

more, it might eventually be possible to enhance the regrowth of less regenerative mammalian tissues once some of these signals and controls are understood.

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Marmosets (*Saguinus fuscicollis*): Are Learning Sets Learned?

Abstract. *Confronted with a novel object, a social group of marmoset monkeys investigated it. If they found food on it they returned to it readily the next day; whoever had led in eating usually did so again. If they did not find food, day 2 responsiveness decreased. These untrained performances were sufficient for one-trial visual discrimination learning.*

Animals tested in the laboratory on a series of object discrimination learning problems typically solve the first ones slowly and require considerable practice before they solve new ones in a single trial (1). This phenomenon has been said to show that the ability for one-trial learning emerges as a result of the training, through a special process called "learning to learn" or learning set formation (2). Our studies of *Saguinus fuscicollis*, a relatively primitive New World primate, suggest in contrast that if these animals have been reared in reasonably normal fashion and if the test situation is designed with consideration for their prior behavioral organization, no further practice and no formal training are required. Thus, progressive improvement in a "standardized" test situation is not necessarily the acquisition of a new ability and might simply be the regaining of previous levels of efficiency after the overcoming of situationally induced negative transfer (3); in everyday life, optimal foraging is hardly the prerogative of Old World primates of presumably high "general intelligence" (4).

Our procedure differed from those of previous investigations in that, inasmuch as most primates typically live and forage in closely knit social groups, we tested our animals in groups rather than

as isolated individuals. We made only the minimum changes in their routine living conditions that were essential for assessing their differential responses to objects related and not related to food. Menzel and Menzel (5) found (i) that with nonfood objects family groups of *S. fuscicollis* quickly detected any novel or changed object; (ii) that they investigated only a few minutes and showed little recovery the next time the same object was encountered, a day or more later; and (iii) that the order in which the various group members approached any given object was not fixed, but varied from trial to trial according to test conditions. We hypothesized that a sufficient basis for one-trial associative object discrimination learning would be any set of mechanisms, however they might originate, that would lead animals to investigate objects or classes of objects that might contain food, to return to those that contained food on last encounter (win-stay), and to not return (or return less readily) to those that did not (lose-shift) (6). To demonstrate such learning without formal training we needed to incorporate into the same sort of test some objects containing food and to show that the animals immediately perform in a win-stay fashion with them while continuing to perform in a lose-

shift fashion toward nonfood objects.

The social group that we tested consisted of a 9½-year-old female, her 6½-year-old mate, and their three sets of twins (females aged 0.60 years and males aged 1.60 and 2.35 years). All animals other than the male parent had been born and raised in captivity. None had been tested before. Preliminary training consisted of placing their customary food pan in a test apparatus rather than in its usual location and recording their behavior toward it until they seemed well habituated. The test apparatus was a 45 by 60 by 60 cm wire mesh cage with a wood floor and a 25 by 15 cm swinging door on one side. It was left in the home cage permanently and was located at a low elevation with no branches touching it. (Except at test times the animals rarely went into or onto it.) The home cage was a 3 by 4.3 by 4 m section of an indoor room, furnished with a hutch box for sleeping and a number of small trees and overhead branches. Food and water were continuously available.

The test objects were mostly household articles; they were novel to the animals and presumably easily discriminable from one another. They were randomly designated as food or nonfood objects. Jam, honey, or some other treat was smeared onto or inside of the food objects; objects had to be manipulated in different ways in order to discover what, if anything, they contained.

A successive discrimination or "go, no-go" procedure was used. First, we started a timer that produced a "beep" every 15 seconds and positioned chairs about 1 m from the home cage; one of us entered the home cage, placed a single test object on the floor of the apparatus, and closed the apparatus door. When the timer sounded again, the observer left the home cage, closed its door, and sat down. When the timer sounded again, and independently of the animals' behavior, he opened the apparatus door by means of an attached string. We recorded which individuals were on the apparatus just before the door opened (as the timer sounded), the exact order in which they entered the apparatus and took their first licks at the food, which individuals were on or in the apparatus at the moment of each timer beep, and general qualitative notes. Observation continued for 7½ minutes; then the object was removed. A single trial was given each day and intertrial intervals were at least 22 hours.

Before putting food on any novel object we first conducted two trials with each of six nonfood objects, to assure that the animals' behavior was typical

lose-shift performance. In the second phase of testing, six objects had food on them and six did not; three successive trials were given on each, without interpolated trials on other objects, but food and nonfood objects were otherwise presented in an irregular order. In the third phase, three sets of objects (each consisting of a food and a nonfood object) were given three trials per object, with the object presentation order varied from one trial to the next (7). In the retention phase we randomly presented the last nine nonfood objects and all seven objects on which the animals had actually found the food for a fourth trial each. No object had food on it this time and all had been cleaned of odors. The length of time between trials 3 and 4 averaged 3 weeks (range, 9 to 77 days) and was equalized for the two classes of objects.

Figure 1 shows the group's moment-to-moment reactions toward the objects (8, 9). On trial 1 the animals were highly reactive but approached the object warily. The first to enter the apparatus was nearly always one of the two oldest offspring, and the order in which the eight group members entered was statistically reliable across the several objects (Kendall's coefficient of concordance $W = .34$, $P < .001$). No differences in response toward the two classes of objects were seen on any measure until after someone uncovered the food (which did not occur until trial 2 on food objects 1 and 3 and did not occur at all on two other objects); thus the animals could not detect the food at a distance through uncontrolled cues (10). A single, distinctive "food call" or a few licks at the food by its discoverer sufficed, however, to attract others (especially the youngest animals, which still obtained some food from the hands or mouths of their elders) to the object. With food objects the number of individuals increased on or in the apparatus until the food ran out or some had their fill and left; with nonfood objects the number decreased. Although physical competition for food or objects was rare, some individuals typically waited until others left before entering the apparatus.

On trial 2 and thereafter the only objects that induced a wary approach were those that had induced stronger caution (if not a distinctive "alarm call") on the preceding trial. With 11 of the 15 nonfood objects there was a lose-shift decrease from trial 1 to trial 2 in the number of animals on the apparatus before the door opened [$t(14) = 2.66$, $P < .02$], and with 13 of these objects the number of time intervals spent in or on the apparatus decreased [reliability across objects:

$t(14) = 3.49$, $P < .01$; reliability across animals: $t(7) = 6.69$, $P < .001$]. With the seven objects on which the marmosets found food, however, the pattern was win-stay. For example, on the trial subsequent to the discovery of food, only one object showed a decline (from the previous trial) in the number of animals on the apparatus before the door opened; with each of these seven objects the ordinal number of the trial (trials 1 to 3) correlated perfectly (Spearman $\rho = 1.00$) with the speed with which the food was found ($P < .001$). Whether the differences between food and nonfood objects were assessed across individuals or across specific objects, they are significant at or beyond the .02 level on each measure. The evidence for one-trial visual discrimination learning in these animals' first problems resembles that at the asymptote of training in the

typical primate learning set experiment.

The data provide strong evidence for one-trial learning on the part of individuals as well as the group as a whole. Even though all but the two youngest and one of the next youngest animals discovered the food on at least one object, with five of the seven objects whichever individual had discovered it on trial x (the trial of discovery) uncovered it first on trial $x + 1$; the two deviant cases involved the parents, who let their offspring eat first under routine conditions and throughout preliminary training also. The rank orders in which the eight animals ate on trial x and on trial $x + 1$, within any given food object were significantly correlated (median $\rho = .66$, $P < .001$). Only 5 percent of the similar possible correlations across different food objects (for example, trial x , object A and trial $x + 1$, object B) were

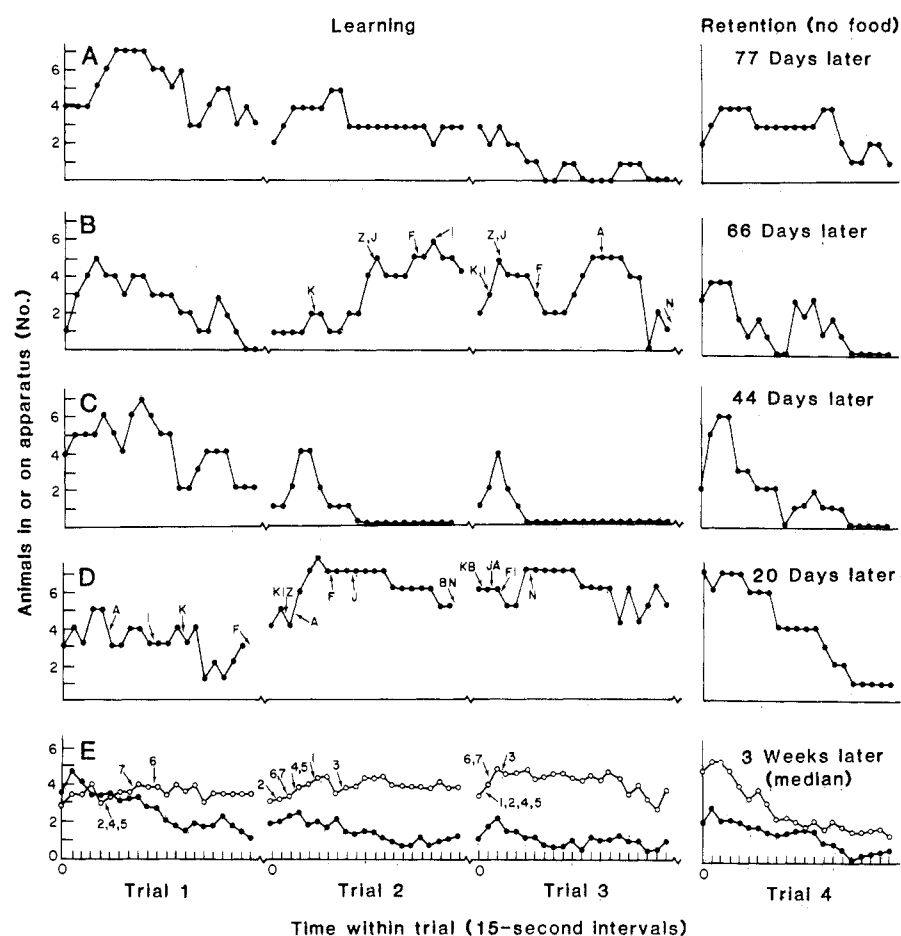


Fig. 1. One-trial group learning about food and nonfood objects, and retention of object discriminations. Each graph shows the number of group members on or in the test apparatus at each 15-second beep of the timer, across the first 5 minutes of any trial. (A to D) Raw data for representative objects of each class: (A) mirror (no food); (B) jar with peanut butter (first food object); (C) milk carton (no food); and (D) vine with chocolate sauce. (E) Averaged data of the last nine nonfood objects (filled circles) and all seven other objects on which the animals found food (open circles). Numbers above the curves in (E) give the ordinal number of each food object and the time at which food was found (8); letters above the curves in the top panels refer to individual animals and show their latency and rank order to eat. (Initials: Z and A, female and male parents Zoe and Alex; K and N, 2.35-year-old males Koni and Niko; B and F, 1.60-year-old young adult males Blaze and Flame; I and J, 0.60-year-old, juvenile females Natalie and Noelle.)

as high as this (median, .20). The last figure is comparable to that found for trial 1 and trial 2 approach orders to unchanged nonfood objects (5). These results are as one would expect if marmosets (like humans) remember self-generated information better than information from others (11). The marmosets may have deferred socially to those who had initially discovered the food, but a more parsimonious hypothesis is that the discoverers were the most discriminating and eager.

Differential response to the two classes of objects was still very clear on the retention trial ($P < .01$ on each measure). Most food objects evoked food calls as soon as they were sighted; no nonfood object did. With nonfood (but not food) objects the number of days elapsed between trials 3 and 4 and the amount of time spent on or in the apparatus were correlated ($r = .69$, $P < .05$); either these objects tended to be forgotten eventually or the animals simply rechecked even old and unproductive objects after enough time had elapsed. Here, both win-stay and lose-shift performances could be viewed as special cases of varying optimal return time (4). Obviously, animals do not stay indefinitely at a food object but rather leave and return after a time or when the object in question has probably replenished its food supply.

In subsequent experiments we have replicated all of the above findings in a variety of contexts, including tests with no food reward after the trial of discovery, with simultaneous presentation of as many as 30 test objects, and with test objects behind a visual blind (in which case some group members took their cue exclusively from a leader). We do not predict how the same animals would do if tested in social isolation in an unfamiliar cubicle with more customary learning set procedures. It would be surprising, however, if free-ranging members of this species are incapable of the same sorts of performances reported here. Why they might be so skilled is an open question. Even 1-month-old infants have an effective strategy for obtaining solid foods, namely, "Take your cues, if not the food itself, from others." As long as any family member is curious enough to check new objects and tolerant enough of food sharing or stealing, and food is sufficiently abundant, others fare well. It is no doubt when social strategies are insufficient for them that individuals lose-shift and use asocial or antisocial strategies instead (12). Not only for *S. fuscicollis* as contrasted with other species but also for infants as contrasted

with adults, the most pertinent question for students of foraging is not how they compare in general learning ability or intelligence but rather what sorts of problems each animal faces and what strategies are sufficient for solving them (3, 4).

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4. For recent reviews of foraging theory, see A. C. Kamil and T. D. Sargent, Eds., *Foraging Behavior: Ecological, Ethological and Psychological Approaches* (Garland, New York, 1981); J. R. Krebs, in *Handbook of Behavioral Neurobiology*, P. Marler and J. G. Vandenbergh, Eds. (Plenum, New York, 1979), vol. 3, p. 225. Probably the strongest single set of evidence against the view of learning set theory (2) that one-trial learning of visual discriminations requires much training and is a good cross-species index of intelligence is recent research on insects [for example, R. Menzel and J. Erber, *Sci. Am.* **239**, 102 (July 1978)].
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7. The reason for this gradual introduction of food and of randomization of object presentation orders is that for most animals, *S. fuscicollis* included, the odds of finding food on any particular object or in any specific location less than a half cubic meter in size must be small—and any large departure from normative odds might be expected to produce over-responding and breakdown of lose-shift behavior. Our animals, however, were little affected by 50 percent reward and randomized orders of object presentation. In the next experiment, trial 2 discrimination of food from nonfood objects was still better than chance over 40 objects presented four at a time, one trial per object per day, with intertrial intervals of a few minutes and (overall) no differential reward for win-stay or lose-shift performance.
8. The female parent died suddenly of undetermined causes during week 1 of phase 4. Her data are excluded from trial 4 and from Fig. 1E. All results remain essentially identical.
9. We exclude from Fig. 1 and from the statistical analyses the two so-called food objects on which the animals never discovered the food.
10. *Saguinus fuscicollis* have highly developed olfactory and scent-marking systems [G. Epplé, in *Primate Behav.* **4**, 195 (1975)]. Precautions taken included control tests in which food or food odors were placed in objects toward which the animals were previously habituated. Responses were no different from those to an unbaited object until the animals came within a few centimeters of the object. Scent-marking of the test objects was seldom observed.
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Long-Term Consistency of Dominance Relations Among Female Baboons (*Papio cynocephalus*)

Abstract. At maturity, female baboons in the Amboseli National Park of Kenya generally attain a rank position among adults near to that of their mothers. However, the age of a female's mother and the difference in ages between sisters also influence the rank acquisition process. These latter demographic variables, which are sensitive to changes in resource availability, may account for the close association both within and among primate species of specific patterns of rank organization and specific environmental conditions.

Long-term studies of provisioned and captive macaques have shown that at maturity a female generally attains a dominance rank position immediately beneath that of her mother and above that of her older sisters (1). We have observed the dominance relations among adult females in a wild population of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park of Kenya for a comparably long term. Our analysis of

the ranks of identifiable females in our main study group, Alto's group, is based on 10 years of observations, an interval roughly equal to the adult life expectancy of a female baboon (2, 3). The data support the prevailing notion that for many species of Old World monkeys the rank of a daughter at maturity is strongly influenced by that of her mother. However, examination of the case histories of Amboseli baboons suggests that the rank