

Pigeons' (*Columba livia*) spatial reference memory is stable over long retention intervals

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Pigeons received training sessions in which a 3×3 matrix of pecking keys was lit with red light. Pecking a particular key (but not the other eight keys) produced grain reward on an intermittent schedule. After this key-location discrimination was learned, subjects received occasional, non-rewarded test sessions, followed immediately by a "relearning" session. The time between these test sessions, which comprised a reference memory retention interval, varied from 1 to 30 days. No significant forgetting was found, even at the longest retention interval. This finding stands in marked contrast to typical results for pigeons tested on spatial working memory tasks (such as delayed matching to sample) in which forgetting is rapid. Our findings are consistent with Bond, Cook, and Lamb's (1981) suggestion that the pigeon's foraging ecology has favored the development of proficient reference rather than working memory.

Although several bird species are thought to have exceptional spatial memory abilities (e.g., Balda, Bunch, Kamil, Sherry, & Tomback, 1987), a common view is that pigeons are not proficient in processing spatial information. Evidence for this hypothesis has come from several studies. Wilkie and Summers (1982) found very rapid forgetting of pecking-key location in delayed matching to sample. Bond, Cook, and Lamb (1981) studied pigeons in the radial-arm maze and found little evidence that their subjects could remember arms that were previously visited and depleted of food. Subsequent research, which employed special training conditions (Roberts & Van Veldhuizen, 1985), different mazes (Olson & Maki, 1983; Wilkie, Spetch, & Chew, 1981), and an open-field feeding environment (Spetch & Edwards, 1986), demonstrated that pigeons have the capacity to remember recently visited locations. However, in most studies demonstrating a spatial memory ability in pigeons, retention of location has been relatively short. For example, Roberts and Van Veldhuizen (1985) found substantial forgetting with a 6-min retention interval.

It has been suggested that the reason for pigeons' relatively poor performance on spatial memory tasks might be related to the species' foraging ecology. Because pigeons seem to often feed from areas that are not easily depleted during a single feeding bout, Bond et al. (1981) suggested that a tendency to return to locations where they had recently fed (a *win-stay* strategy), as well as a tendency to remember these locations (i.e., an accurate *reference memory*, see Honig, 1978), may have evolved in this

species. Because of the way they feed, a proficient "working memory" may not have developed in pigeons. Thus, pigeons' poor performance in spatial memory tasks may be due, in part, to the fact that many of these tasks require both a win-shift strategy and an accurate working memory.

Although Bond et al.'s (1981) hypothesis may be a reasonable one, evidence for it has come primarily from the poor performance of pigeons tested on working memory tasks. To the best of our knowledge, the good performance on spatial reference memory tasks expected from this hypothesis has been demonstrated in only one published study. Roberts and Van Veldhuizen (1985, Experiment 6) baited only four of eight arms in a radial maze and found that their pigeons readily learned which arms always contained food and which arms never contained food. Although these investigators demonstrated good spatial reference memory in the pigeon, they did not test the robustness of this type of memory by imposing significant retention intervals. That was the purpose of the present research. Although there are many spatial reference memory tasks that we could have employed, we chose a key-location discrimination procedure. The primary reason for this choice was that we have used this procedure in our previous studies of pigeons' spatial working memory (Wilkie, 1983a, 1983b, 1984, 1986, in press; Wilkie & Kennedy, 1987; Wilkie & Summers, 1982); its use here permitted a more direct comparison of pigeons' performance on working and reference memory tasks.

METHOD

Subjects

The subjects were 4 Silver King pigeons (originally obtained from Vancouver Island Mountain Squab, Nanimo, B.C., Canada). They had been trained previously on delayed matching of key location. Throughout the experiment, the subjects were maintained at approximately 90% of their free-feeding weights and had ad-lib access to water, crushed

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oyster shells, and health grit in their home cages. When not being tested, all subjects were individually housed in large plastic mesh cages.

Apparatus

The apparatus used in the present study has been described in detail elsewhere (e.g., Wilkie & Summers, 1982). Each of three test chambers contained a 3×3 matrix of identical pecking keys that could be illuminated from the rear by a red light-emitting diode. From the pigeons' perspective, the keys were numbered as follows:

1	2	3
4	5	6
7	8	9

The key matrix was located above a small opening that allowed the subjects access to a standard grain dispenser. To the right and left of the key matrix were two lights that illuminated the test chamber.

Data collection and experimental control were carried out by a Data General NOVA 3 computer, operating under RDOS and the MANX programming language (Gilbert & Rice, 1979).

Procedure

All subjects had been previously trained to keypeck in the present apparatus; therefore, no preliminary training was necessary. Throughout the experiment, the rewarded key (S+) was the 1 key for 2 subjects and the 5 key for the other 2 subjects. All subjects were tested 5 days/week, Monday to Friday.

Initial training. All subjects were trained to peck the S+ key on a CRF schedule. Each peck to the correct key produced 5-sec access to mixed grain. A peck to any of the other eight keys resulted in a 5-sec timeout, during which all keys and the houselights were darkened. A session lasted until the subject had received 60 reinforcers. This training was continued for 5 days, with one session being given per day. The subjects were then given an additional session of CRF training, in which incorrect responses provided no feedback: Responses to any of the eight incorrect keys were recorded, but did not result in a timeout.

Next a variable ratio (VR) schedule was introduced. The average number of correct responses required to receive grain was 10. These responses did not have to be made consecutively. Responses to any of the incor-

rect keys produced no feedback. Each subject received eight sessions, comprised of 60 reinforcers each, during this phase.

Testing and relearning. During this phase, all sessions consisted of a 15-min nonreinforced exposure to the illuminated key matrix, followed immediately by a normal session of 60 reinforcers as described in the previous section. A total of 12 retention tests were conducted, with retention intervals ranging in length from 1 to 30 days. The order in which the retention tests were run was as follows: 3, 3, 2, 2, 1, 7, 7, 14, 14, 30, 30, and 1 days.

RESULTS

All subjects quickly learned the key-location discrimination. Relative responses to the positive key over the last 3 days of training averaged .97, .98, and .98, respectively.

Figure 1 shows relative responses to the positive key as a function of the retention interval separating test sessions. Relative responding to the positive key during the 15-min nonrewarded test was generally around .80, very much higher than chance, $\frac{1}{9}$ or .11. Although performance at the 30-day retention interval was slightly lower than performance at the other retention intervals, this decline in accuracy in the key-location discrimination was not statistically significant when analyzed in a repeated measures analysis of variance [$F(5, 15) = 2.8, p > .05$]. The difference in performance on the first and second tests at each retention interval also was not significant [mean first test = .831, mean second test = .797, $F(1, 3) = 5.12, p > .05$], showing that the additional reinforced practice following the first test did not facilitate performance on the second test.

The fact that relative responding during all retention tests was lower than the levels displayed at the end of training is probably attributable to the fact that pecking was

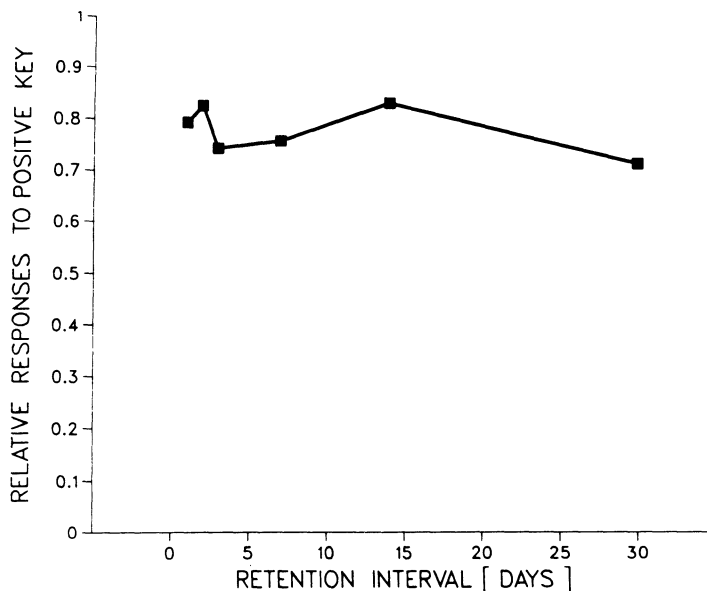


Figure 1. Relative responses to positive key location during tests conducted after various retention intervals.

intermittently reinforced during training but not during test sessions. That is, during training sessions the occurrence of food reward could signal to the subject that the key being pecked was the correct one. During the non-rewarded retention sessions, the subjects had to rely exclusively upon memory to determine which key was correct. Relative responding scores during rewarded training thus probably overestimated the subjects' ability to remember the correct key location.

The subjects trained to peck key 1 performed similarly to those trained to peck key 5. Averaged over all the retention intervals the former subjects averaged .829 relative responses to the positive key; the latter subjects averaged .80.

DISCUSSION

When pigeons are given working memory tests in Skinner boxes, such as those employed in the present study, they can remember the location of the key presented as the sample on a trial, but only for a retention interval of a few seconds (e.g., Wilkie & Summers, 1982). In contrast, the subjects in the present study remembered the location of the rewarded key across retention intervals spanning many days. This finding replicates the observations of Roberts and Van Veldhuizen (1985) that pigeons have good spatial reference memory, and shows in addition that this memory is not subject to quick forgetting. Our finding is also consistent with other results from our laboratory. Wilkie, Willson, and Kardal (in press) trained pigeons to discriminate pictures of geographic locations and then tested the subjects for retention of this discrimination after 60 days. The subjects showed good retention of this discrimination. Each of these studies supports the suggestion of Bond et al. (1981) that the foraging ecology of pigeons has been conducive for the evolution of good reference rather than working memory abilities. Because pigeons often feed in locations that are not necessarily depleted in one visit, a stable reference memory of typically good feeding sites would be advantageous, as would the use of a win-stay strategy.

Another factor in the pigeon's foraging ecology that might inhibit the development of working memory is that feral pigeons tend to feed in groups (e.g., Giraldeau, 1984). Therefore, because the distribution of food resources within a feeding site is likely to be constantly changing due to the foraging of flockmates, an egocentric working memory representation of that distribution would not be of much use.

Although our results support a link between foraging ecology and reference memory ability, there are several reasons for not unconditionally accepting the hypothesis presented by Bond et al. First, the data supporting the hypothesis are strictly correlational. A correlation between memory abilities and foraging ecologies does not necessarily mean that the latter has shaped the former. Because pigeons show good reference memory in nonspatial tasks (e.g., Vaughan & Greene, 1984), it might be that proficient reference memory is a general ability rather than one evolved to meet the demands of one particular problem (i.e., finding adequate food) faced by an animal. Second, although some information about the foraging ecology of the pigeon seems to be well established (e.g., Giraldeau & Lefebvre, 1987), some seems to be based more on generalizations by authors of popular publications that do not present empirical data. More rigorous scientific observation and study of the feral pigeon's feeding habits are needed before we can increase our understanding of the putative relationships between foraging ecology and memory.

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