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Social foraging in marmoset monkeys and the question of intelligence

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A social group of five saddle-back tamarins (*Saguinus fuscicollis*) were allowed 15 min per day in a sizeable room adjacent to their home cage. Every other day two additional novel test objects were placed in the room; one contained food on first presentation, and the next day the locations of both were sometimes moved. From the outset, and even when there were 30 objects to choose from, the animals were acute in detecting the novel objects and in remembering the objects and the locations in which they had found food. Whichever individuals had eaten first were among the first to approach the next day. Subsequent tests showed that such one-trial learning was not dependent on object-novelty; that the animals probably remembered all 30 objects and the location of each; and that they spontaneously performed what amounts to generalized delayed matching to sample. The data match or surpass the asymptotic performances of other marmosets on, for example, learning set tasks but are consistent with what is known about the foraging habits of wild *S. fuscicollis*. Optimal foraging theory is less likely to be an overestimate of animals' mental capacities than previous studies are an underestimate.

1. Introduction

Taxonomists and psychologists alike have in the past often characterized marmosets (family Callitrichidae) as 'squirrel-like', 'primitive' primates. These characterizations are, however, misleading (Ford 1980; Garber 1980). Not only the distinguishing morphological features of these animals (diminuitive body size, tendency towards reproductive twinning, claw-like nails on all digits other than the hallux, and some aspects of their molar dentition) but also many features of their locomotor, postural and other behaviours and their ecological and social organization could well be relatively recent and interrelated adaptations rather than retentions of the traits of their primitive New World primate ancestors (Moynihan 1976; Szalay & Delson 1979). Ford (1980), in fact, argues that marmosets represent a clear case of phyletic dwarfing. Severely limited space and food resources, and interspecific competition for these resources, are among the most obvious candidates for the major selective forces that might have led to their dwarfing.

But regardless of how marmosets originally came to be as they are, there is no question that their foraging strategies today are quite different from those of other taxa, and from one another (Dawson 1979; Izawa 1978; Mittermeier & van Roosmalen 1981; Terborgh 1983). As Terborgh (1983, p. 94; see also Milton 1981; Richard 1981) puts it, the most important characteristic of fruits from the standpoint of their differential exploitation by primates is not their size, texture, colour, construction or taxonomic status but their characteristic concentration in space and time; and the saddle-back tamarin, *Saguinus fuscicollis*, seems to have a unique strategy, at least by contrast to the various non-*Saguinus* species in the same region, in going

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for fruits that occur in tiny, scattered incremental units and that furthermore ripen in a piecemeal fashion. This pattern of ripening implies that only a very small amount of food is available for eating in any given locus on any single occasion, and also that a reliable (though scanty) supply can be obtained at the same loci over a period of many weeks. Such facts, Terborgh believes, will be of the utmost significance for understanding the behavioural, social and ecological organization of *Saguinus* more generally.

Ecologically oriented students of animal learning would surely concur (for example, Johnston 1981; Kamil & Sargent 1981; Kamil & Yoerg 1982). Indeed, such facts might help to explain the sorts of laboratory data on learning and memory that we ourselves have been obtaining over the past several years. Conversely, from our data we would predict that not only are feral *S. fuscicollis* capable of foraging for the above sorts of resources in a relatively optimal fashion, but also that the mechanisms by which they do so entail exceptionally rapid learning and an ability to remember from one day to the next the visual appearances and the relative positions of many objects simultaneously. To be more specific, our data strongly suggest that at least when these animals are tested in a sufficiently 'naturalistic' fashion, they require no training beyond that which they have already picked up 'on their own' in their home environment to show performances which students of learning would construe as evidence for 'cognitive maps' (Menzel 1978; Tolman 1948) and 'win–stay, lose–shift' strategies with respect to objects and locations (Levine 1959; Kamil & Yoerg 1982; Olton 1979). Here we shall not review the results of our already-published studies (Menzel & Menzel 1979; Menzel & Juno 1982). Instead, we shall report four of our more recent tests, which extend our earlier findings, and should dispel the doubts of those students of learning set formation (Schrier & Thompson 1984) who believe that these findings do not entail anything on a par with what primates do on Harlow's (1949) classical tasks. (See also Menzel & Juno 1984.)

2. GENERAL METHOD

The animals used in this study were five laboratory-born sibling adult *S. fuscicollis*: twin males Koni and Niko (4.5 years old), twin males Blaze and Flame (3.5 years old) and a female, Natalie (2.5 years old). They had received extensive testing in situations that involved the presentation of a single test object at a time, in precisely the same locus (for example, Menzel & Juno 1982), but this was their first test involving multiple test objects that were presented simultaneously. Their regular diet had always been given to them every day in the same food pan and usually in the same location. The largest room they had ever been in since birth was their present home cage, which consisted of a 3 m by 4.3 m by 4 m section of a slightly larger indoor room.

Inasmuch as *S. fuscicollis* typically live and forage in social groups rather than alone, we tested them as a group, simultaneously. Testing consisted of opening a guillotine door to the adjacent 6 m by 4.3 m by 4 m room and recording for a period of 15 min the precise order in which, and the time (to the nearest 15 s) at which each individual entered this test room, returned to the home cage, or approached or made physical contact with any of 30 previously designated and widely dispersed points in the test room. Further qualitative notes were also made. Observations were recorded verbally by tape recorder and timed with an electronic timer which sounded a clearly audible beep every 15 s.

Testing was conducted before the morning feeding. As soon as the 15 min 'trial' had elapsed the animals were given their customary morning rations in their home cage, and the door to

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the test room was closed until the next day. (Almost always they had already returned home before 15 min was up.) Each room was furnished with a network of dead trees and branches, via which the monkeys could reach virtually any point in the rooms, from floor to ceiling.

'Pretraining' consisted of allowing the animals to explore the previously novel test room 15 min per day for 10 days (by which time they seemed well habituated to the room and to the procedures) and then adding a number of small cardboard tags to serve as location markers, and giving the animals an additional two 15 min trials to habituate to them. Formal testing began the next day.

3. Test 1: reactions to novel food and non-food objects

This test was similar to those used elsewhere (Menzel 1971; Menzel & Menzel 1979, experiment 1). The most important single difference, procedurally speaking, was that some objects contained food. If *S. fuscicollis* can readily learn and remember the visual appearances and the locations and the orientations of almost any given object (Menzel & Menzel 1979), few cognitively inclined investigators would, of course, see much reason to doubt that they could also learn and remember which of these same objects had contained edibles. From this point of view, the data contain few surprises.

Method

Two new test objects were introduced into the test room every two or three days (for example, an aspirin bottle and a small bow made of red ribbon; a white plastic bag and a tin can). One object of each such pair was randomly selected as the 'positive' or food object and in it or within 25 cm of it were hidden 10 small pieces of candy. The other, 'negative', object contained no food, but (on problems 6–16) as a control for odours, the same amount of candy had been left in it for at least 10 min, and then removed just before the test began. In two problems the positive object contained food both on trial 1 and on trial 2; in all others it contained food only on trial 1. The two locations in which the objects were to be placed were selected in a non-systematic fashion from among the 30 tagged spots in the room, and then a coin-toss determined which object would be in each of these locations. In eight of the 16 problems that were thus presented over a period of 34 days the locations of the two newest objects were changed on trial 2. Twice they were directly swapped (the typical procedure in the traditional two-choice discrimination learning experiment), and the remaining six times the objects were moved to other locations, sometimes displacing older objects to a new location, and other times going themselves to new locations. Rather than discard each pair of objects after a few trials, we discarded only two objects (of which the animals remained somewhat cautious). Old objects remained in the same places from one day to the next, unless displaced by a new object. Thus, the number of test objects in the test room increased cumulatively as the experiment progressed. Unless noted otherwise, the statistical significance of the data was assessed with Monte Carlo simulation techniques.

Results and discussion

Trial 1 performance, and a general description of the animals' search strategies

As expected (cf. Menzel & Menzel 1979), the animals were from the outset very skilled at detecting the new objects on trial 1 of any given problem. They could not initially tell which

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of the two novel objects was 'positive' and which was 'negative'; in 7 of 16 problems they approached the latter object before they went to the former. However, only 2 of the 32 novel objects were approached later than one would expect by chance; and in 7 of the 16 problems the positive object was the first object in the room to be hit ('chance' expectancy = 1.72; $p < 0.001$), and all nine exceptions involved responding first either to the negative novel object or to an object that had been positive on a preceding problem.

In some respects the group's behaviour was very different from that seen in tests in which no objects ever contained food (Menzel & Menzel 1979). On entering the test room the animals fanned out from one another and scanned different sections of the room, as if operating as a team and actively searching for the food. They often moved at very high speeds. Koni and Natalie usually travelled together, with Koni in the lead. The number of problems in which each animal made the first object approach to be recorded on trial 1 was: Koni 10, Niko 0, Blaze 0, Flame 2, Natalie 4. The number of problems in which each was first to eat was: Koni 4, Niko 0, Blaze 2, Flame 1, Natalie 9. The last three (youngest) animals seemed by far the most reliant on cues from others, and Natalie excelled in opening the containers. Niko was typically the last to enter the room and foraged at the opposite sides of the room from Koni; in a subsequent test we removed Koni from the group and Niko immediately took over his role as 'leader'. In general, each individual followed a somewhat different strategy which was undoubtedly influenced as much by its relationships with others as by any other contingencies. Each also had at least a few locations it tended to check before anyone else.

On first detecting the food, the animals very often made a distinctive 'food call', which brought others over towards the object. (An 'alarm call' by an animal who was cautious of an object produced an even more marked group reaction. All group members typically raced over with piloerected tails and 'mobbed' the object together.) Individuals very rarely stayed at the food object until all food was gone. Typically, they grabbed a few pieces of food and ran off with it several metres. As a result, on most trials each of the five animals managed to get some food (even though any one of them would easily have consumed the total quantity that was available, if given the opportunity), and obvious agonistic behaviours towards one another were rare. Obviously, they also had to remember the locus of the food source if they were to check it out again, unless by chance they could get some cues from one another. They did clearly remember, for they usually returned to the food object after having finished their food, by-passing but ignoring other objects in the process. Other indications of their (short-term) memory, which were verified more thoroughly in subsequent tests, were the tendencies of individuals to seldom check unbaited or relatively old objects more than once or twice in a trial and to avoid checking unbaited objects that had recently been checked by a group-mate.

Learning and long-term memory

Figure 1 shows the sequence in which the first five or more objects were approached for the first time (by any animal) in each of the first 10 problems, both on trial 1 and on trial 2. (Usually most of the objects were approached at some time during the 15 min trial.) Table 1 shows the total number of 15 s intervals in which the five animals were scored as approaching or touching each of the objects on each trial that entailed no food in any object. (Each individual could receive a maximum of one count per object per interval.) It is obvious from these data that the effects of a single reinforced trial, and of relative novelty, could usually be detected for several days.

In 15 of 16 problems the first object in the room to be approached by any animal on trial

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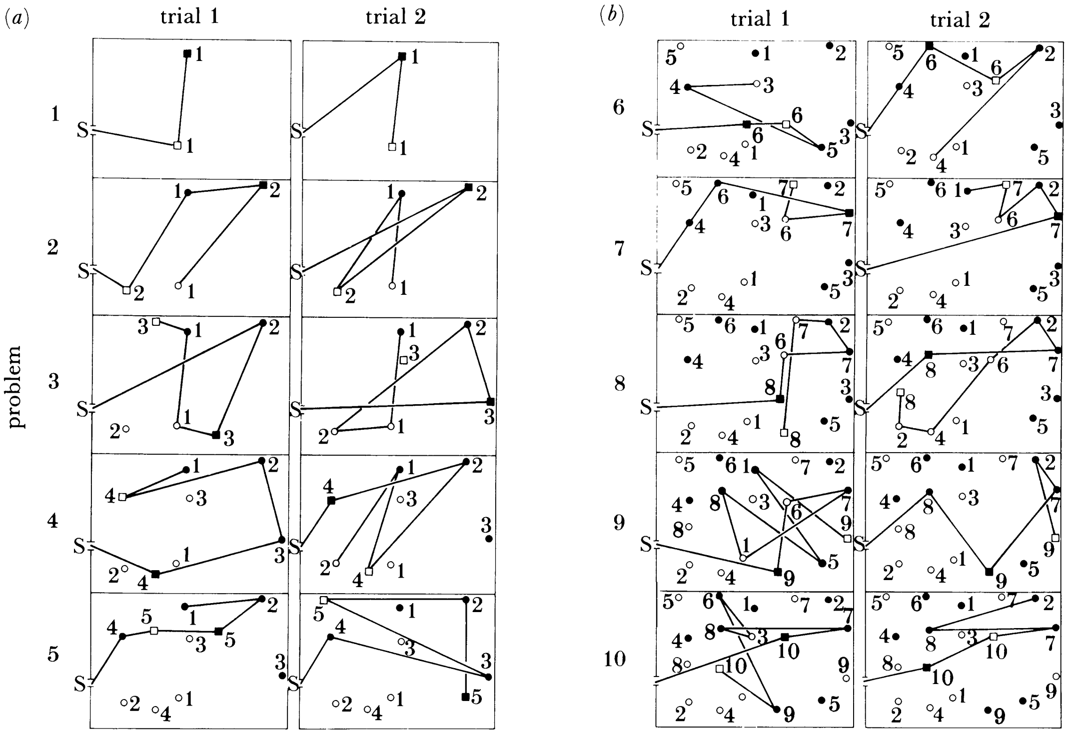

FIGURE 1. Maps of each trial in the first ten problems of test 1, excluding trial 3 of problem 7. The travel line shows the sequence in which the first five or more objects were first approached by any member of the group. Squares represent the newest objects; filled symbols the 'positive' objects; open symbols the 'negative' objects; and numbers the ordinal number of the problem on which each object was first introduced. Object locations varied from floor to ceiling, and the trees and tree limbs by which the monkeys traversed the room are not shown, so the actual relative travel-distances between objects are not very accurately portrayed. The locations of the two newest objects are incorrectly shown on trial 2 of problem 4; they should be the same as on trial 1 of that problem. The positive object was, however, approached first, as shown.

2 was one from which they had once obtained food; in 14 of these cases this object was one of the two newest positive objects. The most novel positive object was approached sooner than its equally novel, negative mate on trial 2 in 9 of the first 10 problems and in 13 of 16 problems overall; if each individual were to be scored separately on this same measure, their scores would average 75% 'correct' (range 70–80) in the first 10 problems, which is on a par with what other marmosets have achieved at the asymptote of their performance on Harlow's learning set task (Miles & Meyer 1956; Pournelle & Rumbaugh 1966). Four of the five individuals also spent more 15 s time intervals at any and all previously 'positive' objects than they spent at any and all negative objects, on every single trial (in the first 10 problems) on which none of the objects actually contained food. Still further, if one treats the various individuals as 'yoked controls' for one another and examines the correlation, within any given positive object, between the order in which each animal ate on trial 1 and the order in which it approached the same object on trial 2, the median Spearman ρ is 0.68 ($p < 0.001$). (In 12 of 16 problems whichever individual had been first to eat on trial 1 was among the first two animals to approach the positive object on trial 2, and in 13 of 16 problems this object was the first object in the room that this individual approached.) No comparable reliability in the social approach order was observed within the negative objects (median $\rho = 0.30$); and of all possible 240 correlations between trial 1 of any given positive object and trial 2 of the other positive objects the median

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TABLE 1. THE BASIC DESIGN OF TEST 1, TOGETHER WITH DATA ON THE TOTAL NUMBER OF 15 S TIME INTERVALS SPENT, BY ALL FIVE GROUP MEMBERS, AT EACH OBJECT ON THOSE TRIALS IN WHICH NO OBJECTS CONTAINED FOOD

		pairs of objects																															
test		1		2		3		4		5		6		7		8		9		10		11		12		13		14		15		16	
day	prob.	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
2	1	6	5																														
4	2	4	2	67	7																												
6	3M	4	0	15	2	28	0																										
8	4	3	1	20	3	2	0	13	8																								
10	5M	5	6	4	2	4	0	16	1	25	10																						
12	6M	8	0	9	9	1	3	17	2	1	3	39	12																				
15	7	3	1	9	6	4	0	2	9	6	1	18	12	45	3																		
17	8M	0	0	3	7	1	0	4	12	23	2	0	1	8	2	26	8																
19	9	0	1	4	2	×	0	0	6	3	1	0	8	6	0	9	0	15	18														
21	10S	0	0	2	5		0	1	5	2	0	0	×	17	0	13	0	12	6	25	15												
24	11S	9*	0	1	8		0	2	9*	2	2	0		9	0	5	3	3	0	5	11	29	34										
26	12M	5	10*	11*	9		0	7	6	2	1	3		3	0	3	3	7	2	3	5	8	7	25	12								
28	13	7	3	1	3*		0	6*	0	9	0	0		6	0	4	12	2	0	6	5	8	6	6	4	42	17						
30	14M	7	0	0	0		7*	2	6	8	1	9*		3	0	7	0	4	1	2	6	8	10	4	0	16	0	34	7				
32	15	3	0	1	2		1	0	3	1	3	0		14*	0	1	0	8*	0	9	4	1	10	1	1	9	1	8	0	45	27		
34	16	1	3	2	1		2	0	2	6	0	0		7	5*	0	0	4	0*	6	4	2	4	3	1	9	0	3	11	12	8	15	6

M, new object moved ×, object removed S, new object swap location *, old object moved

Scores along the diagonal are the trial 3 data for problems 7 and 11, in which the 'positive' (A) object contained food on trial 2 as well as trial 1; otherwise, they are trial 2 data. The 'negative' (B) objects in problems 6–16 contained food odours on trial 1.

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ρ is 0.25 and only 15% were as high as 0.68. Thus, individuals as well as the group as a whole showed clear evidence of one-trial learning, and the group data are not attributable to any fixed 'leadership hierarchy'.

In addition to discriminating between the 'positive' and 'negative' objects the animals also remembered the places in which they had found food. Thus, for example, the median ρ between the trial 1 order in which the animals ate and the trial 2 order in which they approached the location the positive object had occupied on trial 1 was 0.80 ($p < 0.001$), and this despite the fact that in some cases no test object was currently in that locus, and their approaches were sometimes made relatively late in a trial. In almost all problems, some food had spilled from the object on trial 1 as animals manipulated the object (twice, all of it spilled onto the ground, a metre or more beneath the object). The same individual that had retrieved it from any given spot stared at that same spot on trial 2, often making 'food calls' in the process and then looking at the spot the container had occupied on trial 1.

We found no evidence that very close spatial contiguity between food and cue object was essential for one-trial learning (cf. Jarvik 1956). It is clear, too, that the marmosets did not follow *either* a 'win–stay, lose–shift' strategy with respect to objects *or* the same sort of strategy with respect to locations; they followed *both* but simply attached a slightly lower priority to the latter. A major source of difficulty for them in more traditional tests, where two objects directly and repeatedly swap the same two locations is, we would think, not that they are 'naive' or 'poor learners' but that they learn too much, and therefore are confused by the strange 'rules of the game'. How could their feral counterparts manage to get back to a specific object in their native home range, which might exceed 30 ha in size, if they did not have a 'locational' strategy as well as an 'object' strategy? Indeed, we believe that the most accurate description of their achievements is that, with or without obvious reinforcement for so doing, they learn and remember the layout and structure of their environment: their 'rules of responding' being instantiations of that knowledge rather than substitutions for, or explanations of, it. Stated otherwise, learning to approach or avoid particular objects and locations is probably a special case of cognitive mapping rather than vice versa (Menzel 1978; Nadel & Willner 1980; Tolman 1948).

4. Test 2: learning with already-familiar objects

Here we sought to determine whether the results of the preceding tests were dependent upon the use of novel objects, or whether one-trial learning and 24 h memory could also be demonstrated with 'old' objects. The animals were given no cue on trial 1 (other than odour and other uncontrolled cues); the crucial question was what they would do on trial 2.

Method

On 16 occasions over the course of 20 trials, one object was selected from the 30 test objects that were left in the room from test 1 and baited with food on two successive trials. This object was selected at random, with the restriction that it not have contained food during the previous five trials. Odd-numbered objects ('problems') received their second baiting ('trial 2') at the same time that even-numbered ones were baited for the first time ('trial 1'). Throughout the first eight such problems, the locations of all objects remained constant. In the remaining eight problems, the location of the baited object was swapped with that of some other object on

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'trial 2', this other object being selected by the same criteria as above. Between the eighth and ninth problems we gave the animals two runs in which no objects contained food or were moved. If the animals did not find the food within 15 min on trial 1 of any given problem we entered the test cage, tapped on the baited object as soon as one or more monkeys looked out of the home cage or otherwise attended to us, and then withdrew and sat down again at our observation stool about 1 m from the cage. (Usually they approached the object we had tapped without going to more than one other object first.)

Results and discussion

On 15 of the 16 critical test trials the marmosets approached whichever object contained food for the second time sooner than they approached the one that contained food for the first time; the latter objects were approached no sooner than chance. In 6 of the 8 problems on which the baited object was moved on trial 2, the same object was approached sooner than the other object which now occupied its old location; both exceptions resulted from the animals' apparent failure to detect the baited object for a time, for as soon as they spotted it they raced for it. The mean rank of the baited objects in the approach sequence on trial 2 was 5.7 (median = 2.5; 'chance' = 15.5; $p < 0.001$); only the two mentioned just above were approached later than expected by chance, and only one as late as it had been on trial 1. The objects that occupied their old (trial 1) locations were also approached sooner than expected by chance (mean rank = 6.3, median = 6; $p < 0.01$ difference from 15.5 and from their trial 1 score). Either the animals remembered the location in which they had found food, or they responded to the change in objects *per se* (see the next test), or both.

Almost all failures to go first to the objects that were baited for the second time involved prior response to the objects that had been baited on the immediately preceding problems; and within almost every trial there was a statistically significant correlation between the relative recency and frequency with which any given object had contained food and the order in which it was approached. Obviously, it is not necessary that an object be novel to demonstrate one-trial learning in *S. fuscicollis*; and although these animals have highly developed olfactory systems (Epple 1975), odour cues in the present study were not effective at long range.

5. TEST 3: DETECTION OF CHANGES IN OBJECTS AND THEIR LOCATIONS

Here we tested further how well the animals remembered both the visual appearances and the locations of test objects from one day to the next, as evidenced by their ability to detect change.

Method

A total of 15 trials were given, one per day. On five trials, two of the 30 test objects in the room were selected at random and their locations were directly swapped with one another; a coin toss decided which object was to contain food. On the remaining 10 trials one randomly picked object was removed from the room (for a single trial: it was repositioned in its old place the next time), and where it had been we placed a 'new' object that was visually identical to some third object that was already in the room. Either this 'new' object or its old visual counterpart contained food, five trials being given, in haphazard order, with each of these two possibilities. In this test and the preceding one all of the 30 objects were used at least once as a critical test object; thus, assuming that the animals could detect all of the above changes,

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it would be difficult to explain this fact without also assuming that they remembered all of the objects and all of their locations. (Note also that before test 2 only half of the objects had ever had food available in them, and only two had had food available in them more than once.)

Results and discussion

On the five trials in which the locations of two of the objects were directly swapped, the mean rank of the 10 objects in question, in the approach sequence, was 4.4 ($p < 0.001$). On the 10 trials in which the old object had been removed from the room and replaced by one that matched a third object somewhere else in the room, the mean rank for the former, 'new' object was 3.4 ($p < 0.001$) and on all 10 trials this object was hit before its 'old' counterpart.

The old counterpart objects were approached somewhat sooner than they had been on the previous trial (mean ranks = 15.1 and 19.8, respectively; $p = 0.05$) but no sooner than the average object (mean rank = 15.5). However, with more than half of them it was our strong impression that the monkeys had detected the similarity between them and the corresponding 'new' objects. For example, one animal seemed to eye the old object from a distance (too great to qualify as an unequivocal approach), went elsewhere for a while, repeated this sequence one or more times, and then not only it but several others went for the object en masse, making 'food calls' even before reaching it, and even though it did not in fact contain any food. It was as if they initially had only a vague premonition and thus hesitated in acting on it unless someone else also seemed to be looking at the same object.

6. TEST 4: GENERALIZED DELAYED MATCHING-TO-SAMPLE AND NON-POSITIONAL DELAYED RESPONSE

In our next experiment, we tested these anecdotal impressions with a different procedure. Our primary purpose was, however, as follows. Given the animals' acute ability to detect whenever an object in a given locus was not the same object that was there on the preceding trial, any procedure that is aimed at experimentally disentangling 'object' discrimination from 'locational' discrimination by moving objects about from one trial to the next might create as many problems and confounds as it solves. We wished, therefore, to see whether we could demonstrate object discrimination without moving any of the test objects.

Method

Ten of the 30 test objects were discarded. Each day for 57 days a single trial was given; on each trial one of the 20 remaining test objects was selected at random (with the provision that it had not contained food for at least five trials), and baited. Before the test trial began, a different but visually almost identical ('sample') object was presented to the marmosets in their home cage. For the first 40 trials it contained five small pieces of candy and it was placed in the animal's cage and left there until they had found and eaten the candy. Following this it was removed and (about 1 min later) the door to the test room was opened. For the remaining trials we simply held the 'sample' object in front of the cage and let the monkeys watch as we dropped 10 pieces of candy into it. They could not touch the object and were not given any food. Then we stepped out of their home room and commenced the test run in the usual fashion. The sample objects were hidden from the animals' sight in all cases.

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Results and discussion

The monkeys' relative latencies to approach the critical test object after having been given these cues ('day 0') are shown in figure 2, along with the corresponding scores for the same object on the immediately preceding and following trials. (Some of the last tests are omitted because we did not have complete information on trials following the single reinforced trial.) The mean rank approach score for day 0 was significantly lower than that of the average object and of the preceding trial even in the first 20 tests ($p < 0.05$ in all cases), and very clearly so for all 40 tests with the first (matching to sample) procedure ($p < 0.001$) and for the tests with the second (non-positional delayed response) procedure ($p < 0.001$). Overall, the critical test object was approached sooner on day 0 than on the preceding day on 85% of the tests.

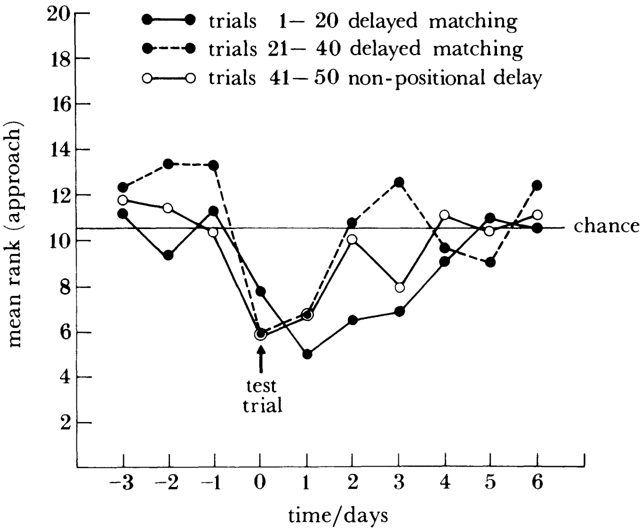

FIGURE 2. Relative latencies to approach the test objects in test 4, before, on and after the day they had encountered a 'sample' object in their home cage. (In this test there were 20 objects in the room; the first to be approached by any animal received a rank of 1, and so forth.)

The data strongly suggest that the major 'improvement' that occurred with practice was attributable largely to the monkeys' decreasing tendency to go first to the objects that had been baited on the immediately preceding trials. In other words, memories of the previous day's run in the test room were initially a more important determinant of performance than memories of what had occurred a few minutes earlier in the home cage, and to reveal to an outside observer what we now presume they actually knew about the objects, they had to 'learn to forget'. The lack of any decrement in performance when we switched from the first procedure to the second shows, further, that food reinforcement during the cue-giving phase of the trial was not essential. In this experiment there was, coincidentally, little systematic relationship between the order in which the various individuals had obtained food from an object in their home cage and the order in which they approached the matching object in the test room (median $\rho = 0.25$).

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7. Conclusions

Marmoset intelligence, as we see it, is whatever marmosets do, especially if it gives them an advantage over their competitors. The data strongly suggest that any other species might be hard put to do appreciably 'better' than *S. fuscicollis* on the same tasks, in the same test situation, with nothing more by way of prior instructions or training. It is worth noting further that in all of our experiments (including others in which we tested several social groups that contained infants) it has typically been the youngest animals that are most successful in getting the food. The rankings of marmosets relative to other species and of younger animals relative to older ones which one might obtain in more orthodox laboratory tasks might, of course, be very different; but it is our guess that such rankings might rest as much as anything on testing the animals alone in an isolated cubicle, with conditions that are strongly 'loaded' against any animal that is stressed or distracted by such isolation or that is not customarily a solitary forager.

Speaking more generally: although 'the ability to quickly solve new problems' or 'to apprehend the relationships between novel presented facts and organize one's actions accordingly' constitute the major ingredients of most definitions of intelligence, most 'standardized' tests of this hypothetical process, if not this definition as such, amount largely to roundabout definitions of *human* intelligence. Before animals are confronted with any given test situation, every species if not every individual has faced a different set of problems and developed a different set of strategies for solving them. These strategies might well all be optimal. Furthermore, depending largely upon how one's test situation and test criteria are loaded for or against it, almost any animal might in principle be made to rank either at the top or at the bottom of one's unidimensional quantitative scale of so-called correct responses. Such a point of view is directly complementary to the view that differences in intelligence are matters of degree rather than of kind: as, for example, is implied by Darwin's doctrine of 'mental continuity' and Harlow's analogous position that within any given species or age groups, types of learning that appear qualitatively distinct actually only represent different stages in the same, single, continuous quantitative function. It is, however, no less Darwinian a view; and in our opinion it provides a better 'explanation' of the present data. We do not, of course, imply that there are many investigators left today who would attempt to rank order species as to their relative 'general intelligence', let alone base such a ranking on any single index.

What is it about the behavioural organization of *S. fuscicollis* that makes the present sorts of tasks so simple for them? First of all, they are (even for primates) highly alert, visually curious and reactive to almost any sort of novelty or change. Secondly, they habituate to most objects quite rapidly, and show little or no spontaneous recovery of responsiveness on subsequent encounters with the same (unchanged) objects (Menzel & Menzel 1979, 1980). This is not a common propensity in Old World primates, at least in captivity; the 'advantage' that *S. fuscicollis* have here is that they are less manipulative. Thirdly, one class of objects towards which they do not thus habituate are those that proved to be edible, or to contain edibles, on last encounter (Menzel & Juno 1982). And, finally, being first in their group to locate food very likely provides additional (social) reinforcement, for foraging seems to be a team effort, involving a considerable amount of reciprocal altruism. All this, however, is an account of performance rather than of knowledge or perception. If the animals did not also know the nature and relative positions of the objects in question, these behavioural propensities would not do them much good. It is, of course, an open question how well they would do on problems that

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call for something other than a 'win–stay, lose–shift' strategy; and it is quite conceivable here that their skills are much more specialized, and less flexible, than those of (say) rhesus monkeys or chimpanzees.

It should not be forgotten, either, that assessments of an animal's intelligence rest not merely on the structure and apparent adaptiveness of any given performance, and how well it might fit some logical definition, but also on what we know (or assume) about how that performance originated. Regardless of what an insect can do (see, for example, Menzel & Erber 1978; Gould & Gould 1982), most people would hedge at calling it a cognitive genius, and the same is true of circus animals and robots. Partly for this reason, one of us (C.J.) is currently investigating the ontogenesis of one-trial learning in infant marmosets, within a 'normal' group context. It is a safe bet that some learning is involved; our guess is that much of it is social learning, particularly that which serves to wean infants from relying directly on their elders for food.

To most of humanity some animals quite simply look smarter and seem to act smarter than others. The fact that the smart-looking ones happen to be our own fairly close kin is no accident, and it makes us cautious about our own biases and prejudices. This, however, is only to say that judgments regarding intelligence might best be viewed as folk taxonomy rather than scientific taxonomy, and that no taxonomist should trust any external 'field marker' implicitly, let alone treat it as a sufficient definition of his or her genotypic concepts. Species do not have any platonic 'essence'; and neither does intelligence. At the same time, folk taxonomy is probably not completely mistaken, and some 'field markers' are indeed fairly trustworthy. In some cases they furnish as good an initial source of research ideas as any. Thus, for example, the first time we ever laid eyes on *S. fuscicollis* they impressed us as highly intelligent, largely because they seemed so alert, visually curious, and reactive towards us as strangers or indeed towards almost any novel event in their inferred visual and auditory field. All of the tests we devised amount, in retrospect, to little more than introducing some additional minor novelty or change into their environment, to test whether these first impressions were true or false, or in what senses they were true or false. Other researchers might have learned just as much about marmosets by some other strategy; but we doubt that we would have; and to say that *questions* about animal intelligence are 'outdated' or 'scientifically useless' would be short-sighted.

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Discussion

P. Garrud (*University of St Andrews, U.K.*). I should like to ask about something puzzling in the results from the one-trial object discrimination task. Why do the marmosets return sooner to the previously baited member of any particular pair than to the unbaited object, not only on the trial immediately following the baited trial but also on nearly all the ensuing trials? This seems surprising when:

(i) the animals ate all the food on the first trial in any case;

(ii) the animals have revisited that object at least once (on the next trial) and found it empty;

(iii) they are presented with a series of problems, all of which have this general form: that the new object baited on any trial is never baited thereafter.

E. W. Menzel. This might be a redescription of the results that you note rather than an explanation, but I'd say that even without special training on our part *Saguinus fuscicollis* have very strong 'win–stay' strategies and excellent memories. The results might be surprising or puzzling in the light of what other animals do in other situations, but they are quite consistent with Terborgh's field data on the foraging habits of wild *S. fuscicollis* and with what our own laboratory animals do every day in their home cages and in our other test conditions. They become less puzzling, too, if one thinks of some other well-known analogies. For example, rats and hummingbirds tend to 'win–shift' or 'alternate' with respect to locations at the outset of many experiments, and to persist at this to some degree and for some time despite an

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experimenter's not rewarding them for it with food. Their specific response strategy is different, but in other respects there are many commonalities.

Actually, too, the effects of a single reinforced trial were not as long-lasting as you suggest: after several unreinforced trials with the same objects these effects were no longer statistically significant; and with repeated tests of the same sort they diminished. (See here figure 2 for a graphic representation of these points, from our fourth experiment.) Although it initially goes against their grain, marmosets can also learn to 'win–shift', just as rats and hummingbirds can learn to 'win–stay'. Thus, for example, in one of our later experiments our animals learned to go sooner on trial 2 to objects that had had a piece of inedible paper in them on trial 1 (and that were baited with food on trial 2) than to objects that had contained food on trial 1 (but contained nothing on trial 2).

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