atlas (Baylé et al., 1974). On the basis of the recent chick atlas (Puelles et al., 2018), lesions were located at the level of planes 14 to 20, mainly in the subdivisions 1 and 2 of the hippocampus, without reaching the dentate gyrus primordium.

DISCUSSION

Our results support previous lesion studies (Hampton and Shettleworth, 1996; Fremouw et al., 1997) demonstrating that the hippocampus is engaged in the functioning of spatial memory in birds. Previous studies demonstrated that injections of 0.1 μL (10 mg/mL; Patel et al., 1997; Bailey et al., 2009) or injections of 0.1 to 0.5 μL (100 mg/mL; Watanabe and Bischof, 2004) of an ibotenic acid solution induced a partial excitotoxic lesion of the hippocampus, sufficient to impair spatial memory performance in birds. The present study evidenced that bilateral injections of 0.2 μL of NMDA solution (10 mg/mL) were also suitable to produce a lesion of the hippocampus. The avian hippocampus has a relatively high density of glutamate receptors, including NMDA receptors (Herold et al., 2014). This makes this brain region in birds sensitive to the adverse effects of NMDA injections, in a similar way to the mammalian hippocampus.

The size of the lesion obtained in the present study appeared quite small compared to those obtained by aspiration or electrolytic lesions, 2 techniques often used to achieve hippocampal lesions in birds (Fremouw et al., 1997; Colombo et al., 2001; Tommasi et al., 2003; Kahn and Bingman, 2009). This relatively small size of the lesion could be related to a potential tissue recovery. Previous studies in birds have shown that, following lesions, a complete tissue recovery could be observed in the striatum (Kubikova et al., 2014) and the High Vocal Center (Scharff et al., 2000). Moreover, tissue recovery seems to be faster following neurotoxic lesions than electrolytic lesions and mediated by recruitment of new neurons. As the hippocampus in birds also

integrates newborn neurons (Barnea and Pravosudov, 2011), we cannot totally exclude that the size of the lesion reported in the present study was minimized by potential tissue recovery. The lesions produced by NMDA injections appeared restricted to the anterior hippocampus. Together with the fact that NMDA injections produce neurotoxic lesion and spare fibers of passage, these findings may suggest a specific role of the anterior hippocampus in spatial memory. However, further studies will be necessary to characterize with precision a possible specific role of different hippocampal sub-regions in spatial learning and memory in quail.

The present study provided evidence that the effect of the hippocampal lesion depends both on the task considered (spatial vs. cued or spatial) and the phase (habituation vs. acquisition vs. test phase). This specificity of the effect of the lesion strongly suggests that the lesion has no general effect on the locomotor activity or motivation of the quail. If the lesion had a general effect on motivation or locomotor activity, a difference between lesion and control birds should have been observed during the habituation phase, when all the cups were rewarded. An effect of the lesion on motivation would have also produced a similar effect on the latency to find the rewarded cup in the training phase of both the spatial and the spatial or cued tasks, as in the 2 tasks, birds had to find mealworms hidden in an opaque cup. Rather, the specificity of the effect of the lesion on the latency to find the reward during the learning phase of the spatial task suggests the lesion only impaired learning performances when the spatial location was the main relevant information to find food in the arena. When animals could learn the task using a memory system based on the color of the cup (cue-based memory), the lesion did not produce any significant effect. This is confirmed by the probe test conducted in the dual spatial or cued task that showed that both the sham-operated and lesioned quail similarly followed the relocated white cup. Altogether, our results support previous lesion studies (Hampton and Shettleworth, 1996; Fremouw et al., 1997; Tommasi et al., 2003) or cellular imagery studies (Mayer et al., 2016) demonstrating that the hippocampus is engaged in the functioning of spatial memory in birds.

As mentioned, the effect of the lesion was probably not permanent and essentially observed during the early phase of training of the spatial task. In line with this, previous studies have shown a similar transient effect of the lesion of the hippocampus on spatial learning and memory performances (Morris et al., 1982; Fremouw et al., 1997). These findings were indeed at the origin of the demonstration there are multiple memory systems into the human and non-human animal brain (Squire, 1992; Clayton and Krebs, 1994; White and McDonald, 2002; Poldrack and Packard, 2003; Packard, 2009; Mayer and Bischof, 2012; Squire and Dede, 2015; Mayer et al., 2016). Indeed, animals can use different memory systems to learn a task. Previous studies even showed the level of training can influence the relative use of

multiple memory systems. Indeed, rats trained to learn the location of a reward in a maze preferentially use their spatial hippocampus-dependent memory after few days of training and shift to a cue-based dominant response with extended training (Packard and McGaugh, 1996). Such findings may contribute to explain the results obtained in the present study. During the early phase of training of the spatial task, the hippocampus-dependent memory system would be required for the quail to solve the task. Thus, quail with a lesion of the hippocampus would exhibit a deficit in learning during the early phase of the spatial task. With training, the impairing effect of the lesion would decrease because overtraining would be associated to a shift to the use of a hippocampus independent memory system. Finally, the impairing effect of the lesion would be specific of the spatial task and absent in the spatial or cued task because, in this task, thanks to the presence of a colored cup, birds would preferentially use a hippocampus independent cue-based memory system.

In a recent study, we demonstrated that quails were able to solve both the spatial and the dual spatial or cued tasks (Lormant et al., 2018). The present study confirms this finding and provides evidence that, in quail, a dissociation may exist between a hippocampus-dependent spatial memory system and a hippocampus-independent cue-based memory system, regarding both the cognitive processes engaged as well as the neural substrates that underline the 2 systems. The development of specific learning and memory tests in this model may represent an important step for future studies dedicated to a better understanding of the neurobiological bases of learning and memory in birds.

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