The procedure described below was followed in examining the ability of the extended MWC model to accommodate the cited data (*8, 9*). First, Eq. 2 with coefficients given by Eqs. 4b (denoted for brevity by Eq. 2 + 4b) and Eq. 3 + 4c were simultaneously fitted to the data for $\alpha_2\beta^{+CN}{}_2$ and $\alpha^{+CN}{}_2\beta_2$, respectively, in order to determine best-fit values of the five parameters of the extended MWC model. The following values were obtained by fitting to the cyanmet hybrid data only: $k^\alpha_T = 0.0235$ torr^{-1}, $k^\alpha_R = 1.63$ torr^{-1}, $k^\beta_T = 0.0124$ torr^{-1}, $k^\beta_R = 1.25$ torr^{-1}, $L = 8169$. With these parameter values, the functional dependence of y on log p was calculated for $\alpha_2\beta_2$, $\alpha_2\beta^{+CN}{}_2$, and $\alpha^{+CN}{}_2\beta_2$ by using the extended MWC equations 1 + 4a, 2 + 4b, and 3 + 4c. The resulting curves are plotted together with the data in Fig. 1. It may be seen that, whereas the parameter values given above provide a satisfactory fit to the data for the two cyanmet hybrids (as expected), they do not provide a satisfactory fit to the data for normal hemoglobin.

An attempt was then made to find a set of parameter values which would simultaneously provide a satisfactory fit of Eqs. 1 + 4a, 2 + 4b, and 3 + 4c to the combined data for the cyanmet hybrids and normal hemoglobin. Although many initial combinations of parameter values were tried, the search was unsuccessful. As an example of the type of results obtained, curves of y versus log p are plotted in Fig. 2 for all three species; the curves are calculated from the following parameter values: k^α_T and k^β_T as above, $k^\alpha_R = k^\beta_R = 4.0$ torr^{-1}, $L = 9.52 \times 10^6$. It may be seen that these parameter values provide a satisfactory fit to the data for normal hemoglobin but do not provide even an approximate fit to the data for the cyanmet hybrids. It was found to be generally true that the better a set of parameter values fit the data for normal hemoglobin, the worse it fit the data for the cyanmet hybrids (and vice versa), irrespective of the particular parameter values selected. It may therefore be concluded that the extended MWC model is too restricted by the assumption expressed in Eqs. 5 to be capable of simultaneously accommodating the oxygen saturation data for both cyanmet hybrids and normal hemoglobin.

The procedure described below was followed in examining the ability of the extended Coryell model to accommodate the same data. First, Eqs. 2 + 6b and 3 + 6c were simultaneously fitted by least squares to the data for $\alpha_2\beta^{+CN}{}_2$ and $\alpha^{+CN}{}_2\beta_2$, respectively, in order to determine best-fit values of the parameters k_0, α, and β. The values of these three parameters were then fixed accordingly, and Eq. 1 + 6a was fitted to the data for $\alpha_2\beta_2$ to obtain best-fit values of γ and δ. The parameter values obtained in this manner are: $k_0 = 1.40$ torr^{-1}, $\alpha = 0.73$, $\beta = 0.30$, $[\gamma,\delta] = [0.58, 0.084]$ (*13*). With these parameter values, the functional dependence of y on log p was calculated for $\alpha_2\beta_2$, $\alpha_2\beta^{+CN}{}_2$, and $\alpha^{+CN}{}_2\beta_2$ by using the extended Coryell equations 1 + 6a, 2 + 6b, and 3 + 6c. The resulting curves are plotted together with the data in Fig. 3. It may be seen that, in contrast to the extended MWC model, the extended Coryell model is capable of simultaneously accommodating the oxygen saturation data for both cyanmet hybrids and normal hemoglobin.

The purpose of this report is not to demonstrate that the particular sequential model considered here (the extended Coryell model) provides an adequate description of ligand binding in hemoglobin. Indeed, there are several reasons for believing that it is highly oversimplified. Nonetheless, we have unequivocally demonstrated that if the widely accepted view that the cyanmet hybrid hemoglobins are similar or equivalent in structure and subunit interactions to their partially oxygen-liganded analogs is correct, then the cooperative ligand binding of hemoglobin is more properly described by some model of the sequential type than by any two-state concerted model.

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13. Because γ and δ enter symmetrically into Eq. 1 + 6a, it is not possible to determine which of the values in brackets corresponds to γ and which to δ without additional information.
14. I thank H. A. Saroff for helpful suggestions.

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Spontaneous Remembering after Recall Failure

Abstract. *Verbal free recall of lists of 20 items increased on repeated recall attempts, without any further presentation of each word after it had been recalled just once. Such restricted presentation resulted in long-term storage and retention of almost all 20 items, as shown by their eventual spontaneous retrieval without further presentation. Most items that failed to be recalled were retrieved again later without any further presentation, indicating that such failures represent retrieval failures rather than loss from storage and that free recall verbal learning requires retrieval from long-term storage.*

In order to show that recall failures during free recall verbal learning represent retrieval failures rather than loss of (information about) items from long-term storage (LTS) and to separate the effects of presentation on encoding and retrieval, the subjects in this study of spontaneous remembering were presented, on each trial, only those items not yet recalled at all, instead of all items in the list. Since such restricted presentation involves the presentation of each item only until it has been recalled once, while the subject attempts to recall all items in the list on each recall trial, the development of recall during such verbal learning can be examined without confounding due to continuing presentation. Each subject was tested individually; he was read a list of 20 items at a rate of 2 seconds per word and was asked for free recall of all items in the list in any order immediately after presentation. After this initial presentation of the entire list, the subject was presented only those items that had not yet been recalled at all, before he again attempted to recall all of the items in the list. Learning was

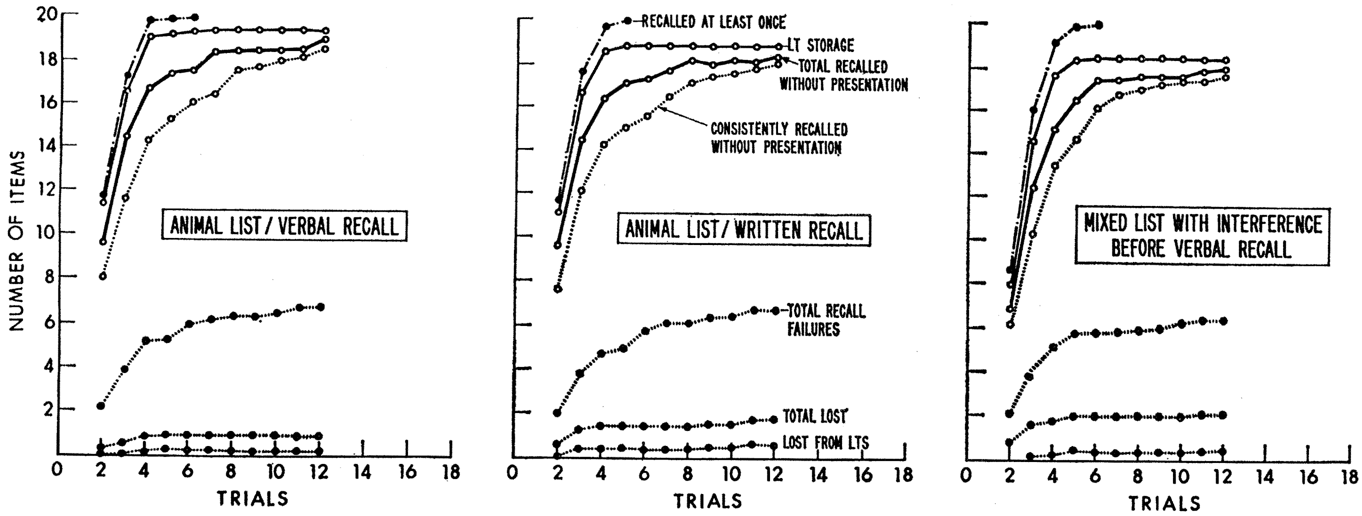

Fig. 1. Verbal free recall learning by restricted presentation, without further presentation of each item after it has been recalled just once. Long-term storage (LTS) is the number of items already in storage before each recall trial; retrieval from LTS is shown by recall without presentation. The lower curves show the cumulative total of all recall failures, of those recall failures never retrieved again, and of those recall failures apparently lost from LTS.

carried through 12 recall trials; since almost all items had been recalled at least once by the fourth trial, there were scarcely any presentations after this. Initial storage in LTS is demonstrated by eventual spontaneous recall; since items are not presented again after initial recall, spontaneously retrieved items must have been stored on (or before) the trial of initial recall, providing an excellent estimate of the number of items in LTS on each trial. Retention of LTS alo is demonstrated by spontaneous retrieval without further presentation after recall failure and shows that most recall failures are retrieval failures.

Three groups of ten normal, young adult subjects, who were paid for their participation, were studied. The first group learned a list of 20 animals by verbal free recall, and the second group learned the same list by written free recall (*1*). The third group learned a list of 20 unrelated items by verbal free recall, for the purpose of demonstrating that increasing retrieval of items without further presentation does not depend on the use of a limited category of items for learning (*2*). This third group also was subjected to verbal interference, before each recall attempt, by requiring these subjects to recall spontaneously ten items from a new category designated after each trial, in order to show that increasing retrieval without further presentation involves retrieval from LTS rather than rehearsal of previously recalled items (*3*). Finally, it is important to note that all subjects were encouraged to extend their recall on each recall attempt by continuing to search for more items even after it became difficult. Such extended recall may be necessary to demonstrate increasing retrieval without further presentation, since subjects in verbal learning experiments may simply terminate retrieval search when it becomes difficult (*4*).

Figure 1 shows the very similar results obtained from all three groups. Even though each item was presented only until it was recalled for the first time, nearly all of the 20 items entered LTS, as shown by eventual spontaneous retrieval without any further presentation on some later trial. Long-term storage is shown in Fig. 1 as the minimum number of items that were in storage before each recall trial. The total number of items recalled without further presentation, which reflects retrieval from LTS, continued to increase throughout learning without any further presentation, so that an increasing proportion of the items retained in LTS was recalled. Most of the items recalled from LTS without further presentation also were recalled consistently on all subsequent recall attempts throughout learning; once an item was spontaneously retrieved after previous recall failure, it usually was consistently retrieved thereafter (*5*). Although retrieval failures may extend over many recall attempts when such restricted presentation is used, there were very few recall failures after an item was spontaneously retrieved. Of the 20 words, about 14 were recalled on every trial, starting with their first recall; only about 1 word was never retrieved again after the first recall; and the remaining 5 words were recalled, then not retrieved, and then retrieved spontaneously without presentation (*6*).

The lower three cumulative curves in Fig. 1 show the total number of all recall failures throughout learning, the number of all those recall failures without later spontaneous retrieval, and the number of only those recall failures without later spontaneous retrieval involving items that clearly had been in LTS before recall failure (as indicated by at least one retrieval from LTS without presentation). The finding that most of the recall failures later were retrieved again on some subsequent trial without further presentation indicates that most recall failures represent retrieval failures rather than loss of (information about) items from LTS. The items that were spontaneously retrieved after previous recall failure were usually retrieved from LTS late during the recall attempt in which they were recovered (mean output position, 15.1, 15.4, 13.9, respectively, for the first, second, and third groups).

Essentially the same findings were exhibited by all subjects in all three groups. The rapid storage and effective retrieval of the mixed list of unrelated items was not very different from the storage and retrieval of the animal list, even with verbal interference before each recall attempt. This confirms that such recall without presentation does involve retrieval from LTS (rather than recall from short-term retention by rehearsal of previously recalled items), and that the effectiveness of retrieval appears to be a function of the number of items in the list to be retrieved (7) but not of the number of items in the potential search space in LTS.

These findings appear to indicate that free recall verbal learning may require retrieval from LTS and that most recall failures after initial recall represent retrieval failures rather than loss of (information about) items retained in LTS. Apparently, presentation of items only until they have been recalled at least once is sufficient for storage and retention of almost all items, as demonstrated by subsequent spontaneous retrieval without any further presentation. Once an item has been spontaneously retrieved from LTS the probability of subsequent retrieval is very great, so that retrieval from LTS increases without further presentation. There is very little support in these data for the assumption that (information about) items is lost from LTS during verbal learning. These results support the assumptions previously made in the analysis of verbal learning by selective reminding (8) that items remain in LTS and that recall failures may reasonably be regarded as retrieval failures.

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References and Notes

1. The items in the animal list were: dog, fox, horse, buffalo, lion, rhinoceros, elephant, antelope, bear, lamb, rat, raccoon, sheep, llama, goat, cheetah, squirrel, beaver, donkey, and turtle.
2. The items in the mixed list were: Chicago, hand, tulip, zebra, carpenter, brandy, clarinet, Norway, train, cup, slippers, tennis, lemon, pigeon, corn, desk, spider, garlic, elm, and shark.
3. The following categories were used for verbal interference by spontaneous retrieval before recall of the list to be learned: names of states, boys' names, articles of clothing, verbs, colors, occupations or professions, musical instruments, foreign countries, trees, girls' names, relatives (types of), and natural earth formations.
4. Both extended recall on each recall attempt and many recall attempts (without further presentation) seem to be needed to obtain the maximum spontaneous retrieval from LTS necessary to evaluate storage, retention, and retrieval accurately. Since the subject must learn that it is possible to retrieve additional items by such extended recall, it is important to provide enough time and encouragement to allow maximum retrieval from the very first trial on. This also requires the subject to try to recall all items in the list, rather than just some self-selected part of the list. Our subjects have reacted positively to the challenge of achieving their own maximum retrieval without further presentation.
5. Such consistent retrieval from LTS on all subsequent recall attempts without any further presentation may also provide an estimate of list learning. We would ordinarily say that a list has been learned when the subject can consistently recall all of the items in that list without any further presentations. Therefore, it would also seem reasonable to say that when a subject can recall half of the items consistently on all subsequent recall attempts, without any further presentation of those items, the subject has learned a (smaller) list of just those items (and has learned half of the entire list to be learned), since this seems to be what we mean when we say that a list has been learned. The cumulative number of items that are consistently retrieved from LTS on all subsequent recall attempts should therefore provide an estimate of list learning for comparison with item learning.
6. F. I. M. Craik [*J. Verb. Learn. Verb. Behav.* **7**, 996 (1968); *ibid.* **9**, 143 (1970)] has shown that items from short-term storage are not recalled at delayed testing after presentation and testing of other lists, even though they are recalled at immediate testing. This effect is shown in the present data by failure to retrieve about one item again after the first recall. Since retrieval from LTS may occur only after many recall attempts, this effect would have been greater if repeated retrieval attempts had not been used.
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Coyote Predation Control by Aversive Conditioning

Abstract. *Conditioned aversions were induced in coyotes by producing lithium chloride illness in them following a meal, and the effects upon eating and attack behavior were observed. One trial with a given meat and lithium is sufficient to establish a strong aversion which inhibits eating the flesh of that prey. One or two trials with a given flesh (lamb or rabbit) specifically suppresses the attack upon the averted prey but leaves the coyote free to attack the alternative prey. A method of saving both prey and predator is discussed.*

Predation of lambs by feral coyotes, in the public lands of the western United States, has led to a sharp controversy between naturalists who wish to see this carnivore survive in its natural habitat and stockmen who wish to reduce sheep losses to predatory coyotes. The principal method of controlling predation has been simply to kill the coyotes, employing bounty hunters, traps, and lethal poisons. These methods do not distinguish between the sheep killers and other coyotes (*1*). We are devising behavioral methods which spare both prey and predator.

If an animal eats a poisoned meal and survives, it will develop an aversion for the flavor of that meal. Such conditioned aversions have been studied most extensively in the rat, which is an omnivore specialized in seeking and testing new sources of food, including many plants which could be toxic (*2*). Several general questions arise: (i) Can such aversions be as readily established in a feral carnivore which preys principally on animals? (ii) Will gustatory aversions inhibit attack behavior directed at olfactory, auditory, and visual aspects of living prey? (iii) Can the inhibitory effect be limited to a specific prey (for example, lambs), leaving other options (for example, rabbits) open to the predator?

Our subjects were seven adult coyotes, approximately 2 to 4 years of age, maintained in individual dog runs. Five coyotes were removed from their feral den at approximately 3 weeks of age. Three (male "Brujo" and females "Luna" and "Coty") had hunted rabbits in the desert, while two (male "Feisty" and female "Dizzy") had no hunting experience. All were relatively domesticated and readily attacked both lambs and rabbits. The male "Sam" and female "Mary" were trapped as adults and were shy feral animals, each with an amputated forepaw, a result of the trapping. After several months of habituation to captivity Sam attacked and ate rabbits, but refused to attack lambs even when they were placed in his pen for hours. Mary would not attack either animal.

Our general procedure was to maintain the animals on one "safe food" and then present a "poison food" laced with lithium chloride or followed by an intraperitoneal injection of lithium chloride. In the hamburger experiment, four coyotes (Brujo, Coty, Luna, and Mary) were maintained on dog food and given fresh hamburger on two occasions. On the first hamburger trial the meat contained 6.0 g of lithium chloride in 31 capsules (No. 4 gelatin coated with a cellulose acetate compound). All the animals became ill and vomited after that meal (*3*). Three days later the animals were presented with unpoisoned hamburger and refused to eat the meat. After the hamburger test, they ate a full ration of dog food, indicating the aversion was specific to hamburger (see Fig. 1). During the attack experiment, each coyote was placed in an individual pen approximately 4 by 5 by 4 feet high (1 foot = 0.3 m). The individual