

INHIBITION TRAINING IN WOLVES AND DOGS

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ABSTRACT

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A theoretical model previously proposed by the first author hypothesizes that dogs (*C. familiaris*) should perform better than wolves (*C. lupus*) on training tasks in which (1) cues are arbitrarily selected by the experimenter, (2) reinforcement is administered by the experimenter, and (3) the to-be-learned behavior has no perceptible, functional connection with the reinforcement. To test this hypothesis, four Eastern wolf pups (*C. l. lycaon*) and four Alaskan Malamute pups (*C. familiaris*) were administered a passive inhibition task at seven weeks of age and an active inhibition test (leash training) at 11 weeks of age. Significant differences in the predicted direction were obtained for all task variables.

INTRODUCTION

A theoretical model proposed by the first author (Frank, 1980) argues that natural selection has favored evolution in the timber wolf (*Canis lupus*) of two concurrent systems of information processing. The more recently acquired system is characterized as "cognitive" and is believed to have evolved in response to pressures that accompanied the rise of group hunting and that are relaxed under conditions of domestication. Accordingly, the model argues that wolves should perform complex problem-solving tasks better than domestic dogs (*Canis familiaris*). This hypothesis is supported by subsequent empirical comparisons of wolf and dog performance on a variety of tasks designed to tap such capacities as insight into means-ends relationships, serial organization of behavior, cognitive mapping, internal representation (imagery), and foresight (Frank, 1983, Frank and Frank, 1982a).

A repertoire of relatively closed behavioral programs comprises the more primitive "instinctual" system described by the model. Whether the behaviors governed

by this subsystem are genetically preprogrammed or are locked in during the course of postnatal development by "innate teaching mechanisms" (Lorenz, 1969. cf. Hailman, 1969, Gould, 1975), they (1) exhibit little plasticity and (2) are elicited by very specific stimulus configurations. In contrast, the model points out that virtually all domesticated species, including the dog, are selected (incidentally or otherwise) for tractability, that is, (1) behavioral plasticity, which is reflected in high behavioral variability, and (2) responsiveness to a broad range of stimuli. The paper therefore recommends that these hypothetical differences be tested by comparing wolf and dog performance on the sorts of *training* tasks employed by Scott and Fuller (1965). These are distinguished from *problem-solving*, or insight learning, tasks (which we used to tap complex cognitive functioning) on the basis of three criteria: (1) Cues are arbitrarily selected by the experimenter; (2) reinforcement is administered by the experimenter; (3) the to-be-learned behavior has no perceptible, functional connection with the reinforcement. These criteria *minimize* the likelihood that cues will either release *functional* behaviors that might be fortuitously appropriate to the task or that cues will afford the animal "*insight*" as to the correct response. Conversely, they *maximize* demand on the animal's *capacity for cue utilization* and, if the task requires either synthesis or modification of behavior, *behavioral plasticity*. We do not, of course, assume all training tasks to be equally loaded on both components of tractability. It is reasonable to suppose, for example, that performance on sensory discrimination tasks depends more on cue utilization than behavioral plasticity and that inhibition tasks, such as those discussed in the present paper, place relatively more emphasis on behavioral plasticity.

The Inhibition Test described by Scott, Shepard and Werboff (1967) and the Leash Training Test devised by Scott and Fuller (1965, pp. 207-211) satisfy our three criteria, and it is therefore hypothesized that domestic dogs should perform better than wolves on both tasks.

EXPERIMENT 1: INHIBITION TEST

METHODS

Subjects

Wolves. In May of 1980, four Eastern wolf pups (*C. l. lyones*), one male and one female from each of two litters, were acquired at 11 days (± 24 h) of age from the Carlos Avery Game Park, Forest Lake, Minnesota, and fostered on an eight-year-old female wolf approximately 67 days after ovulation. Details of their acquisition, first six weeks of maintenance, socialization, feeding, and disposition are reported elsewhere (Frank and Frank, 1982a).

Dogs. In most systematic comparisons of wolf and dog behavior, the domestic breeds chosen for study have been selected largely on the basis of availability

(e.g., Zimen, 1972, Bakarich, 1979). This practice, however, introduces the risk of confounding species characteristics with breed characteristics. In the course of its domestication, the dog has been subjected to a variety of selection pressures that now differentiate it from the wolf. These include selection for increased fecundity (Fox, 1971), reduced wildness, and reduced tooth size (Scott and Fuller, 1965). In addition, Scott and Fuller (1965) point out that individual dog breeds have been variously selected for extremes of size, distinctive morphological features and deformities, and a host of specialized behavioral, cognitive and sensory attributes. These breed-specific traits account in large measure for the differences reported by Scott and Fuller in their comparison of training and problem-solving performance in cocker spaniels, basenjis, beagles, Shetland sheepdogs, and wirehaired fox terriers (1965, pp. 205-258) and might likewise be expected to produce differences between wolf and dog performance that would obscure the effects of domestication per se. We therefore sought a breed of dog that has been relatively free of selection for specialized traits likely to influence performance on the tasks included in our research program³, and the Alaskan Malamute seemed admirably suited to our needs. First, it is among the so-called "lupine" breeds, that is, dogs that have retained their wolf-like size and general morphology (Mech, 1970). Second, historical and contemporary authorities on the breed indicate that there is little evidence of selection for behavioral, cognitive, or sensory attributes (See Riddle and Seeley, 1976). Third, the Malamute is numbered among the northern forest breeds that evolved in the same boreal environment as the timber wolf. Moreover, although it might be argued that one or two other breeds satisfy these conditions equally well, the Alaskan Malamute is the only such breed that, like the Eastern timber wolf, is indigenous to North America. Finally, Frank (1980) speculates that the underlying mechanism by which domestication has produced changes in the dog's information processing system is neoteny. In this connection Coppinger and Coppinger (1982) have recently proposed a taxonomy by which dog breeds are classified according to degree of neoteny and suggest that the "heelers" and the northern forest breeds comprise the least neotenus group, that is, dogs whose morphology and behavior most resemble the "adult," or wild, form. This system is based largely on the Coppingers' interpretation of various domestic dog behaviors as modified forms of wild-type predation behaviors and insofar as it postulates relationships between behavior and morphology, contradicts findings reported by Scott and Fuller (1965, pp. 339-347). However, if

³Another way to eliminate systematic breed variability would have been to test representatives of several breeds. However, the number of animals required for a project of this kind would have made it impossible to rear them under the same foster-litter conditions as the wolf pups. Furthermore, such data already exist for most of the tests in our program, much of which has been generously made available to us for comparative purposes by J. Paul Scott, John L. Fuller, and their associates.

the taxonomy holds up across other domains of behavior, it will provide further support for our choice of breed.

In May of 1981, we fostered four 10-day-old (\pm 48 h) Alaskan Malamute pups, one male and one female from each of two litters, on the same female wolf who had reared our wolf pups the year before. The pups were introduced to the foster mother approximately 77 days after ovulation and were housed in the same facility, permitted contact with the same members of the animal colony, fed the same diet, administered the same experimental tests, and, in general, subjected to the same regimen as the wolf pups, with three exceptions: The Malamutes weaned themselves more abruptly than the wolves and therefore made an earlier transition to solid food. Second, the domestic pups did not require the same rigorous socialization program as the wolf pups and therefore did not spend as much time in close daily contact with the experimenters. Third, they were allowed somewhat more access to the outdoor enclosure.

Apparatus and procedure

Training was conducted in a 9.75 x 9.75 m outdoor arena constructed of unfinished plywood. South and east walls of the arena were 1.22 m high to admit maximum sunlight. North and west walls were 2.44 m high with a .60 x .60 m window in the west wall approximately 3.7 m south of the northwest corner. All pups had undergone two days of habituation and three days of testing in the arena the preceding week (Frank and Frank, 1982a) and were assumed to be thoroughly familiar with the experimental setting.

The plywood platform (100 x 100 x 10 cm) on which subjects were placed was set against the north wall of the arena near the northwest corner. The 10-cm elevation and the short grass surrounding the platform were intended to provide both kinesthetic and tactile cues when subjects stepped off the plywood. The den-box in which both groups of animals were reared was similarly elevated, and since all subjects therefore had ample experience negotiating a 10-cm artificial cliff, we discounted the possibility that performance might be confounded by systematic differences in fear of unfamiliar heights.

Each pup was fitted with a choke chain tied to an 8-m length of 1/8 in. nylon rope. The rope ran through an eyebolt mounted in the north wall 45 cm above the center of the platform to a pulley, 1.8 m above the platform, and then through a series of eyebolts to the observation window where Experimenter 2 was stationed. Thus, apparatus was essentially identical in design and dimension to that used by Scott, Shepard and Werboff (1967, p. 240, Fig. 1B).

Procedure

Testing was conducted Monday through Friday for two successive weeks beginning on the Monday nearest the pups' 7-week birthday. Before each day's testing pups were confined to their home barn. Each pup was carried from the barn to the arena,

placed in the middle of the platform, and the choke chain slipped over his head. Experimenter 1 then withdrew through a door in the north wall, at which time both experimenters started their stopwatches.

If a pup left the platform before Experimenter 1 withdrew, he was replaced on the platform and the choke chain given a sharp tug. If a pup placed two feet off the platform after the trial began, Experimenter 2 corrected him by pulling on the rope. The trial ended when the pup either achieved the time criterion prescribed for that trial or received five corrections. The number of corrections administered on each trial and the longest time (in minutes) spent on the platform without (or prior to) correction on each trial (intratrial "best performances") were recorded for each pup. Pups were returned to the home barn after testing.

The number of *♂*s and the number of testing days precluded strict daily rotation of testing, so the order in which the wolf pups were tested was quasi-random, subject only to the requirement that no pup be tested either first or last on two consecutive days. The Malamute pups were matched with wolves by age, litter and sex and assigned the same order of testing as their lupine counterparts.

Daily training regimen. The details of each day's training precisely followed the procedures reported in the earlier study:

a. *Day 1.* Each [*♂*] received a preliminary trial which consisted of being held in position on the board by the rope and collar for a five-second period.

b. *Day 2.* Each [*♂*] received a preliminary trial as described and two training trials. Each training trial was run until [*♂*] stayed on the board for 15 consecutive seconds or received five corrections. A trial was scored as "perfect" if *♂* attained the time criterion of 15 consecutive seconds and required no more than one correction.

c. *Day 3.* Each [*♂*] received a preliminary trial and five training trials. On the first training trial, the time criterion was 15 seconds. If this trial was not a perfect trial (two or more corrections), the time criterion for Trial 2 was 15 seconds again. If Trial 1 was a perfect trial, then five additional seconds were added to the 15 seconds, thus making the criterion 20 seconds on Trial 2. With each successive perfect trial, an additional five seconds were added to the previous time criterion. The following exceptions were noted. If *♂* met the time criterion but not the correction criterion for a perfect trial, he proceeded to the next trial at the same time criterion level as before. If this was a perfect trial, he proceeded as previously described. If this was not a perfect trial, then the time criterion was reduced to the next lower time criterion. If *♂* failed the criterion set, on the subsequent trial the time criterion was reduced to the next lowest time criterion. On Trial 5, the time criterion was always the same as the highest level previously passed. If *♂* succeeded in passing all trials, examples of the successive time criteria would be 15, 20, 25, 30, and 30 seconds for the five trials on Day 3.

d. *Day 4.* This day's test schedule was the same as Day 3 with a preliminary trial and five training trials. On the fourth through the 10th day of testing, if *♂* met the highest time criterion he could have met on the previous day, five seconds were added to the previous standard time raise. The time criterion on Trial 1 was 15 seconds, and if *♂* proceeded with a perfect trial and had met the highest time criterion

he could have met, 10 additional seconds were added to the base level of 15. The same considerations as stated above were still in operation. Thus, the successive time criteria could have been 15, 25, 35, 45, and 45 seconds, respectively, for the five trials.

Day 7. This day was the same as Day 4 except that 15 seconds were now added to each successive perfect time score if the animal had met the highest possible time criterion (45 seconds) on Day 4. Thus, the possible time criteria employed could have been 15, 30, 45, 60 and 60 seconds, respectively.

Days 8 through 10. These days were run the same as previously described except that either 20, 25, 30, 35, or 40 seconds could be added to the time criterion of each day for perfect performance if the animal met each day's highest possible time criterion. On Day 10 of the series, [W] performing at the maximum level received extra trials with the time criterion imposed of 1.5, 2, 3, 4, 5, etc., times their previous longest time criterion. This was restricted to a maximum limit of 10 minutes or five extra trials (Scott, Shepard, and Werboff, 1967, pp. 241-242).

RESULTS

Each pup's intratrial best-performance times were totalled over all 42 training trials and these best-performance totals averaged across 3: in each group. Although the bonus time increments awarded for 3: who met the previous day's highest time criterion were administered as described above, bonus times are not included in the analysis summarized below in Table I. This had no effect on the wolves' scores, since no wolf ever met his highest time criterion, but it placed an arbitrary daily ceiling of 120 sec on the Malamute pups for days 3 through 10 and thus

TABLE I

t-test for inhibition test performance in wolves and Malamutes

		Total Intratrial Best- Performance Times (in Min.)	Total Corrections
Wolves	\bar{X}	4.13	185.5
	S^2	5.3	283
Malamutes	\bar{X}	12.33	82.5
	S^2	16.39	4,003
	$\bar{X}_M - \bar{X}_W$	3.50**	-3.15*
	$d.f.$	6	4

*. $p < .025$

** $p < .01$

tended to reduce the difference between the two groups. Nevertheless, the Malamutes accumulated significantly longer intratrial best-performance times than the wolves.

The total number of corrections administered to each pup over all 42 training trials was averaged across the trials in each sample and the means submitted to a t -test, which is also summarized in Table I. Because the wolf and Malamute variances were significantly different ($F_{3,3} = 14.4, p < .05$) we elected to compute degrees of freedom as if sample sizes were unequal (Frank, 1974, p. 298). Unless $s_1^2 = s_2^2$ this calculation will ordinarily yield a value less than $N_1 + N_2 - 2$ and thus a more conservative test. Even so, the wolves received significantly more corrections than the Malamutes.

Since results obtained by Scott et al. (1967) are reported in graphic form, no statistical comparison with our results is possible. However, for purposes of descriptive comparison we have reproduced in Figures 1a and 1b the averages reported for the two variables in the original study, along with the averages for our own study.

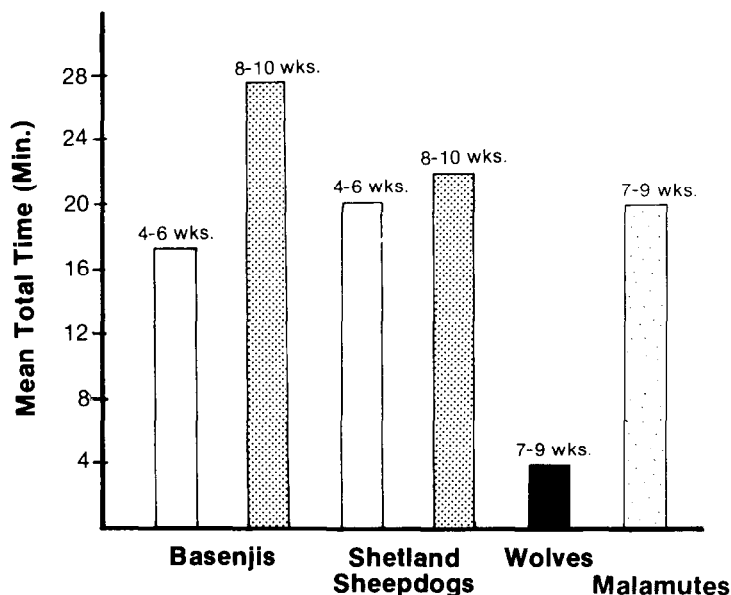


Fig. 1a. Mean best-performance totals over 42 training trials.

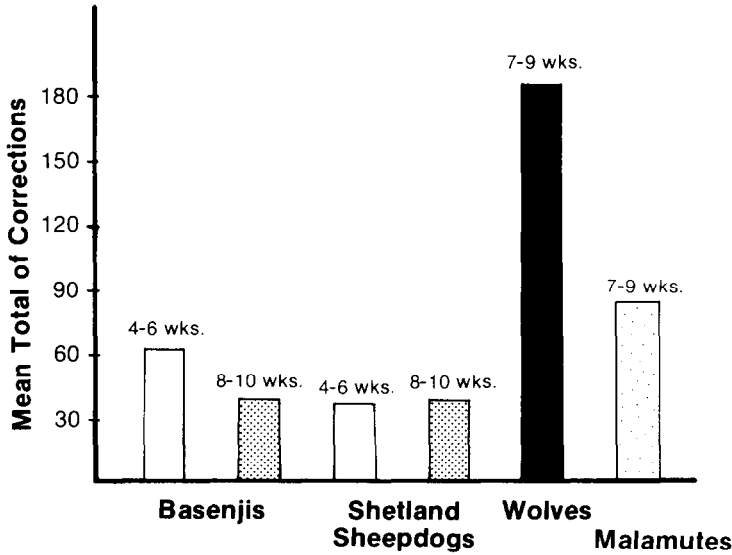


Fig. 1b. Mean total corrections over 42 training trials.

EXPERIMENT 2: LEASH TRAINING

The most salient feature of Leash Training (Scott et al., 1950) is that it must not only extinguish such unacceptable responses as yelping, jumping and tugging, but must substitute other behaviors, viz., walking at the trainer's side with no tension on the leash. It is therefore a test of active-inhibition learning.

METHODS

The procedure, scoring, and physical features of the training course (Fig. 2) conformed as nearly as possible to those prescribed by Scott et al. (1950).

Subjects

Subjects in this study were the same pups used in the experiment reported above. The experiment began when they were 11 weeks old, by which time they were receiving only two daily feedings, which were conducted in the experimenters' house to facilitate accurate daily recording of food intake and body weight and administration of medication and vitamin supplements. This also put us in close contact with every animal at least 2-4 h each day, thereby maintaining some semblance of socialization in the wolf pups.

Besides the inhibition training reported above and the barrier test reported earlier (Frank and Frank, 1982a) all of the pups had, prior to this study, participated in the manipulation and goal-orientation tests reported by Scott and Fuller (1965).

As in the study reported above, order of testing was quasi-random, subject only to the requirement that no pup be tested either first or last on two consecutive days.

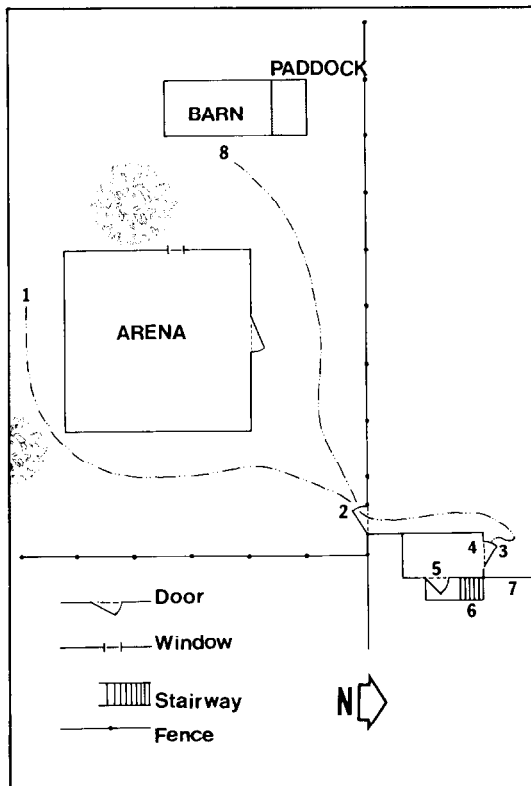


Fig. 2. Leash-training course.

Equipment

Equipment for this test included a choke chain, leash, clipboard, food reward (canned sardines), and two food dishes.

Training

Training to walk on leash was conducted Monday through Friday for two successive weeks beginning on the Monday nearest the pups' 11-week birthday.

Equipment. Before testing all pups were confined to the home barn. Each pup was carried from the barn to a point just east of the southwest corner of the arena (point 1 in Fig. 2), where the choke chain and leash were put on. The pup was then led around the south and west sides of the arena to the gate of the enclosure (point 2) from which he was carried into the experimenters' kitchen (point 7) where the pups ordinarily received their daily feedings. The pup was then fed a tablespoon of fish, carried back into the enclosure (to point 2) and led back to the home barn (point 8), where he was given an additional serving of fish and then returned to the barn. Demerits (see Appendix, below) were not awarded on the return trip.

Procedure. Beginning on Day 3 # was led through the gate (at point 2), two doors (points 3 and 5), and up a short flight of stairs (point 6) into the kitchen (point 7), where food reward was administered while # recorded the pup's score. The pup was then led back to point 8, where (on Days 3-5) he was administered a second serving of fish before being returned to the barn.

Demerits

Each pup was awarded one demerit for each of the following faults:

Balks in open. A balk was scored when # actually had to be dragged over the ground. A maximum of three balks was allowed. If a pup balked more than three times, he was carried to the first door (point 2), placed on the ground and allowed an opportunity to complete the remainder of the course (three doors and one stairway). Additional balks in the open were not scored.

Balks at doors. If a pup balked at any of the doors or the gate, he was carried to the next door and allowed an opportunity to proceed. Thus, # could receive a total of three demerits in this category.

Resistance to leash. Accepts leash (0), fights or bites leash--occasionally (1), about half the time (2), constantly (3).

Position. Slack leash (0), pulls at leash (1), "sunfishes," i.e., sometimes runs off to the side, sometimes pulls ahead, sometimes drags behind (2), drags (3).

Interference with trainer. Stays away from feet (0), crosses in front and occasionally stops so that trainer must sidestep to avoid stepping on pup (1), crosses in front and jumps on trainer at times (2), runs between feet and/or jumps on trainer constantly (3).

Excitement. Quiet (0), whines--occasionally (1), constantly (2), yelps or howls (3).

Each pup's daily score was the total number of demerits received in all categories.

RESULTS

Mean daily demerits for wolves and Malamutes appear below in Table II. Since wolves do not vocalize, scores for Malamutes are given both with and without demerits for vocalization. The six daily means reported by Scott and Fuller (1965, p. 208) for a 19-20-week-old sample of 34 basenjis, 33 beagles, 41 cocker spaniels, 24 Shetland sheepdogs, and 21 wirehaired terriers are also included in Table II, and their similarity to corresponding entries for our sample of Malamutes suggests that both our task and scoring procedures were comparable to theirs.

TABLE II

Mean leash-training demerits for wolves and dogs

Day	1	2	4	5	9	10
Dogs ^a (N=153) ^b	8.7	6.2	4.6	3.6	2.2	1.9
Malamutes (N=4) (Excluding Vocalizations)	9.0 (6.0)	7.0 (4.0)	4.3 (2.3)	4.0 (2.3)	2.0 (1.3)	1.3 (1.0)
Wolves (N=4)	7.3	7.5	9.3	7.8	6.0	6.5

^aFrom Scott, J.P. and Fuller, J.L., 1965. Genetics and the social behavior of the Dog. University of Chicago Press, Chicago, p. 208.

^b34 basenjis, 33 beagles, 41 cocker spaniels, 24 Shetland sheepdogs, 21 wirehaired fox terriers

TABLE III

t-test for differences between mean leash-training demerits^a for wolves and dogs

	Day ₁	Day ₁₀	Improvement: Day ₁ - Day ₁₀ (% as own controls)
$\bar{X}_W - \bar{X}_M$	1.25	5.50	- 4.25
s^2 diff.	0.75	1.26	1.31
t	1.67	4.37**	- 3.23*
n	6	6	6

^aExcluding demerits for vocalization

* $p < .01$

** $p < .005$

Three measures of wolf and Malamute leash training performance were considered. The first analysis compares the average number of demerits for wolves and Malamutes ($\bar{X}_W - \bar{X}_M$) on Day 1. The second compares average demerits for the two species on Day 10, and the third compares the two groups' average improvement, the difference between Days 1 and 10 $(\bar{X}_1 - \bar{X}_{10})_W - (\bar{X}_1 - \bar{X}_{10})_M$. These three differences were each submitted to a *t*-test for samples of unequal size (Frank, 1974, p. 295). The difference on Day 1 was not significant, but as predicted, the Malamutes received fewer demerits on Day 10 and showed greater improvement over the 10 days of training than the wolves. The statistical tests are summarized in Table III.

DISCUSSION

Results of the experiments described above confirm our hypothesis that dogs should perform better than wolves on tasks in which (1) cues are arbitrarily selected by the experimenter, (2) reinforcement is administered by the experimenter and (3) the to-be-learned behavior has no perceptible, functional connection with the reinforcement. Our findings therefore support the theoretical argument that domestic dogs have been selected for tractability, that is, cue-receptivity and behavioral plasticity. Although the cues in our experiments were complex, situational stimulus configurations (the apparatus, setting, etc.) rather than simple, highly salient signals, such as one might employ in a sensory discrimination study, the two tasks demanded, respectively, passive and active modifications of the initial responses and so clearly favored the more behaviorally plastic congener. These theoretical implications should, however, be regarded as provisional for several reasons.

A major deficiency of our study was that both measures involved forced learning rather than reward learning. More specifically, both experiments employed mechanical restraint administered by a choke chain. It is uncertain whether the dog was first domesticated in the capacity of scavenger, beast of burden, hunting or herding partner, or companion, but whatever the role of the modern dog's immediate forbear, we might suppose that one of the most fundamental prerequisites to his continued association with humankind was tolerance for external restraint of various behaviors, including aggression and locomotion (cf. Scott and Fuller, 1965). Indeed, we believe that this was one of the major pressures favoring selection for tractability. Furthermore, it is likely that these inhibitory demands were both expressed and enforced by much the same assortment of pushes, pulls and manipulations one finds used today by traditional pastoralists, dog owners, and parents of preverbal children. Thus, if we view our results as evidence of *dog's leash performance*, the data concur with the theoretical model. If, however, we view our results as evidence of *wolf's leash performance*, other interpretations become equally plausible. It might be argued, for example, that tolerance for restraint

in wild animals is detrimental to reproductive fitness. The wild animal who placidly tolerates the sorts of restraint most commonly encountered in a natural setting (a trap, seizure by a predator, entrapment in a rockslide, etc.) is unlikely to leave offspring after his first such experience. Given this circumstance it is even possible that wolves have evolved an innate escape response to such restraint.

Although this interpretation accounts for our results with no recourse to hypothetical differences in the general behavioral plasticity of wolves and dogs, it is flawed in two respects: First, when wolves are neck-pinned by dominant wolves or humans (in the case of socialized wolves) the usual response is to freeze. Nor is this response limited to immediate "hands-on" restraint; L. David Mech (personal communication, 1971) has observed the same response in wild-trapped wolves neck-pinned with a forked stick. Second, the Malamutes were no less resistant to the choke chain than the wolves in the early trials of both studies (Recall, for example, that there was no significant difference between leash-training demerits awarded to the wolves and Malamutes on Day 1.). Their superior overall performance was attributable to precisely the sort of behavioral accommodation that would seem to bespeak greater behavioral plasticity. Nevertheless, there is substantial evidence of species-specific constraints on learning (e.g., Hinde and Stevenson-Hinde, 1973; Seligman and Hager, 1972), which suggests that these experiments, especially the Inhibition Test, should be conducted using a variety of reinforcers, both positive and negative. Support for this caveat surfaced during informal behavior-shaping exercises that we introduced to keep the wolves habituated to handling during a hiatus in the testing schedule. All shaping was conducted in the home barn, and single nuggets of kibble were used as reinforcement. Since we were also using this opportunity to explore the range of behaviors that might be subject to shaping, different tasks were assigned to different wolves. One was the Inhibition Test, for which we deliberately selected the animal who had performed most poorly when originally tested. During the Inhibition Test she had received 205 corrections (of 210 possible), logged zero seconds on more than half of her 42 training trials, and had remained on the platform only 12 seconds on her best single intratrial performance. On her first day of food-reinforced inhibition she remained on the platform for 2 minutes and by the third day exceeded 10 minutes.

Finally, we should point out that our results can be explained wholly in terms of interspecific differences in social behavior, with no reference at all to cognitive functioning. Scott (1980) points out that dogs exhibit an almost unique capacity to form attachments to humans that are as strong as most conspecific bonds, and we have likewise reported elsewhere (Frank and Frank, 1982b) that our Malamutes exhibited an early and persistent preference for human social partners,

while our wolf pups manifested an equally unequivocal preference for interaction with canids. Insofar as dogs' social orientation may be accompanied by a relatively greater sensitivity to human behavioral cues and insofar as training is a form of social communication (cf. Pryor, 1981), our procedure would necessarily tend to favor dogs. In this connection, Zimen (1981) suggests that the wolf's orientation toward humans may be mediated by two independent, single-locus genetic characters: high vs. low interest in humans and high vs. low fear of humans. The most socializable specimens (presumably the foundation stock of domestic dogs) are of the high interest/low fear genotype. The subspecies of wolf used in our study occupies a range more nearly on the fringes of human habitation than any other extant North American subspecies and has therefore been exposed to more intense human predation. This would tend to select against both high interest and low fear, and, indeed, none of our four wolves exhibited this phenotype. It is possible that a larger sample (or a sample including broader representation of wolf subspecies) would have included specimens whose social orientation toward humans facilitated performance on our training tasks.

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