

end of the spermatheca. If so, the displaced sperm would remain a threat to the current male. Cyclical copulation may function to repeatedly displace previously stored sperm to the distal end of the spermatheca, thus neutralizing the recurrent threat. The actual mechanism of sperm precedence has been discovered for only one species of insect (14). Whether this problem can be resolved for *A. herberti* (15) remains to be determined.

In *Scatophaga stercoraria* (L), the yellow dungfly, the last male to mate was responsible for 80 percent of the offspring subsequently produced until another mating occurred. Parker (16) determined that males of *S. stercoraria* could probably displace fully all previous sperm by increasing the duration of copulation with each female, but for some reason, dungfly males do not do this. Parker developed a model which revealed that the amount of displacement in *S. stercoraria* should stabilize at the optimum, yielding the maximum overall fertilization rate for males, but not the maximum possible egg gain to a male from a given mating (8, 16).

Abedus herberti males, in contrast, invest in matings and appear to have virtual certainty of paternity. This turns Parker's question around. Why should the water bug paternity assurance system be so nearly perfect? Male water bugs lack the opportunity to optimize their overall fertilization rate because egg-covered males are rejected as mates by females (6). Because of this limitation on the absolute number of eggs a male water bug is allowed to fertilize, individual males have apparently been under intense selection to maximize egg gain from each mating. Even the smallest fault in paternity assurance by male brooders would provide an opportunity for cheaters (males that mate repeatedly, but decline to brood eggs); and the frequency of cheaters would probably quickly increase to equilibrium, with the level of opportunity provided by careless brooders.

This reasoning suggests that the first brooder in a population of predominantly nonbrooders must have been adapted for a high level of paternity assurance. Members of the subfamily Lethocerinae (17) (nonbrooding giant water bugs) are believed to have a common ancestry with the Belostomatinae. Modern *Lethocerus* males repeatedly mate an individual female and may guard her between bouts of copulation (18). Multiple mating and guarding of an appropriated female by male insects apparently is an adaptation to prevent sperm

displacement from subsequent matings by another male (8, 19). It is not difficult to envision a pattern of alternating bouts of copulation and oviposition evolving from the lethocerine system, and under suitable ecological conditions (such as absence of, or limited, emergent vegetation, intense predation, and egg parasitism), it might have been advantageous for females to begin depositing their eggs on their mates' backs, and for males to begin brooding them.

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proximal end; the ejaculatory opening at the distal end was plugged with silicon rubber.

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12. The remaining infertile eggs failed to hatch and were removed by the vasectomized male 42 days after pairing. The female that produced the eggs had been allowed to copulate only once with a normal striped male 30 days before. It seems probable that the single coupling provided insufficient sperm to fertilize all of the female's eggs. *Abedus herberti* males usually copulate three or four times before receiving the first of a female's eggs.
13. In replicate five, the second male (No. 17) died before the eggs on its back hatched. Twenty-one of 99 eggs hatched, and only six nymphs were of the wild-type phenotype. This anomaly suggests that the wild type (+ +) male (No. 17) experienced sexual dysfunction (perhaps related to senescence) at the time of the male's pairing with the previously mated + + female. This event was significant in that it further dramatized male risk, and demonstrated the utility of previously stored sperm as a female backup system.
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20. I thank G. A. Parker, R. L. Trivers, and J. Alcock for reviewing early versions of this paper. Supported by NSF grant DEB 76-24332. Arizona Agricultural Experiment Station MS 2924.

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Dr. Guthrie and *Felis domesticus* Or: Tripping over the Cat

Abstract. *The principal reactions described in Guthrie and Horton's classic learning monograph appear to have been caused by the mere presence of the experimenters. Neither escape nor food reinforcement is necessary for the establishment of such responses. They are species-typical "greeting" reactions, readily elicited by the sight of human observers.*

For almost half a century, most research in instrumental (operant) conditioning has been conducted without regard for the natural behavior of the animals used as subjects (1, 2). A recurrent consequence of this tradition has been the failure to recognize species-typical reactions that are critical in certain learning situations. The pigeon's "operant" key-pecking response, for example, was not identified as a simple grain-pecking reaction, and a generation of investigators therefore believed that they had taught tens of thousands of pigeons, individually, how to peck. The implications of this error have been only partially explored (3).

Failure to recognize the common avian peck was not an isolated aberration (4). We report here the discovery of another such oversight, this time from one of the two classic studies of learning in domestic cats (5, 6).

In the puzzle-box experiments of Guthrie and Horton (5), cats were photo-

graphed and observed as they learned to escape from a small, glass-fronted chamber. A conspicuous escape door in the front of the chamber could be opened by jostling a slender, vertical rod about 1 foot away. The ability of cats to master so simple a task was not in question, but great importance was attached to the manner in which their "learning" was expressed. The animals' responses were described as highly stereotyped, with long series of movements repeated "in remarkable detail" from trial to trial. Several different reactions were recorded, but the commonest was that shown in Fig. 1. The stereotypy of this behavior was interpreted as evidence for a process of learning by stimulus-response contiguity (5, 7), and the tracings shown in Fig. 1 were widely reprinted in support of that conclusion. Elsewhere, the same stereotyped reactions were cited as evidence of "superstitious" operant conditioning (8).

Neither interpretation is warranted.

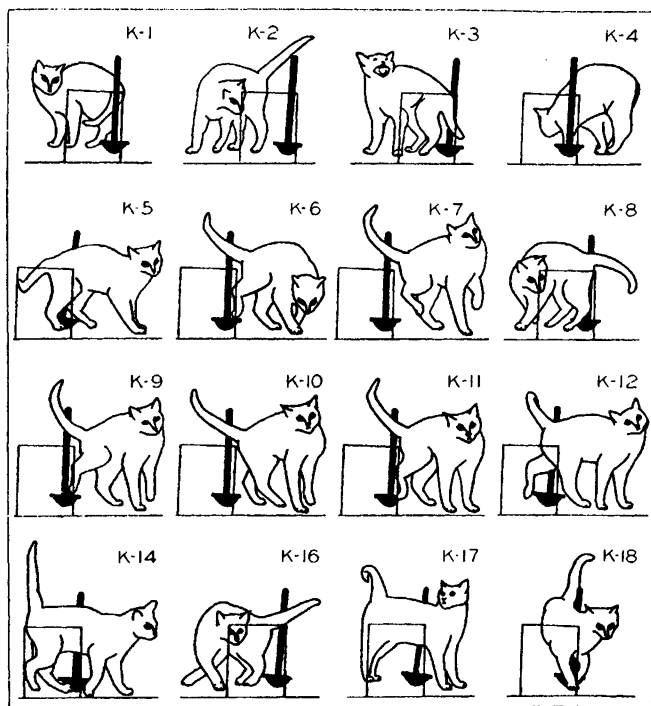


Fig. 1. From Guthrie and Horton (5). The stereotypy of these reactions was taken as evidence, first of contiguity learning (5, 7), and later of "superstitious" operant conditioning (8). [Figure courtesy of Peter Smith]

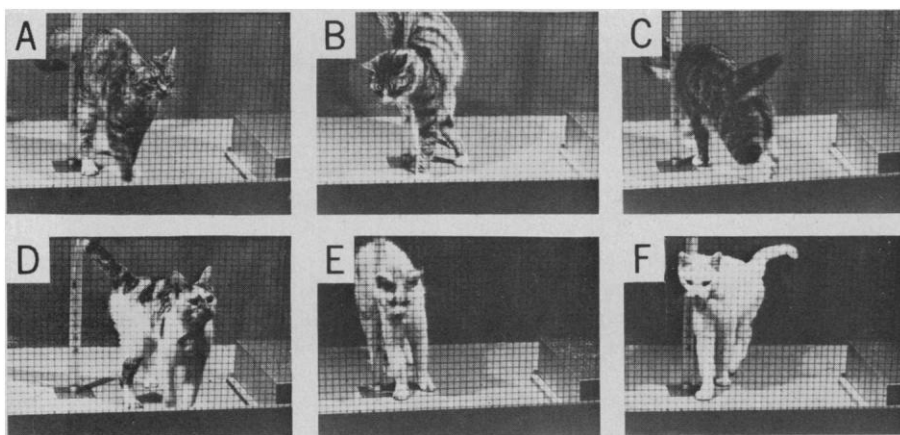


Fig. 2. Species-typical greeting reactions (*kopfchengeben*) elicited by the mere presence of a human observer. Compare with Fig. 1.

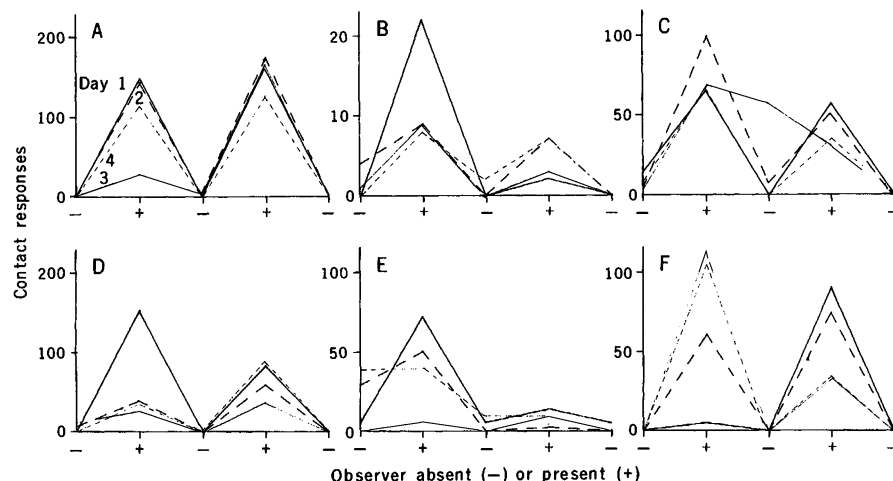


Fig. 3. Frequency of contact with the vertical sensor rod as a function of the presence or absence of a human observer. The peak response rates arise from greeting reactions as illustrated in corresponding panels of Fig. 2. The few responses recorded with the observer absent were due primarily to pawing or tail chasing.

The reaction shown in Fig. 1 did not originate in the puzzle box. It is species-typical in many of the *Felidae*, including lions, tigers, jaguars, ocelots, and domestic cats (9, 10). Known as flank rubbing, head rubbing or *kopfchengeben* (10), it occurs in courtship and in "greeting" rituals (9-11). Typically, the target animal is brushed with head, arched back, and raised tail as the cat moves sinuously past. Alternatively, the behavior may be performed without contact, or redirected to nearby inanimate objects. Redirection is especially likely when the animal to be "greeted" is distant or inaccessible. Past failures to recognize this response (5, 7, 8) are surprising, since domestic cats often treat humans as conspecifics, either rubbing their shins persistently or redirecting the response to nearby doorposts, appliances, or furniture.

We recently observed such redirected rubbing in apparatus similar to that used by Guthrie and Horton (12). The response was first performed spontaneously by two experimental animals. When we watched unobtrusively (13), the reaction did not occur; but when we were visible, the animals rubbed heads, flanks, or tails against the (convenient) vertical rod. To document this, we arranged for an observer to enter and leave the room systematically during each of four experimental sessions. Each daily session lasted for 50 minutes, with an observer present during minutes 10 to 20 and 30 to 40. The effects of human presence are evident in Figs. 2, A and B, and 3, A and B.

Although never rewarded for rubbing, the animals had received food in the experimental chamber. This proved entirely irrelevant. Figures 2C and 3C show the results of retesting the second animal in a well-learned, food-free condition. To avoid uncertainty, we then repeated the study with "naïve" animals, never fed as part of any experiment (14). Each naïve cat was simply placed inside the experimental chamber. When an observer entered the room, the animal approached and rubbed the accessible vertical rod, as shown in Figs. 2, D to F, and 3, D to F (15).

When Guthrie and Horton set out to study the stereotypy of learned behavior, they chose to observe at close range the reactions of individual animals (16) while rewarding them for contact with the vertical sensor rod. In retrospect, their methods were self defeating. (i) They failed to consider the animals' species-typical repertoires. (ii) Both experimenters and as many as eight guests sat

in front of the glass-fronted chamber, unconcealed by any blind (17). (iii) Each trial began with the animal's reintroduction into this setting, making "greetings" especially probable. (iv) The vertical rod, intended as a neutral response sensor, provided an almost ideal target for redirected rubbing. Thus, efficiently if inadvertently, the experimenters arranged to evoke the species-typical reactions which they, and many others, failed to recognize and which were construed as evidence for particular learning mechanisms (18).

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References and Notes

- Historically, this tradition reflects, and was reflected in, the transition from Thorndike's era (2) to that of Skinner [B. F. Skinner, *Behavior of Organisms* (Appleton, New York, 1938)]. For Thorndike, the instrumental response repertoire was fundamentally a subset of the species-typical repertoire. But Skinner's "operant" responses were said to be of arbitrary form and were defined, not by their topographies, but rather, by their consequences. Thus, whereas Thorndike's system required both observation of subjects and knowledge of their natural behavior, Skinner's required neither.
- E. L. Thorndike, *Psychol. Rev.*, **Suppl. 2** (1898).
- It now appears that the operant key-pecking topography arises from Pavlovian conditioning of the grain-pecking reaction and that operant response-shaping techniques are unnecessary [B. R. Moore, in *Constraints on Learning*, R. A. Hinde and J. S. Hinde, Eds. (Academic Press, London, 1973)]. The traditional misinterpretation has also had social implications, in that the impression of technical competence created by the animal research contributed to the spread of operant techniques in psychotherapeutic and related situations.
- See also R. C. Bolles, *Psychol. Rev.* **77**, 32 (1970).
- E. R. Guthrie and G. P. Horton, *Cats in a Puzzle Box* (Rinehart, New York, 1946).
- Thorndike's original monograph (2) also dealt with the reactions of cats in puzzle boxes, but his apparatus and techniques were very different from those of Guthrie and Horton, and his data were not compromised.
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- The term "greeting" is not entirely apt. Although rubbing may indeed be most probable when animals meet, it may also recur from time to time throughout an encounter.
- The front of the 120 by 85 by 85 cm chamber was constructed of hardware cloth; other surfaces were wooden. No escape door was required. The response sensor was a vertical Lucite tube, 2.5 cm in diameter. Suspended from the ceiling of the chamber, it passed through a small, metallic floor plate, and was clad with copper at that point. The cladding and plate formed a normally open, circular switch which could be closed by a force of 0.05 N. Closure operated remote counters and clocks and drove a cine camera (Beaulieu R16B) mounted 2 m from the chamber in a heavy sound-attenuating box.
- Unobtrusive observations were made from a blind by closed-circuit television and by means of switch-operated camera, counters, and clocks.
- The 2.6- to 3.7-kg adult female cats were obtained from the colony of Dalhousie Medical School, where they had been held briefly for inoculations and quarantine. Between experimental sessions the animals were housed in groups of two or three.
- A fourth naïve animal, tested briefly, made 6.5 rubbing responses per visit and none between visits. Two other cats were screened, but simply slept in the apparatus. While all four waking cats conformed to the pattern described, it is not universal. Occurrence of the reaction undoubtedly depends upon the nature and timing of previous interactions with humans.
- Data were presented from only 16 of their 52 cats. A few of these made pawing or biting reactions of possibly Pavlovian origin, or escape reactions resembling those described by Thorndike (2). Apart from rubbing, however, the most common reaction was to strike the rod while rolling upon the floor. "Ecstatic" rolling is closely related to rubbing, but seems to occur at higher levels of excitement.
- According to Guthrie and Horton (5) the experimenters and their visitors sat "in full view of the animal. There were at times as many as ten people observing the performance. Conversation was permitted though visitors were warned not to call out to the animals. In ten cases we attempted to coax an inactive animal into activity. Visitors were present during a total of fifteen experiments" (5, p. 14).
- We have not, of course, set out to demonstrate that learning was everywhere irrelevant to the behavior of Guthrie and Horton's cats (16). We have argued only that their principal data do not constitute evidence of learning by contiguity (5, 7), "superstition" (8), or any other process.
- Supported by the National Research Council of Canada. Our data were reported at the 1977 Northeastern Regional Meeting of the Animal Behavior Society. We thank R. C. Bolles, H. James, E. P. Lovejoy, and N. J. Mackintosh for comments on an early draft of the manuscript.

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Specific Nonopiate Receptors for β -Endorphin

Abstract. Iodinated β -[2-D-alanine]endorphin exhibits specific binding to cultured human lymphocytes. The binding is inhibited by low concentrations of β -endorphin and its D-alanine² derivative, but is not affected by opiate agonists and antagonists, or by enkephalin analogs, β -lipotropin, adrenocorticotrophic hormone, or α -melanocyte-stimulating hormone; this suggests the existence of a specific, non-opiate binding site (receptor) for β -endorphin. The carboxy-terminal region of β -endorphin is essential for this binding activity, since α -endorphin is not active. β -Endorphin may be a circulating hormone with peripheral physiological effects that are not primarily mediated through interactions with opiate or enkephalin receptors.

β -Endorphin, which corresponds to the sequence of residues 61 to 91 of β -lipotropin, exhibits a wide range of pharmacological activities in addition to its central analgesic effects (1). The typical morphinomimetic effects and some other behavioral effects are blocked by specific opiate antagonists such as naloxone

and naltrexone. Among these behavioral effects are excessive grooming behavior (2), catatonic states and wet shakes (3), and profound sedation and catalepsy (4). Some other behavioral effects of β -endorphin, such as the delay in extinction of pole-jumping avoidance (5), are not blocked by opiate antagonists and thus would appear to be mediated by actions independent of opiate receptor sites in the brain.

β -Endorphin-like material is present in the serum of rats and its level is increased by acute stress (6). Significant levels of β -endorphin are not detectable in normal human serum, although it is present in the plasma of patients with certain endocrine disorders (7). In genetically obese mice the pituitary and plasma contents are two to three times greater than in control animals (8). The possible nature of the relation between β -endorphin and stress remains highly speculative. Variations in the secretion of β -endorphin by the pituitary or in its circulating plasma levels are not correlated with changes in the cerebral concentration of the peptide (9). The stress-induced release of β -endorphin from the pituitary may thus have a physiological role totally distinct from the theoretically possible central analgesic effects of the peptide. Moreover, perfusion of β -endorphin into the pancreas reduces the release of somatostatin and increases the

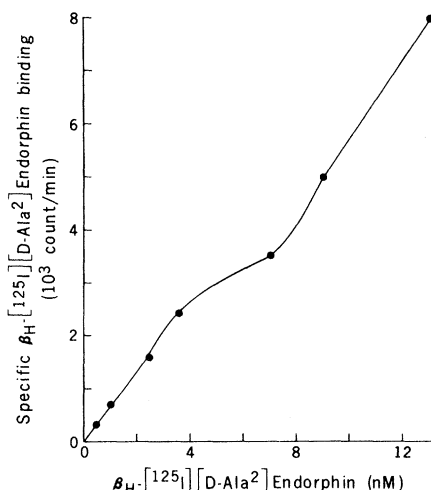


Fig. 1. Saturation binding curve for β -[¹²⁵I][D-Ala²]endorphin to cultured lymphocytes (10^7 cells per milliliter). The curve exhibits a biphasic function in which binding to low-affinity site is linear up to 150 nM (data not shown). Binding was assayed as described for Table 1. Values are the means of three incubations. Very similar data showing such biphasic curves have been obtained in several experiments.