BRIEF COMMUNICATIONS

Rats remember long lists of nonspatial items

K. STEELE and J. N. P. RAWLINS
University of Oxford, Oxford, England

The performance of monkeys on visual recognition tasks similar to those employed with human subjects (e.g., Warrington & Taylor, 1973) has demonstrated a memory for "lists" of at least 20 objects (Aigner et al., 1987). Although similar levels of performance have been noted in rats (e.g., Olton, Collison, & Werz, 1977), the testing paradigms have assessed spatial memory (e.g., a 17-arm radial maze). Although it has recently been shown that rats can recognize trial-unique nonspatial items over retention intervals of at least 60 sec (Aggleton, 1985; see also Aggleton, Hunt, & Rawlins, 1986; Raffaele & Olton, 1988; Rothblat & Hayes, 1987), the storage capacity for such information has not yet been established. The present report concerns an adaptation of Aggleton's method, which we used to determine whether rats have a substantial nonspatial working-memory capacity. Rats were trained on a running recognition task in which they were eventually required to remember lists of up to 32 objects over retention periods of up to 13 min. This procedure may provide a quantitatively controlled assessment of memory in rats that is comparable to human memory tests.

METHOD

Subjects

The subjects were 6 experimentally naive, adult male DA-strain rats (bred in-house, breeders from Bantin & Kingman), weighing 250–325 g at the start of behavioral testing. They were maintained in group cages on a 12:12 light:dark cycle, with lights on at 0800 h. Testing took place during the mornings. Water was available ad lib in the home cage; food was available for 1.5 h/day, at least 10 min after testing.

Apparatus

Testing was conducted in a Y-maze, closely modeled on that used by Aggleton (1985), except that the goalarms were 11 cm longer to allow for an extra door, located half way along the goalarm. There was also a door in the central area from which the arms radiated, which simultaneously blocked access to all three arms. Doors were manually operated. The arms were each 13 cm wide and 20 cm high. The distance from the back wall of the goalboxes to the maze center was 37 cm. Distinctive goalboxes (Aggleton, 1985) could be inserted into the goal arms: these differed in texture, paint de-

sign, and the objects they contained. There were 50 pairs of goalboxes, each different from every other pair (although the two members of a pair were identical).

Procedure

The rats were familiarized with the apparatus and then trained on a nonmatching rule identical to that used by Aggleton (1985). On the first choice trial, a rat in Goalbox A₁ would be offered a choice between an identical (familiar) goalbox, A₂, and a different (novel) goalbox, B₁. If the rat chose the novel goalbox, two 0.045-g reward pellets (Campden Instruments, UK) were dropped into the box, such that they could fall anywhere, and the rat had to search for them. Only the first selection made between any pair of goalboxes was scored. "Familiar" choices resulted in repetition of the same choice between a goalbox from the A pair and B₁ until the correct novel selection was made. During these correction trials (not scored), the positions of the two goalboxes were always interchanged. On the second trial, the rat chose between B₂ and C₁. On the third trial, the choice was C₂/D₁, and so on. This procedure yields a list length of 1, because the familiar goalbox in any trial had occurred one trial before. One member of a goalbox pair was used for the novel presentation and the other for the familiar presentation, so recognition of familiar boxes could not depend on olfactory cues resulting from scent-marking goalboxes at their initial presentation. Goalbox order and left-right position were randomized, and goalboxes were placed in the maze simultaneously. The arm of the maze containing the goalbox chosen by a rat was closed off by lowering a door when an imaginary line joining the rat's ears crossed onto the floor of the goalbox. The rats were thus permitted to obtain tactile and olfactory information by sniffing the edge of the goalbox before making a choice. This they usually did, but equally they sometimes chose without pausing at the edge of the goalbox.

The experiment was run in two replications. Rats 1–3 were trained with only a central door and an intertrial interval (ITI) of 25-sec. Rats 4–6 were trained with central and avenue doors, to prevent them from seeing three goalboxes simultaneously, with a 24-sec ITI. During acquisition, the rats had a 20-min training session each day; the number of trials was variable. Once the rats had learned the basic response rule to a criterion of 80% correct, averaged over 3 consecutive days, list learning commenced.

During list-memory testing, each rat received 50 trials per day. List length was first increased to two: the rat started in A₁, and A₂ was available as the familiar choice on both of the first two choice trials. This enabled a list to be built up: A₂/B₁, A₂/C₁, B₂/D₁, C₂/E₁, D₂/F₁, and so forth. The list length was later increased, for example, to four: A₂/B₁, A₂/C₁, A₂/D₁, A₂/E₁, B₂/F₁, C₂/G₁, D₂/H₁, and so forth. Here, the first four choices established the list. The first scored test trial was B₂/F₁. To correctly reject B₂, a rat had to recall the earlier presentation of B₁, four trials previously. There were thus three intervening items, and 3 × 25 sec (or more, if correction trials occurred) between presentation and test. The goalboxes were presented in a freshly randomized sequence for each day's testing.

Rats 1–3 were given a slow buildup of list lengths, with 3 days at List Length 2, and then 2 consecutive days at each of List Lengths 3–10, 12, 16, and 20. Rats 4–6 were initially given a rapid increase with list lengths of 2, 4, and then 8 on consecutive days. However, they performed poorly at the higher list lengths (data not presented), falling to a level not significantly above chance. We therefore reverted to a slow increase, with 2 further days at List Length 1

This work was supported by a grant from the Wellcome Trust. We thank J. P. Aggleton and P. Reed for their help and advice. Address reprint requests to J. N. P. Rawlins, Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, England.

and then 2 consecutive days at each of List Lengths 2-8, 12, and 16, plus 4 consecutive days at List Length 32.

RESULTS

Acquisition

All rats learned the task. There was no significant difference (t test) in the numbers of trials to criterion in the two replications. Mean performance on the first 50 training trials, at 54% for Rats 1-3 (the original experiment) and 56% for Rats 4-6 (the replication experiment), was not significantly above chance—there was little evidence of spontaneous nonmatching. To reach a performance level of 80% averaged over 3 consecutive days took a mean of 240 trials (not including the trials during the 3-day criterion run).

List Learning

The change from the basic nonmatching procedure used in training to the list-learning procedure produced only a trivial drop in choice accuracy (see Figure 1). In all rats, performance decreased as list length increased [Replication 1, $F(12,24) = 2.64$, $p < .05$; Replication 2, $F(10,20) = 3.72$, $p < .01$], but was still well above chance at even the longest list lengths. For example, the 3 rats tested at the list length of 32 items (retention duration about 13 min) made a combined total of 141 correct choices in 204 trials, for a score of 69% (significantly

above chance; $p < .0001$, binomial test). The rate of decline of choice accuracy seemed rapid between List Length 1 (zero duration) and List Length 6 (duration about 2 min), but more gradual up to List Length 32, with a rise around List Length 8 for Rats 1-3. Overall, Rats 4-6 appeared to perform better than Rats 1-3 (see Figure 1).

DISCUSSION

The high overall levels of performance probably owe much to the high discriminability of items from different trials, because each goalbox pair was a unique complex stimulus, likely to give rise to rich, multisensory memory representations. Since each goalbox pair was used only once per session, confusion between different occurrences of the same pair was restricted to previous days. It is unlikely that the fairly consistent level of performance at the higher list lengths was due simply to a baseline chance level increased by unintended, experimenter-generated cues. First, when list lengths were increased rapidly in Replication 2, performance fell to levels not significantly above 50%. Second, in a previous experiment using the same nonmatching design, the consequences of restricting the number of goalboxes used was assessed so that each appeared more than once in the same test session (Aggleton et al., 1986). This interference procedure produced a drop in choice accuracy with set sizes of up to six, implying that rats remember several of these stimuli, even when the contingencies in force would yield the maximum number of rewards if the rats forgot each goalbox as soon as they had recognized it as familiar on a choice trial.

A further result confirms that the rats learned a generalized skill, and not just the ability to remember the specific 50 goalbox pairs normally used. Rats 4-6 were tested on one day with goalboxes they had never seen before, and still performed well—78% on List Length 4 (significantly above chance; $p < .001$, binomial test).

The results can be considered consistent with a two-store working memory (i.e., a short-term/low-capacity store plus a longer term/high-capacity store) or, alternatively, as consistent with a single, exponentially decaying store. To assess these possibilities, two different forms of linear regression analyses were conducted. In the first, the model considered the forgetting curve as divided into two portions, with the discontinuity occurring after Item 7 or Item 8. Separate slopes were fitted for each portion, so as to mimic the two-store model. These models fitted the data fairly well, accounting for 26% of the variance in the data from Rats 1-3 (with the discontinuity following Item 7), and 32% of the variance in the data from Rats 4-6 (with the discontinuity following Item 8). The alternative model calculated a regression between choice accuracy and logarithmically transformed list length, so as to mimic a classical logarithmic decay function. These analyses produced results very similar to those of the

Figure 1. Performance at different list lengths. The graph shows, for each list length, the percentage of trials that were correct (excluding correction trials). The minimum number of trials per data point is 198. The results give a conservatively low estimate of performance at list lengths above 1 because the effective list length of many trials was increased by correction trials that occurred earlier in a session.

two-store model, accounting for 26.4% and 36.5% of the variance in the data from Rats 1-3 and Rats 4-6, respectively. All the regressions reported were highly significant ($p < .001$), but the similarity in the outcomes using the two different models does not permit a choice of preferable description of the forgetting curves we obtained.

This development of Aggleton's method allows rat memory to be assessed with unusually precise control over the information-processing demands of the task. Although retention intervals inevitably depend to some extent on list length, by varying ITIs it is possible to vary information load for a given retention interval. Minor modification of the procedure, so that a single probe trial follows a serial presentation of stimuli, makes it possible to assess primacy and recency effects: we have found clear evidence of relatively good recognition of the first and last items in a list of five, relative to memory for the intermediate items (Reed, Chih-Ta, Aggleton, & Rawlins, 1989). Furthermore, we found that memory for an intermediate item could be improved by abruptly increasing or decreasing the illumination of a target goalbox at initial presentation (Reed et al., 1989). The goalbox stimuli, unlike stimuli in spatial memory tasks, also allow control of the nature of the information. For example, goalbox pairs can be made more or less similar, to examine the consequences for interference, and scented goalboxes could test olfactory memory. This multiparameter control should give the task unusual flexibility for assessing

memory capacities and the consequences of interventions thought to modify memory.

REFERENCES

- AGGLETON, J. P. (1985). One-trial object recognition by rats. *Quarterly Journal of Experimental Psychology*, **37B**, 279-294.
- AGGLETON, J. P., HUNT, P. R., & RAWLINS, J. N. P. (1986). The effects of hippocampal lesions upon spatial and nonspatial tests of working memory. *Behavioural Brain Research*, **19**, 133-146.
- AIGNER, T. D., MITCHELL, S. J., AGGLETON, J. P., DELONG, M. R., STRUBLE, R. G., PRICE, D. L., WENK, G. L., & MISHKIN, M. (1987). Effects of scopolamine and physostigmine on recognition memory in monkeys with ibotenic-acid lesions of the nucleus basalis of Meynert. *Psychopharmacology*, **92**, 292-300.
- OLTON, D. S., COLLISON, C., & WERZ, M. (1977). Spatial memory and radial arm maze performance in rats. *Learning & Motivation*, **8**, 289-314.
- RAFFAELE, K. C., & OLTON, D. S. (1988). Hippocampal and amygdaloid involvement in working memory for nonspatial stimuli. *Behavioral Neuroscience*, **102**, 355-369.
- REED, P., CHIH-TA, T., AGGLETON, J. P., & RAWLINS, J. N. P. (1989). *Primacy, recency, and the von Restorff effect in rats' nonspatial recognition memory*. Manuscript submitted for publication.
- ROTHBLAT, L. A., & HAYES, L. L. (1987). Short-term object recognition memory in the rat: Nonmatching with trial-unique junk stimuli. *Behavioral Neuroscience*, **101**, 587-590.
- WARRINGTON, E. K., & TAYLOR, A. M. (1973). Immediate memory for faces: Long- or short-term memory? *Quarterly Journal of Experimental Psychology*, **25**, 316-322.

(Manuscript received April 20, 1989;
revision accepted for publication June 22, 1989.)