Evidence for large long-term memory capacities in baboons and pigeons and its implications for learning and the evolution of cognition

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Previous research has shown that birds and primates have a rich repertoire of behavioral and cognitive skills, but the mechanisms underlying these abilities are not well understood. A common hypothesis is that these adaptations are mediated by an efficient long-term memory, allowing animals to remember specific external events and associate appropriate behaviors to these events. Because earlier studies have not sufficiently challenged memory capacity in animals, our comparative research examined with equivalent procedures the size and mechanisms of long-term memory in baboons and pigeons. Findings revealed very large, but different, capacities in both species to learn and remember picture–response associations. Pigeons could maximally memorize between 800 and 1,200 picture–response associations before reaching the limit of their performance. In contrast, baboons minimally memorized 3,500–5,000 items and had not reached their limit after more than 3 years of testing. No differences were detected in how these associations were retained or otherwise processed by these species. These results demonstrate that pigeons and monkeys have sufficient memory resources to develop memory-based exemplar or feature learning strategies in many test situations. They further suggest that the evolution of cognition and behavior importantly may have involved the gradual enlargement of the long-term memory capacities of the brain.

intelligence | primate | bird | categorization | picture processing

Birds and primates have demonstrated a wide variety of cognitive capacities in different settings and are especially adept at learning visual discriminations (1–3). There has been a long and active debate on how such discriminations are learned. One prominent view has been an exemplar approach in which learning is mediated by the memorization of large number of stimulus-specific exemplars (4–7). Previous examinations of the size and durability of associative memory capacity in animals provide some credence for this possibility. Clark's Nutcrackers can remember 18–25 caches in a room containing 69 cache sites for as long as 180–285 days (8) and have been indirectly estimated to retrieve food from 3,000 to 6,000 stored caches over the winter, likely by using memory. In an earlier operant-discrimination task, pigeons were able to memorize up to 320 randomly assigned pictorial stimuli (9). Comparable capacity studies have not been conducted in monkeys, but experimental evidence has demonstrated that objects viewed three to four times continue to be categorized as familiar by macaques 6 months later (10). In addition, macaques could reliably recognize pictures 6 months after an initial brief exposure of 30 sec (11). Despite these remarkable accomplishments of birds and monkeys, we postulated that earlier animal studies did not sufficiently challenge memory capacity over extended periods of time (12) and therefore had underestimated memory size in these different animals. These studies also were limited by their use of different procedures, making precise cross-species comparisons difficult.

We have collected a very large database on long-lasting associative memory in baboons (*Papio papio*) and pigeons (*Columba livia*) by using a task specifically designed to maximally challenge their memory capacities. Our comparative interest in these phylogenetically remote species was motivated by their strong reliance on vision, their demonstrated memory and cognitive capacities, and their representation of the two most predominant lines of vertebrates: birds and mammals. The current data are directly relevant to answering important theoretical questions regarding the mechanisms of memory, discrimination learning, and categorization in animals. They also provide insights about the evolution of memory and its possible contributions to the evolution of cognition and intelligence. For instance, it has been proposed that increased intelligence has been actively selected for over evolutionary time as a consequence of ecological (diet, climate), social (group size, complex sociability), or advanced cognitive adaptations (tool use, machiavellian intelligence, language) (13–18). Our comparison of memory sizes in monkeys and birds suggests that the expansion of memory may have played a critical role as well.

Two baboons and two pigeons were tested in the same memory task in which they had to learn and retain increasingly large numbers of picture–response associations in standard operant settings. On each trial, a randomly selected color picture was presented on a front screen, after which two choice stimuli were illuminated on the right and left sides. Because the correct response to each picture was randomly chosen and permanently assigned at the outset of training, this demanding task required memorization of each picture and its associated response. Animals were tested continuously for 3 to 5 years while the number of pictures in the memory set were progressively increased to challenge their memory capacity.

Results

Fig. 1 shows choice accuracy as a function of increasing memory set size. The monkeys showed an astonishing capacity to remember a very large number of picture–response associations. Averaged over the last 75 sessions of testing, baboons #03 and #09 were 78% and 80% correct with a memory set size of 5,910 and 6,180 pictures, respectively. The pigeons were not nearly as good as the baboons, but they were still quite remarkable. Pigeons Linus and BF (who died prematurely) achieved 62.3% and 67.6% correct with memory set sizes of 3,037 and 1,978 images, respectively.

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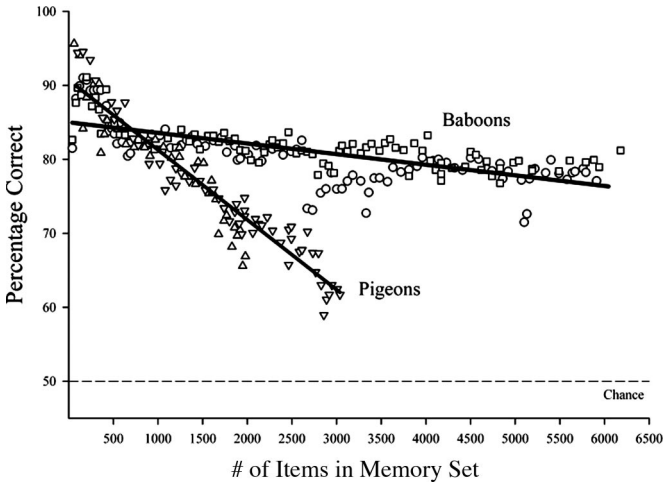

Fig. 1. Large memory capacities in pigeons and baboons. This data represent 3 to 5 years of testing in which pigeons and baboons were tested with memory loads of near 3,000 and 6,000 pictures, respectively. Each point indicates mean accuracy with 1,500 memory trials and is above chance (binomial test, $P < 0.05$). ○, #09; □, #03; △, BF; ▽, Linus. Each line represents the best fitting regression for pigeons ($r = 0.97$, $F(1, 57) = 897.4$, $P < 0.0001$) and baboons ($r = 0.76$, $F(1, 57) = 126.5$, $P < 0.0001$). Linear extrapolation reveals that a memory set size of 14,300 associations would have been required to cause the baboons' performance to decline to levels equivalent to the pigeons' terminal performance. The shallower slope for the baboons reveals their greater capacity to handle large memory loads over testing. The slightly better early performance of pigeons reflects extensive training with the first 40 items in an unrelated experiment.

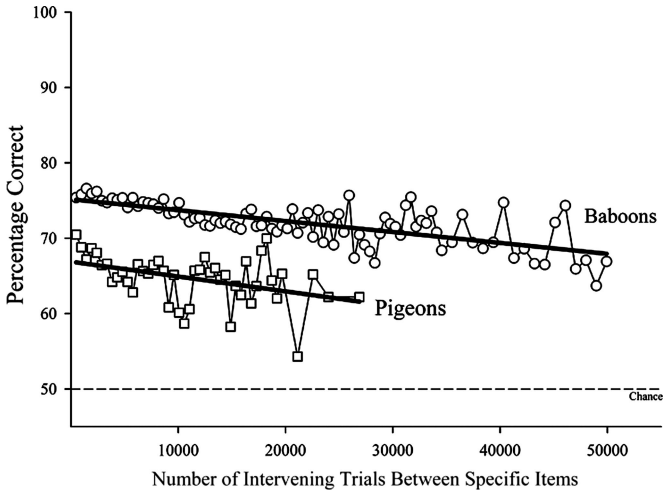

Fig. 2. Similar rates of forgetting in pigeons and baboons. Accuracy was computed as a function of the number of intervening trials, or lag, between two successive presentations of each picture. Baboons maintained 70% correct with lags of 48,000 trials. Pigeons performed above chance (65%, $P < 0.05$) with lags of 20,000 trials. Each line represents the best fitting regression (pigeons, $r = 0.42$, $F(1, 43) = 9.1$, $P = 0.004$; baboons, $r = 0.71$, $F(1, 57) = 86.8$, $P < 0.0001$). Parallel slopes (pigeons = 0.0002; baboons = 0.0001) suggest similar forgetting rates in both species. Longer lags were not analyzed because of small n. Linear extrapolation would indicate that the baboons would need 100,000 trials (≈1 year) to reach a performance level similar to the pigeons at 20,000 trials.

We used two methods to examine memory capacity. The first considered the number of pictures supporting 65% or greater levels of accuracy on average over the entirety of testing. This moderate criterion captured the majority of items that were consistently supporting above-chance performance. These values were 5,016 and 5,093 for #03 and #09 and 1,315 and 1,202 for Linus and BF, respectively. The second method used an all-or-none high-threshold model. This highly conservative model assumes that performance is an additive combination of trials controlled by memory (probability correct = 1) and trials controlled by guessing (probability correct = 0.5), the size of the memory set being estimated by deriving the best fitting proportion of memory and guess trials (12, 19). This model established that at least 3,261 (#03) and 3,605 (#09) picture–response associations were required to account for the baboons' mean performance achieved over the last 75 sessions of testing. The same estimates were 763 and 726 associations for Linus and BF at the end of their testing, although we obtained larger estimates of 986 and 853 picture–response associations 250 and 325 sessions earlier for each pigeon. This relative decline in memory suggests that the upper limit of the pigeons' capacity had been reached and likely exceeded during the course of testing. These findings confirm the initial estimates of Cook *et al*. (12) but with substantially more data over a more extended time period. They suggest that 800 to 1,200 picture–response associations is the maximum capacity of pigeon memory in this picture–response memorization task. Overall, the baboons' long-term memory capacity seemed to exceed that of pigeons by a factor of at least 4 in our various estimates.

We next examined three critical facets of each species' behavior to judge whether the memory dynamics were the same for pigeons and baboons, outside of this capacity difference. With respect to the issue of forgetting, analyses of performance as a function of item lag revealed that both species' memories for specific items could last over several months and tens of thousands of intervening trials (see Fig. 2). This performance extends previous reports about the duration of long-term memory in monkeys and pigeons (9–12, 20) but under considerably greater memory loads. Moreover, forgetting rates as indicated by the slopes of the best fitting lines were found to be of the same order for the two species.

Further evidence of processing similarity was detected in each species' patterns of reaction times. Fig. 3 shows mean choice reaction times for individual baboons (*Left*) and first-peck reaction times for pigeons (*Right*) on old-item trials between the

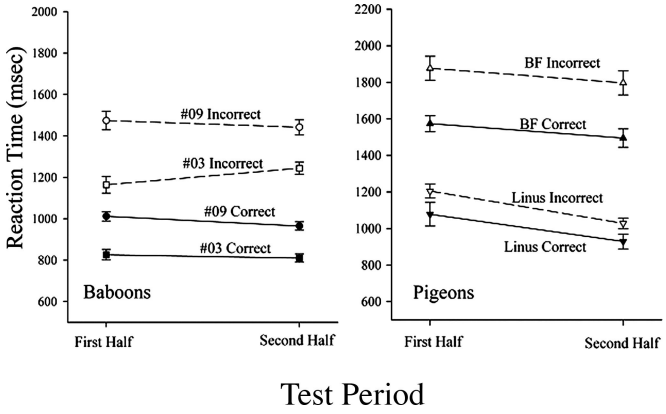

Fig. 3. Parallel memory search in pigeons and baboons. Shown are mean reaction times for correct (filled symbols) and incorrect (open symbols) trials during each half of testing. Reaction times were significantly shorter for correct than incorrect trials (accuracy × test half ANOVAs: #03, $F(1, 40) = 167$, $P < 0.001$; #09, $F(1, 48) = 213$, $P < 0.001$; Linus, $F(1, 48) = 6.3$, $P = 0.015$; and BF, $F(1, 24) = 28$, $P < 0.001$). For these ANOVAs, the data from the first and second halves of testing were divided into 50-session blocks for pigeons and 100-session blocks for baboons, df reflecting the number of blocks for each animal. Parallel memory search is demonstrated by the stable or decreasing correct reaction times with increasing memory loads.

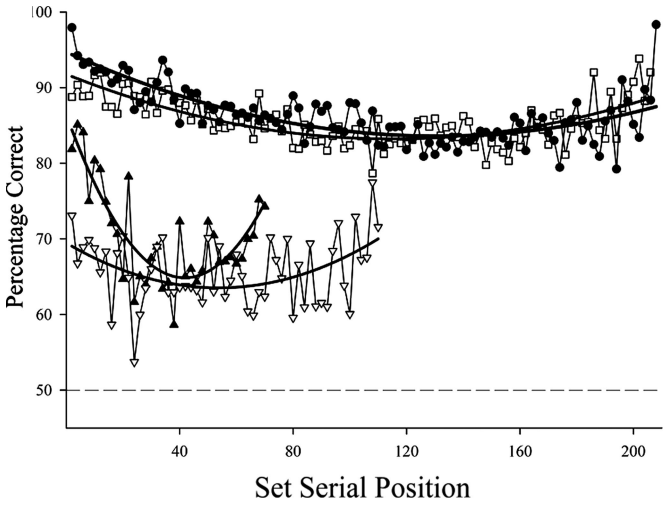

Fig. 4. Similar primacy and recency effects in pigeons and baboons. Shown is the mean accuracy for each animal over the last third of testing as a function of when each image was introduced in the experiment. Serial position functions were computed over 45,600 trials for #03, 49,800 trials for #09, 17,880 trials for BF, and 28,800 trials for Linus. The curves show the best fitting quadratic function for each animal (#03, $r = 0.73$, $F(2, 100) = 58.2$, $P < 0.0001$; #09, $r = 0.78$, $F(2, 101) = 81.1$, $P < 0.0001$; Linus, $r = 0.42$, $F(2, 52) = 5.7$, $P = 0.006$; and BF, $r = 0.73$, $F(2, 32) = 43.5$, $P < 0.0001$. The systematic U-shaped profile of the serial position demonstrates that all birds and baboons experienced similar primacy and recency effects. ●, #09; □, #03; ▲, BF; ▽, Linus.

first half and second half of their respective testing periods. In both species, each animal was significantly faster on correct than incorrect trials. There were no significant increases in reaction time over testing, despite the substantially greater memory load in the second half of the experiment. The independence of response times with memory load indicates that item retrieval was parallel in both species. Also striking is the fact that, for both species, incorrect response times were longer than correct ones. The slower reaction times for incorrect trials may reflect the need for further memory search for poorly recognized items or, alternatively, the generation of competing responses and interference caused by the partial recall of one or more items.

Finally, we computed accuracy as a function of an item's serial position in the overall memory set. To maximize the number of observations for every set, we determined accuracy over the last third of testing as a function of when each image was introduced in the experiment (Fig. 4). Both species showed a U-shaped function, indicating a primacy effect for items introduced early in testing and a recency effect for the newly introduced items. In sum, these cross-species similarities in forgetting, reaction time, and serial position analyses firmly establish that the fundamental memory dynamics of these long-term associations were highly similar, if not identical, in baboons and pigeons. In our task, the two species only differed in terms of their absolute long-term memory capacity.

Discussion

Our research reveals an astonishing ability in baboons to retain long-term picture–response associations. Our estimates indicate they memorized a minimum of 3,500–5,000 items in our task and could have even retained thousands more with continued testing. At a rate of one picture per second, it would take at least 1 h to view their entire memory set, much less engage in the even greater cognitive demands of associating a response to each one. Although the pigeons are clearly more limited, their capacity of 800–1,200 associations is considerable and would represent a rich library of information and experience to draw on during their daily activities. The bigger, but not unlimited, memory of baboons suggests they live in a richer cognitive world than pigeons do. Directly comparable tests of human long-term memory capacity have not been conducted because of practical reasons, but various theoretical estimates indicate we have evolved an enormous capacity for long-term information (19, 21–23). Our results suggest that the ability to store large amounts of information is widespread and substantial in vertebrates, but that memory capacity also varies among species (see also refs. 24 and 25).

One interesting question is why the memory of the pigeons and baboons eventually reached a limit in the task. One candidate source is the unavailability of additional neural circuits to encode and retain large amounts of pictorial information. Variations in encephalization (26) are likely relevant here, as might well be the differential size of important brain components, such as the hippocampus, involved in long-lasting learning and memory. Besides neural limitation, memory limits also might reflect the growing similarity among the items as the memory set expanded, resulting in an increasing interference with continuous testing between the numerous picture–response associations. Although the introduction of other types of stimuli or the availability of more choice alternatives might marginally increase our estimates, we think such modifications would not change the order of magnitude of the capacity estimates generated.

Our research is highly relevant for theories of categorization processes. It offers a strong empirical foundation for exemplar-based theories, as it demonstrates that these two species have sufficient memory resources to use memory-based exemplar or featural learning strategies in many discrimination and categorization experiments. The current research does not rule out that monkeys and pigeons may use generalized concepts in some other settings (27, 28). One key direction for future investigations of animal discrimination learning will be to understand the cognitive interplay between item memorization and concept learning (29).

In a different perspective, our data set also provides important information for our understanding of the evolution of memory systems. Birds and monkeys differ considerably in physiology and evolutionary history. Despite millions years of divergent evolution, they demonstrated highly similar memory profiles with regard to forgetting rates, reaction time, and serial position functions. In both species, picture retention seems to reflect the similar operation of large durable memory systems that can be searched in parallel with the most frequently repeated or most recent items showing the best retention. These functional similarities suggest that the 250 million years of divergent evolution that have occurred since the mammalian/reptilian split may have mainly changed memory capacities but have had little impact on basic memory processes and memory dynamics.

Finally, the current findings are of strong relevance for theories concerning the evolution of animal and human intelligence. Although the exact definition of intelligence remains under debate, we can speculate from our results that a progressive evolutionary growth in long-term memory capacity may have served the development of increasingly complex cognitive functioning over time, especially in primates (2). Clearly, the link between memory size and the most abstract aspects of intelligence must be an indirect one, because conceptual thinking cannot be reduced to simple memory storage and retrieval. Nevertheless, larger memory stores permit a greater amount of information to be retained and eventually compared, which might be essential to discovering abstract relations among items or subsets of items of the highest order. Additional comparative experiments of this type should be aimed at more directly investigating the relation between long-term memory size and cognitive achievement.

Methods

Our subjects were two adult, 18-year-old male baboons (*P. papio*) and two adult male Silver King pigeons (*C. livia*). All animals were tested in the same memory task with minimal modifications made to accommodate each species' size and natural motor and feeding behaviors. The baboons were tested in a Plexiglas chamber that permitted free access to a joystick and full view of a computer screen (see ref. 27 for details). A trial started after monkeys placed a cursor on the fixation point, at which point the picture image was presented central to the screen during 700 ms, immediately after which the two response keys were illuminated. Monkeys had to select, by way of joystick manipulation, the response keys associated to the sample picture. The same procedure was followed for pigeons, except that pecks were required to the picture before making their right/left choice [see Cook *et al.* (12) for details]. For each species, the 120-trial test sessions were composed of 60 "old-item" and 60 "new-item" trials. New-item trials involved two presentations of 30 recently introduced pictures, which were repeated over sessions until subjects reached criterion (20 pictures were used for the first 18 sets). At this point, these new-item pictures were moved to the old-item memory pool and a new set of 30 pictures to memorize was introduced. A session's 60 old-item trials were randomly selected from this ever-increasing pool of previously learned picture–response associations. New-item pictures were introduced in the same order for both species. All trials were reinforced differentially. Incorrect trials gave rise to a time out of either 3 sec (baboons) or 5 sec (pigeons) and were represented immediately until a correct response was given. Correction trials represented after an error were omitted from statistical analysis. A 3-sec intertrial interval followed each trial. Accuracy and response times were recorded. For pigeons, response times were considered as the time elapsed from the onset of the picture to the first peck on the screen [see Cook *et al.* (12) for details]. Cook *et al.* (12) reported a first set of data collected from these pigeons by using this procedure. Here we now report 195 additional test sessions for BF and 770 sessions for Linus. These new data were combined with the previous data set for a total of 895 test sessions for BF (107,400 trials with 53,700 being memory trials) and 1,470 for Linus (176,400 trials with 88,200 being memory trials). Over 3.5 years of testing, baboon #03 participated in 2,280 sessions (273,600 trials), and #09 participated in 2,494 sessions (299,280 trials). Baboons had the capacity to be tested with an average of four sessions a day, whereas the pigeons were limited to one session a day. All pictures were color and were harvested from various sources and resized to 480 × 300 pixels by using photo software.

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