food-induced stress (and eventually starvation) will operate more heavily on birds out of phase of synchrony with their fellow colony members, and specifically on those that are late nesters (*8*). To examine this we analyzed nestling growth and mortality as a function of the temporal position of each nest with respect to the peak date of synchrony for each colony. Two possible indicators of food stress were examined: (i) partial brood reduction and (ii) runt individuals. (i) Avian ecologists frequently distinguish between two broad categories of nestling mortality. Predation generally claims an entire brood since most predators, once having gained access to a nest chamber, remove all young. Losses of one or two individuals from a brood are usually the result of other causes, including disease, accidental death, and, most frequently, starvation (*9*). We regarded partial brood losses of swallows as a probable indicator of food stress. (ii) Bank swallows begin incubation with the laying of the next to last egg, with the result that the clutch hatches asynchronously over a period of 2 or 3 days. If food for the young is abundant, the growth curves converge and siblings become indistinguishable. If food is not abundant, the size differential present at hatching of the last egg can continue or increase. Any individual nestling that was significantly retarded in its development relative to its brood mates was designated a "runt" (*10*). Runts are usually the individuals that will starve if the food shortage is severe enough. Even if they do fledge, their postfledging survivorship can be expected to be considerably lower than that of their brood mates. We therefore interpreted the presence of runts just prior to fledging as further evidence of an increased food stress on those nests.

Figure 2A shows the precision of within-colony synchronization, Fig. 2B shows the occurrence of runt individuals, and Fig. 2C shows partial brood losses, each plotted relative to the peak dates of colony synchronization. The data support our hypothesis since retarded individuals and probable starvation losses both occur much more frequently among late nesters than among any other category.

Several other hypotheses (including predator swamping, increased alertness and predator defense, and pooling of "decision-making" information concerning environmental stimuli) could be advanced to explain the increase in reproductive success that we found in highly synchronized colonies. The effects of most of these hypotheses are additive and their relative importance in promoting synchronized breeding should be expected to vary in different species and in different localities as a function of local ecological factors. The most important factors should be the distribution and predictability of the food supply, the types and abundance of potential nest predators, and the degree of difficulty in predicting optimal times for breeding.

For bank swallows nesting in upstate New York, we propose that the benefits derived from social foraging, coupled with the tendency to leave the nesting colony as soon as the young have fledged, produces one strong selective advantage for precise, within-colony synchronization of breeding behavior (*11*).

STEPHEN T. EMLEN
NATALIE J. DEMONG
Section of Neurobiology and Behavior, Division of Biological Sciences, Cornell University, Ithaca, New York 14853

References and Notes

1. F. Darling, *Bird Flocks and the Breeding Cycle* (Cambridge Univ. Press, London, 1938); I. Patterson, *Ibis* **107,** 433 (1965); G. Orians, *Condor* **63,** 330 (1961); P. Ward, *Proceedings of the XV International Ornithological Congress* (1970), p. 702; K. Immelman, in *Breeding Biology of Birds*, D. S. Farner, Ed. (National Academy of Sciences, Washington, D.C., 1973), pp. 121–147.
2. D. Stoner, *Roosevelt Wild Life Annals* **4** (2), 127 (1936); A. C. Bent, "Life histories of North American flycatchers, larks, swallows and the allies," *Smithsonian Inst. U.S. Natl. Mus. Bull. No. 179* (1942); A. Peterson, *Wilson Bull.* **67,** 235 (1955).
3. S. Emlen and N. Demong, in preparation.
4. Checks were made with an especially designed optical scope. This "ripariascope" had a self-contained light and mirror arrangement that allowed high resolution viewing deep within nest chambers (N. Demong and S. Emlen, *Wilson Bull.*, in press).
5. The average degree of within-colony synchronization (measured as the standard deviation of hatch dates) was 4.3 days. The standard deviation for between-colony synchronization was 11.3 days.
6. These fitness measures are also significantly related to colony size (*3*). The synchrony relationship remains highly significant, however, after colony size effects have been removed (partial correlation coefficient, reproductive success versus synchrony is -0.92, $P = .001$; partial correlation coefficient for the number of fledglings versus synchrony is -0.85, $P = .001$).
7. J. Brown, *Wilson Bull.* **76,** 160 (1964); P. Ward, *Ibis* **107,** 173 (1965); H. Horn, *Ecology* **49,** 682 (1968); D. Lack, *Ecological Adaptations for Breeding in Birds* (Methuen, London, 1968); J. Brown and G. Orians, *Annu. Rev. Ecol. Syst.* **1,** 239 (1970); P. Ward and A. Zahavi, *Ibis* **115,** 517 (1973); J. Krebs, *Behaviour*, in press.
8. Early nesters are deprived of the potential of social foraging at a time when their young first hatch (when most other adults are incubating). Since the energy demands of small nestlings is minimal, a bimodal curve of the effects of food stress is not expected.
9. D. Lack, *The Natural Regulation of Animal Numbers* (Clarendon Press, Oxford, 1954); R. Ricklefs, *Smithsonian Contrib. Zool.* **9,** 1 (1969).
10. All young were examined when 16 days of age. Any individual whose primary feathers showed a retardation, relative to its siblings, of greater than 20 percent of the total feather length was designated a "runt."
11. We thank D. Goldman and D. Rubin for assistance in the field and R. Buskirk, J. T. Emlen, Jr., H. Horn, I. Patterson, and R. Ricklefs for discussions and comments on the manuscript. This report is dedicated to Dr. John T. Emlen, Jr., whose pioneering studies on the social behavior of many groups, including swallows, have provided a continuing inspiration to both his students and kin.

9 December 1974; revised 31 January 1975

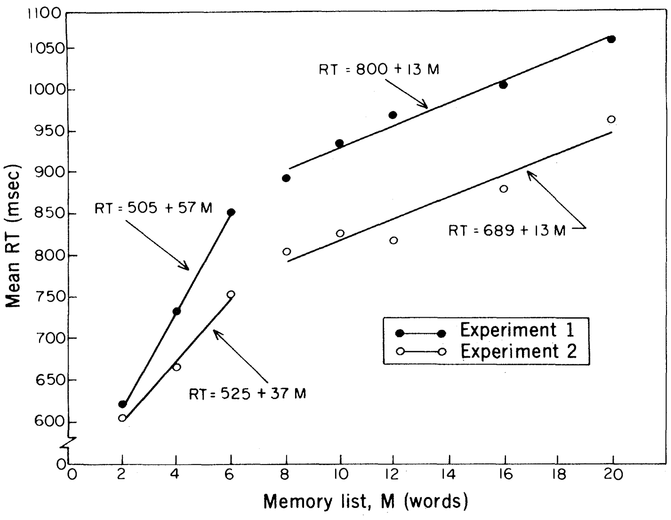
Memory Retrieval from Long and Short Lists

Abstract. *Reaction time in Sternberg's memory retrieval task with both short and long lists is a bilinear function of list length, changing slope at the limits of memory span. Separate long-term and short-term retrieval processes are implied. An alternative one-process model expressed by a logarithmic function is also considered.*

When human subjects must decide whether a stimulus item was present in a short list of memory items, mean reaction time (RT) for the decision is usually a linear function of the number of memory items (*1, 2*). Sternberg (*1*) proposed that the linear function reflects a serial span of memory in which a representation of the stimulus item is compared with representations of each memory item.

Most memory scan experiments have used memory lists short enough to fall within the limits of the span of immediate memory (the number of items that can be recalled without error) (*3*). The limits of immediate memory span are often thought to represent a division between short-term and long-term memory. Because short-term and long-term memory may involve different retrieval processes (*4*), a complete theory of memory retrieval must include an understanding of retrieval from long-term memory and the relation between long- and short-term retrieval.

To determine whether the scan model applies when information resides in long-term memory, we tested lists that exceeded the span of immediate memory and compared performance on these lists with performance on subspan lists. The memory lists were composed of two-syllable, common English words. Subjects memorized lists of 2, 4, 6, 8, 10, 12, 16, or 20 words to a criterion of two consecutive perfect recalls of the list members, in any order. Memorization of a list was followed by a series of trials in which a single test word was presented verbally and the subject decided whether the test word was in the list, pushing one of two buttons to indicate his decision. In experiment 1 we presented each word in any list once, along with an equivalent number of words not on the list (negative tests) (*5*). We presented the test words in a random sequence, which was preceded by one dummy negative test and followed by two dummy tests which were positive or negative with equal probability. This type



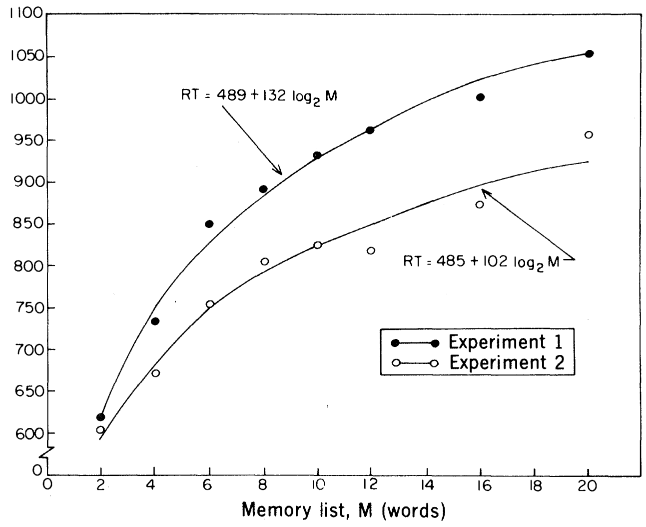


Fig. 1 (left). Mean reaction time as a function of memory list length (positive and negative responses combined). Straight lines represent upper and lower limbs of the best-fitting bilinear functions. Fig. 2 (right). Mean reaction time as a function of memory list length with best-fitting logarithmic functions.

of test sequence eliminates repetition of test items. Repetitions are known to affect RT's in the memory span paradigm (*6*), and number of repetitions is confounded with list length in many experiments using fixed memory lists. After a list was tested, it was discarded and a new list was memorized and tested. No two lists had any common members. We tested each subject on enough different lists of each length to have at least 136 trials at each length. The subjects were five undergraduates obtained from the University of Toronto employment service and paid $2 per hour for participation. The same five subjects served in both experiments. In experiment 2, the same list lengths were used, but there was only one list of each length per subject. Memorization of each list was followed by a random sequence of 40 positive and 40 negative tests. Negative test items were not repeated, but each list item was used as a positive test more than once.

Figure 1 shows mean RT for correct responses as a function of list length in each experiment. Because plots of RT versus list length were parallel for positive and negative responses, the data for the two types of responses were combined. Error rates were low: 2.7 percent of all responses in experiment 1 and 1.6 percent in experiment 2. Logarithmic, exponential, linear, and bilinear functions were fitted to the mean RT's across subjects by the method of least squares (*7*). A bilinear function provided the best fit, with root-mean-square deviations (RMSD's) of 7 and 13 msec for experiments 1 and 2, respectively (*8*). The points at which the best bilinear function changed slope corresponded to a list length of 6.71 words for experiment 1 and 6.83 words for experiment 2. For each experiment, the portion of the bilinear function for shorter lists had a steeper slope than the portion for longer lists [F (1 and 4 degrees of freedom) = 165.86, $P < .01$ for experiment 1, and $F\,(1, 4) = 12.15, P < .05$ for experiment 2]. The slopes for shorter lists were different in the two experiments [$F\ (1,\ 2) = 39.99$, $P < .05$], but the slopes for longer lists did not differ [$F\,(1, 6) < 1$]. The intercepts for the lower limbs of the two bilinear functions were not significantly different [$t\ (2) = 2.42$] (*9*).

The bilinear fit suggests that when memory information exceeds short-term span, the retrieval process is different from that used for subspan lists. The inference of dual processes is further supported by the result that the factor of experiment seems to affect the retrieval process for short lists but not the process for long lists. Both the breakpoint in the crossover to the long-list portion of the function and the slope of the long-list portion are virtually identical in the two experiments. Only the slope of the short-list portion of the function changes across experiments. The selective nature of this effect argues for a dual process model. Other evidence also suggests that retrieval from long and short lists involves different mechanisms (*10*). One possible explanation is that long-term retrieval is sometimes achieved by an accessing mechanism not sensitive to memory list length, but that the same span as that used with short lists is required if this mechanism does not provide enough information for a decision (*11*). The reduced slope reflects an averaging of the effects of list length-dependent and list length-independent processes. However, such a mixed model makes the invariance of the long-list parameters in the two experiments puzzling. A second possibility is that both short-term and long-term memory involve the span of the contents of memory, but that the scanning rate increases after six or seven items have been scanned.

As shown in Fig. 2, a logarithmic function describes the data well (although not as well as the bilinear function), with RMSD's of 12 and 21 msec for experiments 1 and 2, respectively (*12*). Logarithmic functions can be explained by the following type of processing model: The memory items are organized in a way that makes it possible to determine whether the test item was one of the memory items through an efficient classification process. This process consists of a series of decisions, each of which eliminates from further consideration a constant proportion of the remaining memory items. The process continues until all memory items but one have been eliminated. If this last item matches the test item, a positive response is initiated; otherwise a negative response is initiated. The total number of decisions required before a response can be made is a logarithmic function of the number of memory items, and RT could then be expected to increase logarithmically with memory list length (*13*).

DAVID BURROWS
Department of Psychology,
State University College at Brockport,
Brockport, New York 14420

RONALD OKADA
Atkinson College, York University,
Downsview, Ontario, Canada M3J 1P3

References and Notes

1. S. Sternberg, *Science* **153**, 652 (1966).
2. For a review of other reports see R. S. Nickerson, *Psychonom. Monogr. Suppl.* **4** (No. 65) (1972).

➞ G. A. Miller, *Psychol. Rev.* **63**, 81 (1956).

4. For a discussion of this issue ➞ A. W. Melton, *J. Verb. Learn. Verb. Behav.* **2**, 1 (1963).
5. This is a departure from the more traditional procedure in which the entire set of positive and negative items is defined for each subject before the experiment begins.

→ I. Fischler and J. F. Juola, *J. Exp. Psychol.* **91**, 54 (1971).

7. The exact forms of the fitted functions were: linear, RT = $a + bM$; logarithmic, RT = $a + b\log_2 M$; exponential, RT = $a - be^{-cM}$; and bilinear, RT = $a + bM$ if $M \leq M^*$ and RT = $a + bM^* + c(M - M^*)$ if $M > M^*$, where M is the number of items in the memory list and a, b, c, and M^* represent parameters of the various functions. For the bilinear function a is the intercept and b the slope of the lower limb, M^* is the point at which the lower and upper limbs cross, and c is the slope of the upper limb.

8. The RMSD's for the other functions for experiments 1 and 2, respectively, were: logarithmic, 12 and 21 msec; exponential, 12 and 25 msec; and linear, 50 and 31 msec. Deviations from each fitted function were tested for significance by using an F test as described by D. Lewis [*Quantitative Methods in Psychology* (McGraw-Hill, New York, 1960), pp. 351–379]. Only the linear fit for experiment 1 yielded a significant deviation [$F(6, 28) = 5.42$, $P < .01$].

9. The logic of these slope and intercept tests is described by N. Draper and H. Smith [*Applied Regression Analysis* (Wiley, New York, 1966), chap. 1].

→ J. L. Freedman and E. F. Loftus, *J. Exp. Psychol.* **102**, 1085 (1974); B. B. Murdock, Jr., and R. E. Anderson, in *Information Processing and Cognition: The Loyola Symposium*, R. L. Solso, Ed. (Erlbaum, Hillsdale, N.J., in press).

11. See R. C. Atkinson and J. F. Juola [in *Attention and Performance IV*, S. Kornblum, Ed. (Academic Press, New York, 1973), p. 583] for an example of a model in which list length–dependent and list length–independent processes are mixed and the proportion of each determines the slope values for memory retrieval functions.

12. A detailed comparison of bilinear and logarithmic fits was made by analyzing subsets of the data. Each of the five subjects served in ten sessions for experiment 1 and five sessions for experiment 2. Breaking down the data for each subject into two blocks of five sessions for experiment 1 and a single block of five sessions for experiment 2 yielded 15 subsets of data. For each of the 15 subsets the RMSD was smaller for the bilinear than for the logarithmic function. However, the generally good fit for both functions suggests that some caution be used in asserting that the bilinear is preferable to the logarithmic fit.

13. A formal description of such a classification process is provided by information theory [see E. Edwards, *Information Transmission* (Chapman and Hall, London, 1964)]. In information theory terms, the logarithmic relationship results from a process of reducing the uncertainty in the memory list ensemble. For an example of the application of information theory concepts in the Sternberg memory retrieval task, → G. E. Briggs and J. M. Swanson [*J. Exp. Psychol.* **86**, 296 (1970)].

14. Supported by National Research Council of Canada grant A8266. We thank L. Butler for experimental assistance.

22 August 1974; revised 11 February 1975

Focal Attention in the Frog: Behavioral and Physiological Correlates

Abstract. *The prey-catching response of frogs toward small moving objects can be facilitated by small movements of the same stimulus a few seconds earlier, even though initial movements seldom trigger the feeding response. This focal attention phenomenon may be related to the observation that one class of tectal unit continues to discharge for a few seconds following a brief stimulus motion. Together with anatomical data of other investigators, results of the present study suggest that self-exciting neural loops within the tectum mediate this type of selective attention.*

Although the long-standing interest of psychologists in phenomena of selective attention has produced, within the last decade, many new experimental paradigms for human and animal subjects, neurophysiological studies have provided few insights into the underlying mechanisms of those neural filters responsible for selective attention. Among vertebrates, studies of the optic tectum have provided one model of habituation. For example, Lettvin *et al.* (*1*) first noticed that many neurons within the frog tectum habituated rapidly to repeated movements of small buglike objects. Such data seem to correlate well with the locus-specific habituation of feeding behavior by frogs and toads during repeated movements of actual prey objects (*2, 3*). In these species, habituation seems to depend upon extrinsic inhibition of tectal neurons, since appropriate thalamic lesions abolish habituation effects both in overt prey-catching (*4*) and among single tectal neurons (*5*). Habituation effects are prominent in many neurons within the tecta of mammalian species as well (*6*).

The control of visual attention, mediated in part by the optic tectum, is not limited to inhibitory phenomena, since facilitatory effects have also been described. Lettvin *et al.* (*1*) reported that certain tectal neurons in the frog could be "awakened" by one or more short movements of a small spot within the receptive field, and these neurons would continue to respond if the spot continually moved to new portions of the field. Sprague *et al.* (*7*) found that neurons within the cat's tectum could show sudden periods of facilitated response related to signs of arousal in the cortical electroencephalogram. A more definitive study of facilitatory effects on tectal neurons by Goldberg and Wurtz (*8*) relates short-term increments in neural responsiveness to the preparedness of the conscious monkey to make directed eye movements. These observations provide an important entrée into attentional mechanisms, but so far no specific neural circuitry can be identified as the basis of focal attention. The present report includes two experiments which provide further insight into the neural mechanisms of this phenomenon. The first indicates that focal attention occurs during the frog's feeding behavior, and the second reveals a new class of unit in the frog's optic tectum, whose discharge pattern suggests a specific neural model of focal attention.

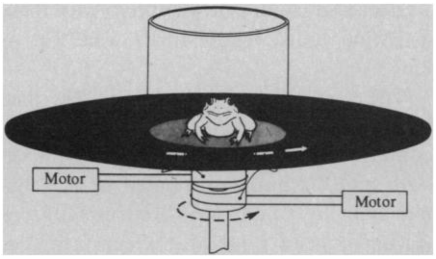


Fig. 1. Apparatus used to study snapping frequency toward dummy prey stimuli. Each yellow wormlike object was independently moved through a short arc when a single pulse activated the corresponding motor. The frog, confined by a transparent cylinder, remains at a nearly constant distance from the stimuli during a series of trials.

My initial observation of attentional effects in the frog's feeding behavior came from tests in which two small prey-objects were manually moved in synchrony 2 to 3 seconds after one object had moved slightly. In this experiment ten frogs directed 85 of 100 snaps toward the stimulus that had moved first, although the initial motion was too small to elicit a snap. In order to gain objective control over these stimuli, I adapted the test method of Ewert (*3, 4*) (see Fig. 1). The 2-cm-long wormlike stimuli were moved by means of motors that were activated by pulses from Tektronix pulse and waveform generators. Since frogs were selected for persistent feeding behavior, motions of less than 0.5 second in duration were required to maintain a low frequency of snaps at the initial motion. In the first paradigm, ten frogs (7 to 8 cm long) were tested for snapping responses toward a single object moving for only 0.3 second through a 5° excursion. This motion was then repeated after a 3.2-second delay. During 100 test trials, these frogs snapped at the initial stimulus motion only eight times, but 75 out of 100 times at second motions. That frogs can be alerted by such a brief motion is obviously adaptive for feeding on insects or worms that move discontinuously.

In order to decide whether the facilitatory effect of prior stimulus motion was a generalized arousal effect or whether it was limited to a spatial locus near the first motion, I repeated the test paradigm five times with the same ten frogs, but interspersed five trials with a new double-stimulus paradigm. In the second case, two prey stimuli were set 30° to 40° apart, and the frog was induced to orient the head directly toward a hand-held stimulus, set momentarily between the test objects. After a 10-second pause one stimulus moved