



Septal area lesions impair spatial working memory in homing pigeons (*Columba livia*)

Ryan M. Peterson*, Verner P. Bingman

Department of Psychology and J.P. Scott Center for Neuroscience, Mind, and Behavior, Bowling Green State University, Bowling Green, OH 43403, United States

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ABSTRACT

The septo-hippocampal system in birds resembles that of mammals, motivating research into the function of the avian hippocampus while surprisingly little attention has been given to the septum. To investigate a possible role of the avian septum in memory, the effects of septal area lesions on a spatial working memory (SpWM) task was tested in homing pigeons. After preoperative training on an analogue eight-arm (feeders) radial maze, now sham-operated control and septal lesioned pigeons were then trained again on the same task of locating the four feeders on the test phase of a trial that were not baited during the sample phase of a trial. During the test phase of a working memory trial, septal lesioned pigeons, compared to both their own preoperative performance and the performance of the controls, required significantly more choices to locate the four baited feeders not baited during the sample phase of a trial, and they made significantly fewer correct responses to the now baited feeders on their first four choices. The results demonstrate that, like its mammalian counterpart, the avian septum plays an important role in SpWM, suggesting that at least some functional properties of the septum are evolutionarily conserved in birds and mammals.

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1. Introduction

Working memory (WM) is the ability to temporarily store, manipulate, and process information used to guide behavior as well as contribute to the storage of information from previously learned episodes (Baddeley, 2003). The ability to employ WM using space as a discriminative stimulus, termed spatial working memory (SpWM), is an adaptive cognitive capacity that supports, among other things, efficient foraging behavior in a range of animal species (Olton, 1985). Robust SpWM ability in many species may explain why they exhibit a propensity to solve foraging challenges on the basis of their spatial characteristics (Balda & Kamil, 1988; Brodbeck, 1994; Brown, Rish, VonCulin, & Edberg, 1993; Hurly, Franz, & Healy, 2009).

The mammalian prefrontal cortex (PFC) and its functional equivalent in the avian brain, the nidopallium caudolaterale (NCL), have been implicated in the control of executive functions such as WM based on observations that damage to either structure

yields WM deficits (mammals: Goldman & Rosvold, 1970; Mishkin, 1957; birds: Diekamp, Gagliardo, & Grüntürkün, 2002; Mogensen & Divac, 1993), as well as unit recordings that have determined that both the PFC and NCL contain populations of neurons that exhibit sustained activity during WM tasks (mammals: Funahashi, 2006; Fuster, 1973; birds: Diekamp, Kalt, & Grüntürkün, 2002; Rose & Colombo, 2005). But in addition to PFC, lesion studies in mammals have found SpWM deficits after damage to the septal area (Numan & Klis, 1992; Numan & Quaranta, 1990; Rashidy-Pour, Motamedi, & Motahed-Larjani, 1996). The origin of this effect is likely due, in part, to the strong connections between the septum and hippocampal formation (HF; Swanson & Cowan, 1979), which is also important for SpWM (Olton, Becker, & Handelmann, 1979).

The avian HF has been extensively studied in the context of spatial cognition such as homing (e.g., Bingman & Mench, 1990), landmark-based navigation (e.g., Gagliardo, Ioalè, Savini, Dell'Omo & Bingman, 2009), and spatial learning (e.g., Kahn & Bingman, 2004) and memory (e.g., Sherry & Vaccarino, 1989; Smulders, Sasson, & DeVoogd, 1995; see also Colombo & Broadbent, 2000). Important in the context of the current study, Good and Macphail (1994) reported SpWM deficits in homing pigeons following aspiration of HF. In contrast to HF, the role of the septum in avian cognition, and spatial cognition in particular, has remained unstudied despite the anatomical connections between the avian septal area and HF (Krayniak & Siegel, 1978a, 1978b; Montagnese, Szekely, Adam, &

Abbreviations: DBB, diagonal band of Broca; FIRST4, first four choices; HF, hippocampal formation; SL, lateral septum; SM, medial septum; NCL, nidopallium caudolaterale; PE, proactive errors; PFC, prefrontal cortex; RE, retroactive errors; SpWM, spatial working memory; TOT-TEST, total choices in test phase; TOT-SAMPLE, total choices in sample phase; WM, working memory.

* Fax: +1 419 372 6013.

E-mail address: rpeters@bgsu.edu (R.M. Peterson).

Csillag, 2004; Montagnese, Zachar, Balint, & Csillag, 2008). The sparse functional research on the avian septal area has predominantly focused on its involvement in heart rate conditioning (Cohen & Goff, 1978) and regulation of social behavior (Goodson, Eibach, Sakata, & Adkins-Regan, 1999), understood based on its efferent projections to the hypothalamus. The dearth of research on the possible relationship between the avian septal area and spatial cognition is perhaps even more surprising given that the avian septum is homologous to the mammalian septum. For example, the neurochemically defined subdivisional organization of the avian septum resembles the mammalian septum (Goodson, Evans, & Lindberg, 2004). Comparative examination of developmental gene expression also reveals similarities between mouse and chick along both the dorsal (pallial) and ventral (subpallial) portions of the septum (Puelles, Kuwana, Puelles, & Rubenstein, 1999; Puelles et al., 2000).

We began this study by hypothesizing that, like its mammalian counterpart, the avian septum participates in the control of SpWM. To test this hypothesis, control and septal lesioned homing pigeons were trained in an analogue radial-arm maze (Spetch & Honig, 1988) to select among eight radially distributed feeders for food reinforcement. The study is designed such that in order to efficiently deplete the available food at the feeders, a pigeon must remember those feeders it had already visited, increasing the WM load after each choice. We predicted that septal lesioned pigeons would display impairment in SpWM by making more choices to feeders that had already been depleted during a trial.

2. Materials and methods

2.1. Subjects

Fourteen unsexed homing pigeons (*Columba livia*), obtained from the pigeon colony at Bowling Green State University, were used in this study. Following preoperative testing (see below), nine birds underwent septal lesion surgery; the remaining five underwent a sham-surgical procedure. Because the current study was the first to examine the spatial cognitive effect(s) of septal lesions in birds, we preferred a larger number of experimental pigeons to eventually explore any relationship between the size and location of the lesions and the size of any behavioral deficits. All birds were housed individually in wire mesh cages (26.7 × 29.8 × 28.6 cm) in a temperature and humidity controlled room and a 12–12 h light/dark cycle (lights on at 07:00). All birds were food deprived to no less than 85% of their baseline weight and allowed ad lib access to grit and water. Each bird's weight and feeding records were monitored daily. All procedures were carried out in accordance with National Institute of Health guidelines and approved by Bowling Green State University's Institutional Animal Care and Use Committee (ICAUC).

2.2. Surgery

2.2.1. Septal lesions

After completion of preoperative testing, nine birds underwent electrolytic lesion of the septum. The pigeons were anesthetized with Isoflurane gas and placed in a stereotaxic apparatus. A portion of the skull was removed to expose the brain and an electrode, a stainless steel insect pin insulated with epoxy (EpoxyLite Corp., Westerville, OH) with an 1.3 mm exposed tip, was inserted into the brain to produce the lesions. Three, bilateral lesion-target coordinates were used to produce the septal lesions: A 6.8, L ± 0.8, V 8.5; A 7.4, L ± 0.8, V 8.5; A 8.0, L ± 0.8, V 8.0. All lesion coordinates were determined using the stereotaxic atlas of the pigeon brain (Karten & Hodos, 1967). For each lesion burn, 3.0 μA of current

was applied for 15 s at the most anterior coordinate and 20 s at the two most posterior coordinates. Following the lesions, the electrode was removed and the skin over the skull was closed with wound clips and swabbed with Betadine to prevent infection. The pigeon was then returned to its home cage and placed on ad lib food and water for 7 days, at which point wound clips were removed and the subject returned to food deprivation.

2.2.2. Sham surgery

Control birds underwent a sham surgical procedure following preoperative testing. The procedure was identical to the septal lesion procedure with the exception that the electrode was not inserted into the brain.

2.3. Testing environment

2.3.1. Testing room

The testing room and food sites used in this study were developed to closely match those of Spetch and Honig (1988). All training and testing occurred in an open-field, testing room approximately 2.74 × 6.4 × 7.77 m with uniform white walls and gray floor (see Fig. 1A). Various 2-dimensional wall posters and three dimensional objects scattered in the room were used to create a spatially heterogeneous environment. All behavior was observed through a small window in a plywood partition separating the testing room and the observer.

2.3.2. Food sites

Food sites (see Fig. 1B) were replicas of those used by Spetch and Honig (1988) and consisted of a platform with a ramp and a feeder. Ramps/platforms were comprised of a wooden ramp (20° incline, 18.5 cm L × 6.8 cm H at the top), which led at the top to a 12 × 29 × 4 cm platform made from a piece of hard foam insulation. The ramp rested on the edge of the platform, which led to the feeder. Feeders, attached to the platforms, were constructed from 2-l milk cartons. The apex of each carton was cut off and a semicircular hole half way down one wall of the remaining carton was made to form an entrance, which led to a food well that a bird could access. Thin poster board was attached to the cartons on the three sides that did not have the entrance to increase the height of the walls to 27 cm. Additionally, 4 cm flaps were also added to the walls on each side of the entrance; see Fig. 1B. The cartons were filled with grit to 10 cm below the lowest point of the semicircular entrance. Throughout the study, the feeders were baited by placing approximately 2.5 g of food (Purina Pigeon Chow, Ralston-Purina, St. Louis, MO) inside the feeder, against the front wall of the carton. Only by standing on top of the platform could a pigeon determine if food was present or not. The purpose for the seemingly complex feeder arrangement was to decrease the probability of a pigeon cycling through the feeders (see Spetch & Honig, 1988).

2.4. Behavioral training and testing

2.4.1. Training

The pigeons were trained to eat from feeders in three phases as described in Spetch and Honig (1988). In phase 1 training, a single food site was placed in the room (site 1; Fig. 1A). Food was placed inside the feeder and along the ramp leading up to it. A bird was placed in the center of the room with the lights turned off. The lights were turned on and the bird had 30 min to ascend the ramp and eat from the feeder. Phase 1 was repeated until the bird consumed all the food from the feeder. Once a bird had eaten all the food it was advanced to phase 2 training. In phase 2 training, four feeders were introduced to the room (sites 2, 8, 4, and 5; Fig. 1A). Food was placed in each feeder and at the top of the ramp. After

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