Title	Effects of hippocampal lesions on spatial short-team memory in pigeons
Sub Title	
Author	古屋, 泉(フルヤ, イズミ) 堀, 耕治(ホリ, コウジ) 渡辺, 茂(ワタナベ, シゲル)
Publisher	慶應義塾大学大学院社会学研究科
Publication year	1995
Jtitle	慶応義塾大学大学院社会学研究科紀要 : 社会学心理学教育学 (Studies in sociology, psychology and education). No.42 (1995.) ,p.9- 15
JaLC DOI	
Abstract	
Notes	論文
Genre	Departmental Bulletin Paper
URL	https://koara.lib.keio.ac.jp/xoonips/modules/xoonips/detail.php?koara_id=AN00069957X-00000042-0009

EFFECTS OF HIPPOCAMPAL LESIONS ON SPATIAL SHORT-TERM MEMORY IN PIGEONS

Furuya, I., Hori, K.,** and Watanabe, S.****

Pigeons were trained on a spatial delayed matching-to-sample task in an operant chamber. After stable performance was established, lesions of the parahippocampus and/or the hippocampus were carried out. The hippocampal lesions did not impair the correct ratio and the distributions of pecking locations for all delays (0.5, 2.0 and 8.0 s). These results suggest that pigeons' spatial short-term memory performance in a small space such as an operant chamber was robust against hippocampal damages.

Key words: Delayed matching-to-sample, Spatial memory, Short-term memory, Hippocampus, Pigeons

INTRODUCTION

Avian hippocampus is a one of the most exciting topics in recent studies of animal spatial memory. Some species of birds, such as marsh tit, store more than thousands of food, each in a separate place, over a period of a few weeks. They should have excellent spatial memory. In fact, the food-storing species showed good spatial memory in a spatial delayed non-matching-to-sample task (Olson, 1991; Olson et al., 1995). Krebs et al. (1989) measured volume of hippocampus of 35 species of birds and found that food-storing birds have larger hippocampus. The species more depending on stored food have larger hippocampus than birds less depending on stored food (Healy and Krebs, 1993). Large memory seems to need large space in the brain. Furthermore, the hippocampus of black-cupped chickadee enlarged on December when this species stored food (Smulders et al., 1995). The enlargement results from neurogenesis of new neurons, because seasonal changes of neurogenesis in the hippocampal area has been reported (Barnea and Nottebohm, 1994). Hippocampal lesions caused deficits in revisiting of cashed sites after storing in the black-cupped chickadee (Sherry and Vacarrino, 1989). Recently, Shettleworth et al. (1995) also reported the hippocampal lesions impaired spatial memory selectively in chickadees.

Avian hippocampus can be divided into three distinctive areas, the dorsolateral part of area parahippocampalis, the dorsomedial part of the area parahippocampalis, and V-shaped hippocampal area enclosed by the ventricles and the midline. Pigeons' hippocampus has been considered to be a homologue of the mammalian structure (Casini et al., 1986; Erichsen et al., 1991; Krayniak and Siegel, 1978). The pigeons are not food-storing species but their ability of homing may suggest that they have some kind of good spatial memory. Hippocampal lesions disrupt navigation task (Bingman et al, 1990a; Bingman et al., 1984; Bingman et al., 1985; Bingman and Mensch, 1990), delayed alteration in T-maze (Reilly and Good, 1987) in pigeons. On the other hand, performance in delayed-alteration task in operant chamber is not impaired by the hippocampal lesions (Reilly and Good, 1987).

The purpose of the present study was to examine effects of bilateral hippocampal lesions on a spatial delayed matching-to-sample task. In this task, the sample stimulus was a lit LED randomly selected from eight horizontally arrayed LEDs. After a delay during which all LEDs were lit, the pigeons should remember the location of the previously lit LED to get a rein-

* JSPS Research Fellow (Department of Psychology, Keio University)
** Department of Physiology, Saitama Medical School, 38 Moro-Hongo, Moroyama, Saitama Japan
*** Department of Psychology, Keio University

forcement. The pecking locations were monitored by a TV camera and analyzed by an image digitizer. Thus, the analysis of the distributions of peck locations for the comparison stimuli could be used to visualize the decay of the short-term memory along time passage.

MATERIALS AND METHOD

Subjects

Four experimentally naive homing pigeons (*Columba livia*) were used. They were maintained approximately at 80% of their free-feeding weights.

Apparatus

The experimental chamber (30×30×30 cm) had a rectangular opening centered in the front panel which provided access to a 2 cm high by 22 cm wide portion of a transparent key at a height of 18 cm above the floor. There were eight red LED lamps (4.5 mm in diameter) behind the key, 2.5 cm apart from center to center. A programming software defined each LED stimulus area at 1.5 cm width. An opening of a food hopper was illuminated by a dim lamp located below the center of the key. Responses were detected by microswitches attached to the response key. Responses were monitored by a TV camera through the transparent ceiling panel. There was a ceiling lamp (AC30W) trans-illuminated through the ceiling panel. The video signal from the TV camera was transmitted to an image memory board of a NEC PC 9801 microcomputer and digitized to decide a peck location.

The experiment was controlled by the NEC PC9801 microcomputer with Photoron FDM98-1 image memory board. For details of this instrumentation, see Hori and Watanabe (1987).

Behavioral Procedure

The subjects were first handshaped to peck an area of illuminated LED, then progressively to a spatial delayed matching-to-sample task. The spatial delayed matching-to-sample task training is as follows.

When the sample stimulus (one of the eight LED lamps) was turned on, a peck at this area (1.5 cm width) turned off the LED and the ceiling light. After a 0.5 s delay, matching stimuli

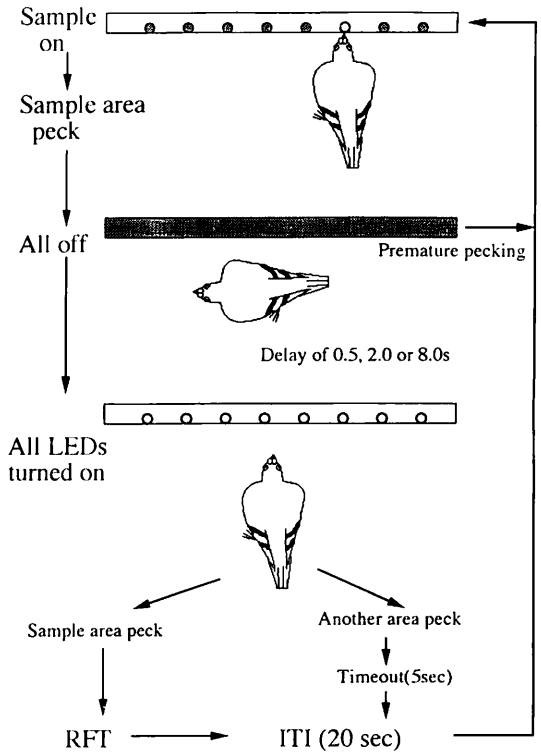

Fig 1. Schematic representations of spatial delayed matching-to-sample task. The subjects must match the sample stimulus, one of the eight horizontally arrayed LEDs after 0.5, 2.0 or 8.0 sec delay. Correct matching response was reinforced by 4 sec access to the food hopper. And followed by a 20 sec ITI (intertrial interval); while incorrect responses produced a five second timeout followed by the ITI. One session consisted of 72-trials.

of all eight LED lamps were turned on. Responses during the delay period produced a five second timeout followed by the correction trial in which the previous sample stimulus was presented again. Correct matching response was reinforced by 4 s access to the food hopper. Then followed by a 20 s ITI (intertrial interval); while incorrect responses produced a five second timeout followed by the ITI. One session consisted of 72-trials. Presentation order of eight positions of the sample stimulus was randomized in each session. If animals showed above 80% correct ratio on this training session,

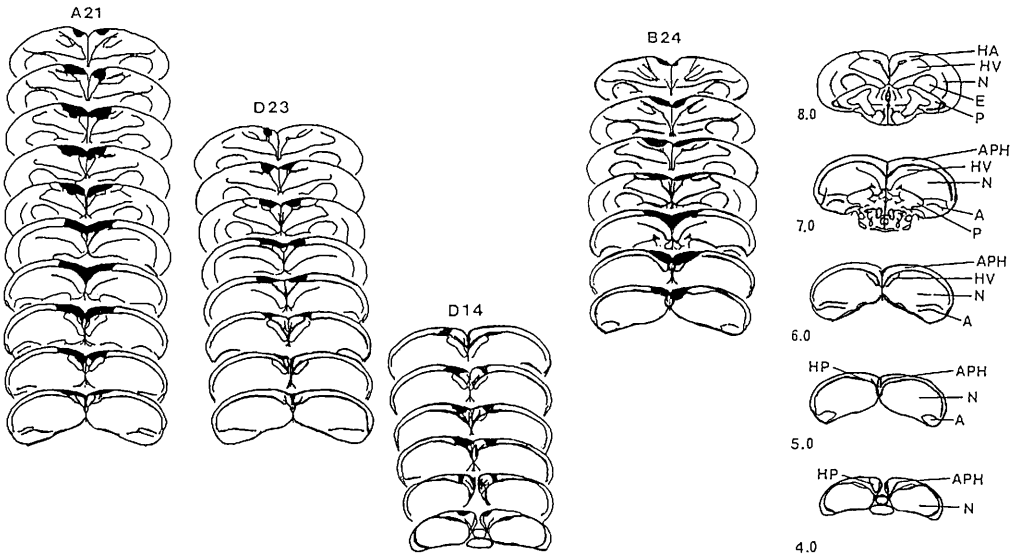

Fig 2. Serial reconstruction of the parahippocampal and/or hippocampal lesions in each subject. HA: hyperstriatum accessorium; HV: hyperstriatum ventrale; N: neostriatum; E: ectostriatum; P: paleostriatum; APH: area parahippocampalis; and HP: hippocampus. Darkened area show extent of lesion damage.

final training phase began. The final phase involved three delays of 0.5, 2.0 and 8.0 s. Presentation order of three delay conditions and the sample stimulus was randomized in each session. The rest of procedures were same as the previous trainings (See Fig. 1).

Training was considered to be complete when animals exhibited a stable performance on the spatial delayed-matching-to-sample task (the correct ratio obtained from ten sessions of each delay did not show tendencies to improve or to decline over successive ten sessions). Afterward, all four subjects received bilateral lesions of hippocampus. Following a 10-day recovery period, 10 sessions of postoperative training began. The procedure of postoperative training was identical with that of the preoperative training.

Surgery

The subjects were anesthetized by ketamine and were fixed in a stereotaxic instrument. A local anesthetic of procaine was then injected into the incision site. Lesions were made by aspiration through a glass pipette. The target coordinates were obtained from the standard pigeon's brain atlas (Karten and Hodos, 1967).

Histology

After completion of behavioral experiment, the subjects were deeply anesthetized by sodium pentobarbital, then perfused with biological saline followed by Heidenhein's solution without mercuric chloride. The brains were removed from the skulls and were kept in 10% formal saline solution for one week, then embedded in paraffin, and cut at 10 μm. Every tenth section was mounted, counterstained with cresyl violet and luxol fast blue, and examined microscopically. Reconstructions of the lesions were made on images of the atlas of pigeons' brain displayed on TV screen conneced to a computer.

RESULTS

Histological Results

Fig. 2 gives reconstructions of damages. The subjects can be divided into two groups according to area of damages. D14 and D23 had restricted damages mostly to the area parahippocampalis. Hippocampus, especially its caudal parts, was mostly intact. A21 and B24 had extended damages to the area parahippocampalis and the hippocampus. The most ventral part of the hippocampus was, however, not com-

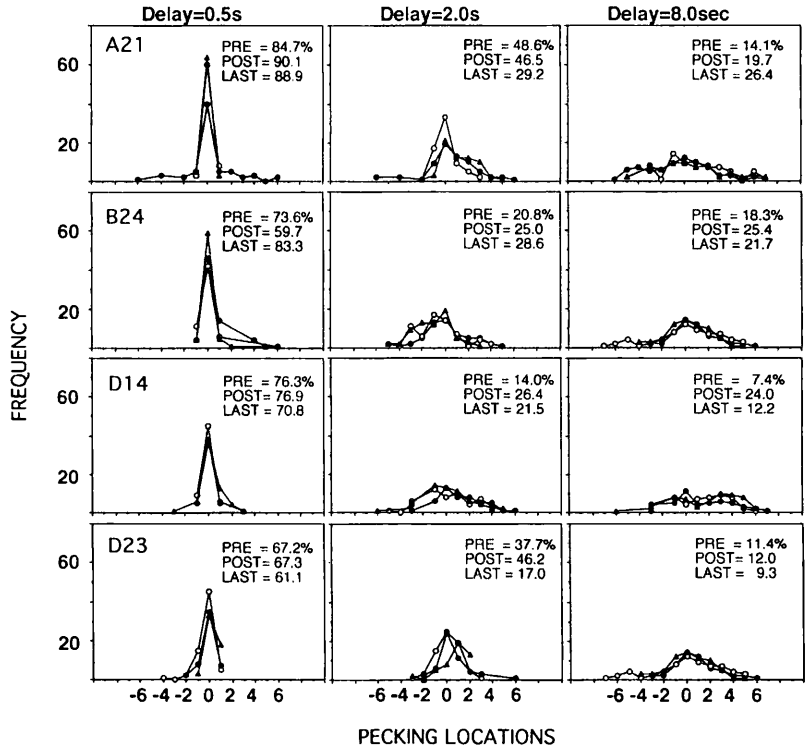

Fig 3. The percentage of correct and the distributions of peck locations for comparison stimuli for each subject(n=4) over the preoperative (last 3 sessions: open circles), the postoperative (first 3 sessions: solid circles) and the last sessions of postoperative (8th to 10th from the first postoperative session: solid triangles). The pecking locations were divided into eight 2.5 cm width portions (the LEDs were centered on the each portion), and the spatial differences between the sample portion and the portion of pecking were calculated. Zero pecking location indicates that the subjects pecked the same portion of the sample presentation. A peck on the rightmost key when the sample stimulus was previously illuminated on the leftmost key would mean +7, and *vice versa*. This would mean a maximum of 7 positive and 7 negative values. This would explain the occurrence of more than 8 plotted points on some graphs.

pletely ablated in their caudal extent. The dorsomedial parts of their hyperstriatum ventrale were slightly damaged. The dorsal part of the caudal neostriatum and the Wulst were also slightly damaged in these two birds.

Behavioral Results

After 80-100 sessions of training, all four pigeons reached the stable performance. Fig. 3 shows the correct percent and the distributions of peck location for comparison stimuli for each subject over the preoperative (the last three sessions), the postoperative (the first three sessions) and the last sessions of postoperative (8th to 10th from the first postoperative session). The pecking locations were divided into eight portions (2.5 cm width and the LEDs were centered on the each portion), and the spatial differences between the sample portion and the portion of pecking were calculated. Thus, the zero pecking location indicates that the subjects pecked the same portion of the sample presentation (but not all these peckings were reinforced because the correct response areas were defined at 1.5 cm width). The negative values of pecking locations represent the pecking portions differed on the left side from the sample portion, and the positive values vice versa.

All animals showed a narrow and steep distribution at the shortest delay and larger variabil-

ity as the duration of delay increased. The subjects showed an inverted U-shape of peck distributions even after 8.0 s delay. After the lesions, no consistent changes were observed in these distributions.

The two-factor ANOVA of randomized block factorial design for the correct ratio (subjected to arc-sine transformation) on lesions and delay showed significant main effect of delay only [$F(2, 6)=70.85$, $p<0.01$]. There were no significant main effects of the lesions [$F(2, 6)=0.60$, $p=0.58$] nor interaction [$F(4, 11)=1.29$, $p=0.33$]. These results have provided no deficits in the spatial delayed matching-to-sample performance after the hippocampal lesions in the operant chamber.

DISCUSSION

The present results clearly showed no deficits in spatial short-term memory after the hippocampal lesions. These results are consistent with the previous study that found no deficits in spatial alternation task in an operant chamber by hippocampal damaged pigeons (Reilly and Good, 1987). However, most of the other hippocampal lesion studies found impairment in spatial memory in pigeons (Bingman et al, 1990a; Bingman et al, 1984; Bingman et al, 1985; Bingman and Mensch, 1990; Reilly and Good, 1987). These discrepancies among hippocampal lesion studies, however, resulted from differences in the experimental settings.

Experiments that showed spatial memory impairments employed fields setting (for example, Bingman et al, 1990a) or mazes (Reilly and Good, 1987). Whereas the experiments that showed no deficits employed operant cambers. Spatial memory in maze or field settings and that in operant chamber have many different characters in decay processes. In the fields setting, spatial memory tolerate 20 min or more (bingman and Mensch, 1990). Similarly, in the T-maze, spatial memory tolerate 15 s to 16 min (Olton and Maki, 1983; Reilly and Good, 1987). In contrast, temporal limits of pigeons' spatial short-term memory in operant chamber were about 10 s or less (Olton and Maki, 1983; Wilkie, 1983; Wilkie, 1984; Wilkie and Summers, 1982).

There are two reasons for these differences. First, there were many extra-spatial cues in the T-maze and the fields setting, so redundant memory traces were possible. The redundancy of memory traces might increase durability of memory trace for long delay. Second, there were many trials separated by relatively short intertrial intervals in a session of most operant chamber studies. These massed trials may produce proactive interference in successive trials. The proactive interference may restrict the performance of spatial tasks in operant chamber (Olton and Maki, 1983). Spatial memory in the T-maze and natural setting based on locomotor activities, while that in the operant chamber such as the present experiment based on visual recognition of stimulus locations.

Hippocampus in birds may have an essential role in spatial memory based on locomotor activities but not in that based on visual cues in small space such as an operant chamber (Reilly and Good, 1987).

These characters of spatial memory can be generalized mammalian studies. The effects of hippocampal lesions on spatial memory in operant chamber were less inconsiderable than that of maze in rats (Aggleton et al, 1992; Walker and Means, 1973; Walker et al, 1970; Walker et al 1972) and hippocampal lesions were ineffective to produce deficits in spatial memory of monkeys in an operant settings (Squire and Zola-Morgan, 1983).

Delayed alternation and spatial delayed matching-to-sample have been sometimes mentioned as 'non-spatial tasks rather than spatial tasks' (Olton and Maki, 1983). As a matter fact, decay time of short-term memory on these task and that of non-spatial task in operant camber, such as conventional delayed matching-to-sample tasks were comparable (Olton and Maki, 1983; Reilly and Good, 1987; Wilkie, 1983; Wilkie, 1984; Wilkie and Summers, 1982).

The hippocampal damages in the present experiment did not affect the pigeons' performance because little locomotor cues were required for the performance of the task. However, non-spatial short-term memory, examined by Konorski pair comparison task, was disrupted by hippocampal lesions in pigeons (Sahgal, 1984 a,b). Thus, no deficits in the present task after hippocampal lesions show that the short-term memory measured in the present task has differ-

ent brain mechanisms from nonspatial short-term memory.

REFERENCES

Aggleton, J. P., Keith, A. B., Rawlins, J. N. P., Hunt, P. R. and Sahgal, A. (1992) Removal of the hippocampus and transection of the fornix produce comparable deficits on delayed non-matching to position by rats. *Behavioural Brain Research*, 52: 61–71.

Barnea, A., & Nottebohm, F. (1994) Seasonal recruitment of hippocampal neurons in adult free-ranging black-capped chiciadees. *Proceeding of Nationall Academy of Sciences*, 91: 11217–11221.

Bingman, V. P., Ioalè, P., Casini, G. and Bagonoli, P. (1990a) The avian hippocampus: evidence for a role in the development of homing pigeon navigation map. *Behavioral Neuroscience*, 104: 906–911.

Bingman, V. P., Bagonoli, P., Ioalè, P. and Casini, G. (1984) Homing behavior of pigeons after telencephalic ablations. *Brain Behavior and Evolution*, 24: 94–108.

Bingman, V. P., Ioalè, P., Casini, G. and Bagonoli, P. (1985) Dorsomedial forebrain ablations and home loft association behavior in homing pigeons. *Brain Behavior and Evolution*, 26: 1–9.

Bingman, V. P. and Mench, J. A. (1990b) Homing behavior of hippocampus and parahippocampus lesioned pigeons following shortdistance releases. *Behavioural Brain Research*, 40: 227–238.

Casini, G., Bingmam, V. P. and Bagonoli, P. (1986) Connections of the pigeon drosomedial forebrain studied with WGA-HRP and H-proline. *Journal of Comparative Neurology*, 245: 454–470.

Erichsen, J. T., Bingman, V. P., & Krebs, J. R. (1991) The distribution of neuropeptides in the dorsomedial telencephalon of the pigeon (*Columba livia*): a basis for regional subdivisions. *Journal of Comparative Neurology*, 14: 478–492.

Good, M. (1987) The effects of hippocampal-area parahippocampalis lesions on discrimination learning in the pigeon. *Behavioural Brain Research*, 26: 171–184.

Healy, S. D. and Krebs, J. R. (1993) Development of hippocampal specialization in a food-storing bird. *Behavioural Brain Research*, 53: 127–131.

Hori, K. and Watanabe, S. (1987) An application of the image processing system for detecting and controlling pigeon's peck location. *Behavioural Brain Research*, 26: 75–78.

Karten, H. J. and Hodos, W. (1967) *A Stereotaxic Atlas of the Brain of the Pigeon, Columba livia.* Johns Hopkins University Press, Baltimore.

Krayniak, P. F. and Siegel, A. (1978) Efferent connections of the hippocampus and adjacent regions in the pigeon. *Brain Behavior and Evolution*, 15: 372–388.

Krebs, J. R., Sherry, D. F., Healy, S. D., Perry, V. H., & Vaccarino, A. L. (1989) Hippocampal specialization of food-storing birds. *Proceeding of Nationall Academy of Sciences*, 86: 1388–1392.

Olson, D. J. (1991) Species differences in spatial memory among Clark's nutcrackers, Scrub jays, and pigeons. *Journal of Experimental Psychology Animal Behavior Peocesses*, 17: 363–376.

Olson, D. J., Kamil, A. C., Balda, R. P., & Nims, P. J. (1995) Performance of four seed-caching corvid species in operant tests of nonspatial and spatial memory. *Journal of Comparative Psychology*, 109: 173–181.

Olton, D. J. and Maki, W. S. (1983) Characteristics of spatial memory in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 9: 266–280.

Reilly, S. and Good, M. (1987) Enhanced DRL and impaired forced-choice alternation performance folowing hippocampal lesion in the pigeon. *Behavioural Brain Research*, 26: 185–197.

Reilly, S. and Good, M. (1989) Hippocampal lesions and associative learning in the pigeon. *Behavioral Neuroscience*, 103: 731–742.

Sahgal, A. (1984a) Adenocorticotrophic hormone and melanocyte stimulating hormone do not affect performance in hippocampuslesioned or control pigeons. *Behavioural Brain Research* 14: 9–15.

Sahgal, A. (1984b) Hippocampal lesions disrupt recognition memory in pigeons. *Behavioural Brain Research*, 11: 47–58.

Shettleworth, S. J., Hampton, R. R., and Westwood, R. P. (1995) Hippocampus and memory for places and colors in a food-storing and a non-storing bird species. Burrows, M., Matheson, T., Newland, P. L., and Schuppe, H. (eds) *Nervous system and behaviour.* Georg Thieme Verlag.

Sherry, D. F., & Vaccarino, A. L. (1989) Hippocampus and memory for food caches in Black-capped chickadees. *Behavioral Neuroscience*, 103: 308–318.

Sherry, D. F., Vaccarino, A. L., Buckenham, K. and Herz, R. S. (1989) The hippocampal complex of food-storing birds. *Brain Behavior and Evolution*, 34: 308–317.

Smulders, T. V., Sasson, A. D., & DeVoogd, T. J. (1995) Seasonal variation in hippocampal volume in a food-storing bird, the Black-capped chickadee. *Journal of Neurobiology*, 27: 15–25.

Squire, L. R. and Zola-Morgan, S. (1983) The neurology of memory: the case for correspondence between the findings for human and nonhuman pri-

mate. In J. A. Deutsch., (ed.) *The Physiological Basis of Memory*, 2nd ed. Academic Press, New York 199–268.

Walker, D. W. and Means, L. W. (1973) Single-alternation performance in rats with hippocampal lesions: disruption by irrelevant task interposed during the intertrial interval. *Behavioral Biology*, 9: 93–104.

Walker, D. W., Means, L. W. and Isaacson, R. L. (1970) The effects of hippocampal and cortical lesions on single-alternation go, no-go acquisition in rats. *Psychonomic Science*, 21: 29–31.

Walker, D. W., Messer, L. G. and Freund, G. (1972) Effect of hippocampal lesions and intertrial interval on single-alternation performance in the rat. *Journal of Comparative and Physiological Psychology*, 80: 469–477.

Wilkie D. M. (1983) Pigeons' spatial memory: III. effects of distractors on delayed matching of key location. *Journal of the Experimental Analysis of Behavior*, 40: 143–151.

Wilkie D. M. (1984) Pigeons' spatial memory: IV. effects of intertrial interval manipulations on delayed matching of key location. *Canadian Journal of Psychology*, 38: 178–195.

Wilkie, D. M. and Summers, R. J. (1982) Pigeons' spatial memory: factors affecting delayed matching of key location. *Journal of the Experimental Analysis of Behavior*, 37: 45–56.