

Behavioral Genetics and Animal Science

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Genetics and the Behavior of Domestic Animals

(Chapter One)

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A bright orange sun is setting on a prehistoric horizon. A lone hunter is on his way home from a bad day at hunting. As he crosses the last ridge before home, a quick movement in the rocks off to his right catches his attention. Investigating, he discovers some wolf pups hiding in a shallow den. He exclaims, "Wow ... cool! The predator... in infant form."

After a quick scan of the area for adult wolves, he cautiously approaches. The pups are all clearly frightened and huddle close together as he kneels in front of the den . . . all except one. The darkest colored pup shows no fear of the man's approach. "Come here you little predator! Let me take a look at you," he says. After a mutual bout of petting by the man and licking by the wolf, the man suddenly has an idea. "If I take you home with me tonight, maybe mom and the kids will forgive me for not catching dinner . . . again."

INTRODUCTION

The opening paragraphs depict a hypothetical scenario of man first taming the wolf. Although we have tried to make light of this event, the fact is that no one knows exactly how or why this first encounter took place. The earliest archeological estimate indicates that it occurred in the late Glacial period, approximately 14,000 years BC (Boessneck, 1985). Another scenario is that wolves domesticated themselves. The presumption is that calm wolves with low levels of fear were likely to scavenge near human settlements. Both Coppinger and Smith (1983) and Zeuner (1963) suggest that wild species which later became domesticants started out as camp followers. Some wolves were believed to have scavenged near human settlements or followed hunting parties; wild cattle supposedly invaded grain fields, and wild cats may have invaded grainaries while hunting for mice. However, the most recent evidence obtained by sequencing mitochondrial DNA of 67 dog breeds and wolves from 27 localities indicates that dogs may have diverged from wolves over 100,000 years ago (Vita *et al.*, 1997).

In any event, wolves kept for companions had to be easy to handle and socialize to humans. Within a few generations, early humans may have turned wolves into dogs by selecting and breeding the tamest ones. Thousands of years ago, humans were not aware that behavior in animals was heritable. However, even today people who raise dogs, horses, pigs, cattle, or chickens notice differences in the behavior of the offspring. Some animals are friendly and readily approach people, while others may be shy and nervous.

GENETIC EFFECTS OF DOMESTICATION

Price (1984) defined domestication as a process by which a population of animals becomes adapted to man and the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events recurring during each generation.' In long-term selection experiments designed to study the consequences of selection for the "tame" domesticated type of behavior, Belyaev (1979) and Belyaev *et al.* (1981) studied foxes reared for their fur. The red fox (*Vulpes fulva*) has been raised on seminatural fur farms for over 100 years and was selected for fur traits and not behavioral traits. However, they demonstrate three distinctly different characteristic responses to man. Thirty percent were extremely aggressive toward man, 60% were either fearful or fearfully aggressive, and 10% displayed a quiet exploratory reaction without either fear or aggression. The objective of this experiment was to breed animals similar in behavior to the domestic dog. By selecting and breeding the tamest individuals, 20 years later the experiment succeeded in turning wild foxes into tame, border collie-like fox-dogs. The highly selected "tame" population of (fox-dog) foxes actively sought human contact and would whine and wag their tails when people approached (Belyaev 1979). This behavior was in sharp contrast to wild foxes which showed extremely aggressive and fearful behavior toward man. Keeler *et al.* (1970) described this behavior:

Vulpes fulva (the wild fox) is a bundle of jangled nerves. We had observed that when first brought into captivity as an adult, the red fox displays a number of symptoms that are in many ways similar to those observed in psychosis. They resemble a wide variety of phobias, especially fear of open spaces, movement, white objects, sounds, eyes or lenses, large objects, and man, and they exhibit panic, anxiety, fear, apprehension and a deep trust of the environment~ They are 1) catalepsy-like frozen positions, accompanied by blank stares; 2) fear of sitting down; 3) withdrawal; 4) runaway flight reactions; and 5) aggressiveness.

Sometimes the strain of captivity makes them deeply disturbed and confused, or may produce a depression-like state. Extreme excitement and restlessness may also be observed in some individuals in response to many changes in the physical environment. Most adult red foxes soon after capture break off their canine teeth on the mesh of our expanded metal cage in their attempts to escape. A newly captured fox is known to have torn at the wooden door of his cage in a frenzy until he dropped dead from exhaustion.

Although the stress of domestication is great, Belyaev (1979) and Belyaev *et al.* (1981) concluded that selection for tameness was effective in spite of the many undesirable characteristics associated with tameness. For example, the tame foxes shed during the wrong season and developed black and white patterned fur, and changes were found in their hormone profiles. This means that the monoestrus (once a year) cycle of reproduction was disturbed and

the animals would breed at any time of the year. Furthermore, changes in behavior occurred simultaneously with changes in tail position and ear shape, and the appearance of a white muzzle, forehead blaze, and white shoulder hair. The white color pattern on the head is similar to many domestic animals (Belyaev 1979) (Figs. 1.1 and 1.2). The most dog-like foxes had white spots and patterns on their heads, drooping ears, and curled tails and looked more like dogs than the foxes that avoided people. The behavioral and morphological (appearance) changes were also correlated with corresponding changes in the levels of gender hormones. The tame foxes had higher levels of the neurotransmitter serotonin (Popova *et al.*, 1975). Serotonin is known to inhibit some kinds of aggression (Belyaev, 1979), and serotonin levels are increased in the brains of people who take Prozac (fluoxetine).

The study of behavioral genetics can help explain why selection for calm temperament was linked to physical and neurochemical changes in Belyaev's foxes. Behavior geneticists and animal scientists are interested in understanding effects on behavior due to genetic influences or those which are due to environment and learning.

A BRIEF HISTORICAL REVIEW OF ANIMAL BEHAVIOR STUDY

This historical review is not intended to be comprehensive; our objective is to discuss some of the early discoveries that are important for our current understanding of animal behavior, with particular emphasis on genetic influence on behavior in domestic animals.

Early in the 17th century, Descartes came to the conclusion "that the bodies of animals and men act wholly like machines and move in accordance with purely mechanical laws" (in Huxley 1874). After Descartes, others undertook the task of explaining behavior as reactions to purely physical, chemical, or mechanical events. For the next three centuries scientific thought on behavior oscillated between a mechanistic view that animals are "automatons" moving through life without consciousness or self-awareness and an opposing view that animals had thoughts and feelings similar to those of humans.

In "On the Origin of the Species" (1859), Darwin's ideas about evolution began to raise serious doubts about the mechanistic view of animal behavior. He noticed that animals share many physical characteristics and was one of the first to discuss variation within a species, both in their behavior and in their physical appearance. Darwin believed that artificial selection and natural selection were intimately associated (Darwin, 1868) and cleverly outlined the theory of evolution without any knowledge of genetics. In "The Descent of Man" (1871) Darwin concluded that temperament traits in domestic animals are inherited. He also believed, as did many other scientists of his time, that animals have subjective sensations and could think. Darwin wrote: "The differences in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind."

Other scientists realized the implications of Darwin's theory on animal behavior and conducted experiments investigating instinct. Herrick (1908) observed the behavior of wild birds in order to determine, first, how their instincts are modified by their ability to learn, and second, the degree of intelligence they attain. On the issue of thinking in animals, Schroeder (1914) concluded:

~The solution, if it ever comes, can scarcely fail to illuminate, if not the animal mind, at least that of man." It is evident that by the end of the 19th century, scientists who studied animal behavior in natural environments learned that the mechanical approach could not explain all behavior.

Behaviorism

During the middle of the 20th century, scientific thought again reverted to the mechanical approach and behaviorism reigned throughout America. The behaviorists ignored both genetic effects on behavior and the ability of animals to engage in flexible problem solving. The founder of behaviorism, J. B. Watson (1930), stated that differences in the environment can explain all differences in behavior." He did not believe that genetics had any effect on behavior. In *The Behavior of Organisms*] the psychologist B. F Skinner (1958) wrote that all behavior could be explained by the principles of stimulus-response and operant conditioning.

The first author visited with Dr. Skinner at Harvard University in 1968. Skinner responded to a question from her about the need for brain research by saying, '~We don't need to know about the brain because we have operant conditioning" (T. Grandin, personal communication, 1968). Operant conditioning uses food rewards and punishments to train animals and shape their behavior. In a simple Skinner box experiment, a rat can be trained to push a lever to obtain food when a green light turns on, or to push a lever very quickly to avoid a shock when a red light appears. The signal light is the '~conditioned stimulus." Rats and other animals can be trained to perform a complex sequence of behaviors by chaining together a series of simple operant responses. Skinner believed that even the most complex behaviors can be explained as a series of conditioned responses.

However, a rat's behavior is very limited in a Skinner box. It's a world with very little variation, and the rat has little opportunity to use its natural behaviors. It simply learns to push a lever to obtain food or prevent a shock. Skinnerian principles explain why a rat behaves a certain way in the sterile confines of a 30 x 30-cm Plexiglas box, but they don't reveal much about the behavior of a rat in the local dump. Outside of the laboratory, a rat's behavior is more complex.

Instincts versus Learning

Skinner's influence on scientific thinking slowed a bit in 1961 following the publication of ~The Misbehavior of Organisms" by Brelands and Brelands. This paper described how Skinnerian behavioral principles collided with instincts. The Brelands were trained Skinnerian behaviorists who attempted to apply the strict principles of operant conditioning to animals trained at fairs and carnivals. Ten years before this classic paper, the Brelands (1951) wrote, we are wholly affirmative and optimistic that principles derived from the laboratory can be applied to the extensive control of animal behavior under non laboratory condition] However, by 1961, after training more than 6000 animals as diverse as reindeer, cockatoos, raccoons, porpoises, and whales for exhibition in zoos, natural history museums, department store displays, fair and trade convention exhibits, and television, the Brelands wrote a second article featured in the *American Psychologist* (1961), which stated, our backgrounds in behaviorism had not prepared us for the shock of some of our failures."

One of the failures occurred when the Brelands tried to teach chickens to stand quietly on a platform for 10 to 12 seconds before they received a food reward. The chickens would stand quietly on a platform in the beginning of training; however, once they learned to associate the platform with a food reward, half (50%) started scratching the platform, and another 25% developed other behaviors, such as pecking the platform. The Brelands salvaged this disaster by developing a wholly unplanned exhibit involving a chicken that turned on a juke box and danced. They first trained the chickens to pull a rubber loop which turned on some music. When the music started, the chickens would jump on the platform and start scratching and pecking until the food reward was delivered. This exhibit made use of the chicken's instinctive food-getting behavior. The first author remembers as a teenager seeing a similar exhibit, at the Arizona State Fair, of a piano-playing chicken in a little red barn. The hen would peck the keys of a toy piano when a quarter was put in the slot and would stop when the food came down the chute. This exhibit also worked because it was similar to a Skinner box in the laboratory.

The Brelands experienced another classic failure when they tried to teach raccoons to put coins in a piggy bank. Because raccoons are adept at manipulating objects with their hands, this task was initially easy. As training progressed, however, the raccoons began to rub the coins before depositing them in the bank. This behavior was similar to the washing behavior raccoons do as instinctive food-getting behavior. The raccoons at first had difficulty letting go of the coin and would hold and rub it. However, when the Brelands introduced a second coin, the raccoons became almost impossible to train. Rubbing the coins together 'in a most miserly fashion]' the raccoons got worse and worse as time went on. The Brelands concluded that the innate behaviors were suppressed during the early stages of training and sometimes long into the training, but as training progressed, instinctive food-getting behaviors gradually replaced the conditioned behavior. The animals were unable to override their instincts and thus a conflict between conditioned and instinctive behaviors occurred.

Ethology

While Skinner and his fellow Americans were refining the principles of operant conditioning on thousands of rats and mice, ethology was being developed in Europe. Ethology is the study of animal behavior in natural environments and the primary concern of the ethologists is instinctive or innate behavior (Eibl-Eibesfeldt and Kramer, 1958). Essentially, ethologists believe that the secrets to behavior are found in the animals genes and in the way the genes have been modified during evolution to deal with particular environments. The ethological trend originated with Whitman (1898), who regarded instincts as congenital reactions which are so constant and characteristic for each species that, like morphological structures, they may be of taxonomic significance. A similar opinion was held by Heinroth (1918). He trained newly hatched fledglings in isolation from adult birds of their own species and found that instinctive movements such as preening, shaking, and scratching were performed by young birds without observing other birds.

Understanding the mechanisms and programming that result in innate behavioral patterns and the motivations behind why animals behave the way they do is the primary focus of ethologists. Konrad Lorenz (1939, 1965, 1981) and Niko Tinbergen (1948, 1951) cataloged the behavior of many animals in their natural environments. Together they developed the ethogram. An

ethogram is a complete listing of all the behaviors that an animal performs in its natural environment. The ethogram includes both innate and learned behaviors.

An interesting contribution to ethology came from studies on egg-rolling behavior in the greylag goose (Lorenz, 1965, 1981). He observed that when a brooding goose notices an egg outside her nest, an innate instinctive program is triggered to retrieve it. The goose fixates on the egg, rises to extend her neck and bill out over it, then gently rolls it back to the nest. This behavior is performed in a highly mechanical way. If the egg is removed as the goose begins to extend her neck, she still completes the pattern of rolling the nonexistent egg back to the nest. Lorenz (1939) and Tinbergen (1948) termed this a "fixed action pattern." Remarkably, Tinbergen also discovered that brooding geese can be stimulated to perform egg rolling on such items as beer cans and baseballs. The fixed action pattern of rolling the egg back to the nest can be triggered by anything outside the nest that even marginally resembles an egg. Tinbergen realized that geese possess a genetic-releasing mechanism for this fixed action pattern. Lorenz and Tinbergen called the object that triggers the release of a fixed action pattern "sign stimuli." When a mother bird sees the gaping mouth of her young, it triggers the maternal feeding behavior and the mother feeds her young. The gaping mouth is another example of sign stimuli that acts as a switch and turns on the genetically determined program (Herrick, 1908; Tinbergen, 1951).

Ethologists also explained the innate escape response of newly hatched goslings. When goslings are tested with a cardboard silhouette in the shape of a hawk moving overhead, it triggers a characteristic escape response. The goslings will crouch or run. However, when the silhouette is reversed to look like a goose, there is no effect (Tinbergen, 1951). Several members of the research community doubted the existence of such a hard-wired instinct because other scientists failed to repeat these experiments (Hirsh *et al.*, 1955). Recently Canty and Gould (1995) repeated the classic experiments and explained why the other experiments failed. In the first place, goslings only respond to the silhouette when they are under 7 days old. Second, a large silhouette which casts a shadow must be used; third, goslings respond to the perceived predator differently depending on the circumstances. For example, birds tested alone try to run away from the hawk silhouette and birds reared and tested in groups tend to crouch (Canty and Gould, 1995). Nevertheless, fear is likely to be the basis of the response. Ducklings were shown to have higher heart rate variability when they saw the hawk silhouette (Mueller and Parker, 1980). Research by Balaban (1997) indicates that species-specific vocalizations and head movements in chickens and quail are controlled by distinct cell groups in the brain. To prove this, Balaban transplanted neural tube cells from developing quail embryos into chicken embryos. Chickens hatched from the transplanted eggs exhibited species-specific quail songs and bobbing head movements.

Do similar fixed action patterns occur in mammals? Fentress (1973) conducted an experiment on mice which clearly showed that animals have instinctive species-specific behavior patterns which do not require learning. Day-old baby mice were anesthetized and had a portion of their front legs amputated. Enough of the leg remained that the mice could easily walk. The operations were performed before the baby mice had fully coordinated movements so there was no opportunity for learning. When the mice became adults, they still performed the species-specific face-washing behavior; normal mice close their eye just prior to the foreleg

passing over the face, and in the amputees the eye still closed before the nonexistent paw hit it. The amputees performed the face-washing routine as if they still had their paws. Fentress (1973) concluded that the experiment proved the existence of instincts in mammals.

The Science of Behavior Today

Two years after the Brelands article, Jerry Hirsh (1963) at the University of Illinois wrote a paper emphasizing the importance of studying individual differences. He wrote, "Individual differences are no accident. They are generated by properties of organisms as fundamental to behavior science as thermodynamic properties are to physical science." Today, scientists recognize the contributions of both the Skinnerian and the ethologists approach to understanding behavior. Modern neuroscience supports Darwin's view on behavior. Bird and mammal brains are constructed with the same basic design. They all have a brain stem, limbic system, cerebellum, and cerebral cortex. The cerebral cortex is the part of the brain used for thinking and flexible problem solving. The major difference between the brains of people and animals is in the size and complexity of the cortex. Primates have a larger and more complex cortex than a dog or a pig; pigs have a more complex cortex than a rat or a mouse. Furthermore, all animals possess innate species-specific motor patterns which interact with experience and learning in the formation of behavior. Certain behaviors in both wild and domestic animals are governed largely by innate (hard-wired) programs; however, experiencing and learning are the most important factors in other behaviors.

A basic principle to remember is that animals with large, complex brains are less governed by innate behavior patterns. For example, bird behavior is governed more by instinct than that of a dog, whereas an insect would have more hard-wired behavior patterns than that of a bird. This principle was clear to Yerkes (1905) who wrote:

Certain animals are markedly plastic or voluntary in their behavior, others are as markedly fixed or instinctive. In the primates plasticity has reached its highest known stage of development; in the insects fixity has triumphed, instinctive action is predominant. The ant has apparently sacrificed adapt-ability to the development of ability to react quickly, accurately and uniformly in a certain way. Roughly, animals might be separated into two classes: those which are in high degree capable of immediate adaptation to their conditions, and those that are apparently automatic since they depend upon instinct tendencies to action instead of upon rapid adaptation.

INTERACTIONS BETWEEN GENETICS AND EXPERIENCE

Some behavior patterns are similar between different species, and some are found only in a particular species. For example, the neural programs that enable animals to walk are similar in most mammals (Melton, 1991). On the other hand, courtship rituals in birds are very species-specific (Nottebohm, 1977). Some innate behavior patterns are very rigid and experience has little effect on them; other instinctive behaviors can be modified by learning and experience. The flehmann, or lip curl response of a bull when he smells a cow in estrus, and the kneel-down (lordosis) posture of a rat in estrus are examples of behaviors that are rigid. Suckling

of the mother by newborn mammals is another example of a hard-wired behavioral system. Suckling behavior does not vary. Newborn mammals suckle almost anything put in their mouth.

An example of an innate behavior that is affected by learning is burrowing behavior in rats. Boice (1977) found that wild Norway rats and albino laboratory rats both dig elaborate burrows. Learning has some effect on the efficiency of burrowing, but the configuration of the burrows was the same for both the wild and domestic rats. The albino laboratory rats dug excellent burrows the first time they were exposed to an outdoor pen. Nest building in sows is another example of the interaction between instinct and learning. When a sow is having her first litter, she has an uncontrollable urge to build a nest. Nest building is hard-wired and hormonally driven because prostaglandin $F_2\alpha$ injections will induce it in sows (Widowski and Curtis, 1989). However, sows learn from experience how to build a better nest with each successful litter.

Other behaviors are almost entirely learned. Some seagulls learn to drop shellfish on rocks to break them open, while others drop them on the road and let cars break them open (Grandin, 1995). Many animals ranging from apes to birds use tools to obtain food. Griffin (1994) and Dawkins (1993) provide many examples of complex learned behaviors and flexible problem solving in animals.

Innate behaviors used for finding food, such as grazing, scavenging, or hunting, are more dependent on learning than behaviors used to consume food. Mating behavior, nesting, eating, and prey-killing behaviors tend to be governed more by instinct (Gould, 1977). The greater dependence on learning to find food makes animals in the wild more flexible and able to adapt to a variety of environments. Behaviors used to kill or consume food can be the same in any environment. Mayr (1974) called these different behavioral systems "open" or "closed" to the effects of experience. A lion hunting her prey is an example of an open system. The hunting female lion recognizes her prey from a distance and carefully stalks her approach. Herrick (1910) wrote, "the details of the hunt vary every time she hunts; therefore, no combination of simple reflex arcs laid down in the nervous system will be adequate to meet the infinite variations of the requirements for obtaining food."

Complex Interactions

Some of the interactions between genetics and experience have very complex effects on behavior. In birds, the chaffinch learns to sing its species-specific song even when reared in a sound-proof box where it is unable to hear other birds (Nottebohm, 1970, 1979). However, when chaffinches are allowed to hear other birds sing, they develop a more complex song. The basic pattern of canary song emerges even in the absence of conspecific (flock-mate) auditory models (Metfessel, 1935; Poulsen, 1959). Young canaries imitate the song of adult canaries they can hear, and when reared in groups they develop song patterns that they all share (Nottebohm, 1977). Many birds, such as the white crowned sparrow chaffinch, and parrot, can develop local song dialects (Nottebohm *et al.*, 1976). Sparrows are able to learn songs by listening to recordings of songs with either pure tones or harmonic overtones. Birds trained with harmonic overtones learned to sing songs with harmonic overtones, but 1 year later, 85% of their songs reverted back to innate pure tone patterns (Nowicki and Marler, 1988). Further experiments by Mundinger (1995) attempted to determine the relative contribution of genetics

and learning in bird song. Inbred lines of roller and border canaries were used in this study along with a hybrid cross of the two. The rollers were cross fostered to border hens and vice versa to control for effects of maternal behavior. The roller and border males preferred to sing innate song patterns instead of copying their tutors. The hybrids preferred to learn some of both songs. Furthermore, canaries are capable of learning parts of an alien song but have a definite preference for their own songs. Comparing these animals to those in Brelands and Brelands (1961) exhibits, birds can be trained to sing a different song, but genetically determined patterns have a strong tendency to override learning. In reviewing all this literature, it became clear that innate patterns in mammals can be overridden. Unfortunately the animals tend to revert back to innate behavior patterns.

THE PARADOX OF NOVELTY

Novelty is anything new or strange in an animal's environment. Novelty is a paradox because it is both fear-provoking and attractive. Paradoxically it is most fear-provoking and attractive to animals with a nervous, excitable temperament. Skinner (1922) wrote that a flighty animal such as the pronghorn antelope will approach a person lying on the ground waving a red flag. Einarsen (1948) further observed that some wild animals will approach various large, dangerous objects such as a power steam shovel. In more recent studies, Kruuk (1972) also observed attraction and reaction to novelty in Thompson's gazelles in Africa. In small groups, Thompson's gazelles are most watchful for predators (Elgar, 1989). Animals that survive in the wild by flight are more attentive to novelty than more placid animals. Gazelles can also distinguish between a dangerous hunting predator and one that is not hunting. The most dangerous predators attract the highest degrees of attraction in the Thompson's gazelle. They often move close to a cheetah when the cheetah is not hunting. Furthermore, when predators walk through a herd of Thompson's gazelles, the size of the flight zone varies depending on the species of predator.

Reaction to Novelty

Confronted with sudden novelty, highly reactive animals are more likely to have a major fear reaction. Examples of sudden novelty include being placed in a new cage, transport in a strange vehicle, an unexpected loud noise, or being placed in an open field. Using various experimental environments, Hennessy and Levine (1978) found that rats show varying degrees of stress and stress hormone levels proportional to the degree of novelty of the environment they are placed in; a glass jar is totally novel in appearance compared to the lab cage to which the animal was accustomed. Being placed in a glass jar was more stressful for rats than a clean lab cage with no bedding.

Livestock and Poultry Reaction to Novelty

Studies of the reaction to novelty in farm animals have been conducted by Moberg and Wood (1982), Stephens and Toner (1975), and Dantzer and Mormede (1983). When calves are placed in an open field test arena that is very dissimilar from their home pen, they show the highest degrees of stress (Dantzer and Mormede, 1983). Calves raised indoors were more stressed by an outdoor arena and calves raised outdoors were more stressed by an indoor arena. The second author is painfully familiar with similar responses in horses. When horses are taken to

the mountains for the first time, a well-trained riding horse that is accustomed to many different show rings may panic when it sees a butterfly or hears a twig snapping on a mountain trail.

Genetic Factors and the Need for Novelty

In mammals and birds, normal development of the brain and sense organs requires novelty and varied sensory input. Nobel prize winning research of Hubel and Wiesel (1970) showed that the visual system is permanently damaged if kittens do not receive varied visual input during development. When dogs are raised in barren and nonstimulating environments they are also more excitable (Walsh and Cummins, 1975; Melzak and Burns, 1965). Schultz (1965) stated, "when stimulus variation is restricted central regulation of threshold sensitivities will function to lower sensory thresholds." Krushinski (1960) studied the influence of isolated conditions of rearing on the development of passive defense reactions (fearful aggression) in dogs and found that the expression of a well-marked fear reaction depends on the genotype of the animal. Airedales and German shepherds were reared under conditions of freedom (in homes) and in isolation (in kennels). Krushinski (1960) found that the passive defense reaction developed more acutely and reached a greater degree in the German shepherds kept in isolation compared to the Airedales. In general, animals reared in isolation become more sensitive to sensory stimulation because the nervous system attempts to readjust for the previous lack of stimulation.

In an experiment with chickens, Murphy (1977) found that chicks from a flighty genetic line were more likely to panic when a novel ball was placed in their pen, but they were also more attracted to a novel food than birds from a calm line. Cooper and Zubeck (1958), and Henderson (1968) found that rats bred to be dull greatly improved in maze learning when housed in a cage with many different objects; however, enriched environments had little effect on the rats bred for high intelligence. Greenough and Juraska (1979) found that rearing rats in an environment with many novel objects improves learning and resulted in increased growth of dendrites, which are nerve endings in the brain.

Pigs raised in barren concrete pens also seek stimulation (Grandin, 1989a,b; Wood-Gush and Vestergaard, 1991; Wood-Gush and Beilharz, 1983). Piglets allowed to choose between a familiar object and a novel object prefer the novel object (Wood-Gush and Vestergaard, 1991). Pigs raised on concrete are strongly attracted to novel objects to chew on and manipulate. The first author has observed that nervous, excitable hybrid pigs often chew and bit vigorously on boots or coveralls. This behavior is less common in placid genetic lines of pigs.

Although hybrid pigs are highly attracted to novelty, tossing a novel object into their pen will initially cause a strong flight response. Compared to calm genetic lines, nervous-hybrid pigs pile up and squeal more when startled. Pork producers report that nervous, fast-growing, lean hybrid pigs also tail-bite other pigs more often than calmer genetic lines. Tail biting occurs more often when pigs are housed on a concrete slatted floor which provides no opportunity for rooting.

Strong attraction or strong reaction to novelty has also been observed by the first author in cattle. Cattle will approach and lick a piece of paper laying on the ground when they can

approach it voluntarily (Fig. 1.3). However, the same piece of paper blowing in the wind may trigger a massive flight response. Practical experience by both authors suggests that highly reactive horses are more likely to engage in vices such as cribbing or stall weaving when housed in stalls or runs where they receive little exercise. Denied variety and novelty in their environments, highly reactive animals adapt poorly compared to animals from calmer genetic lines (Price, 1984).

In summary, in both wild and domestic animals novelty is both highly feared and necessary. Novelty is most desirable when animals can approach it slowly. Unfortunately, novelty is also fear-provoking when animals are suddenly confronted with it.

TEMPERAMENT

In animals as diverse as rats, chickens, cattle, pigs, and humans, genetic factors influence differences in temperament (Murphey *et al.*, 1980b; Kagan *et al.*, 1988; Grandin, 1993b; Fordyce *et al.*, 1988; Fujita *et al.*, 1994; Hemsworth *et al.*, 1990; Broadhurst, 1975; Reese *et al.*, 1983; Murphy, 1977; Tulloh, 1961; Blizard, 1971). Some individuals are wary and fearful and others are calm and placid. Boissy (1995) stated, fearfulness is a basic psychological characteristic of the individual that predisposes it to perceive and react in a similar manner to a wide range of potentially frightening events.] In all animals, genetic factors influence reactions to situations which cause fear (Davis, 1992; Murphey *et al.*, 1980b; Kagan *et al.*, 1988; Boissy and Bouissou, 1995); therefore, temperament is partially determined by an individual animal's fear response. Rogan and LeDoux (1996) suggest that fear is the product of a neural system that evolved to detect danger and that it causes an animal to make a response to protect itself. Plomin and Daniels (1987) found a substantial genetic influence on shyness (fearfulness) in human children. Shy behavior in novel situations is considered a stable psychological characteristic of certain individuals. Shyness is also suggested to be among the most heritable dimensions of human temperament throughout the life span.

In an experiment designed to control for maternal effects on temperament and emotionality, Broadhurst (1960) conducted cross-fostering experiments on Maudsley Reactive (MR) and Non Reactive (MNR) rats. These lines of rats are genetically selected for high or low levels of emotional reactivity. The results showed that maternal effects were not great enough to completely mask the temperament differences between the two lines (Broadhurst, 1960). Maternal effects can affect temperament, but they are not great enough to completely change the temperament of a cross-fostered animal which has a temperament that is very different from that of the foster mother. In extensive review of the literature, Broadhurst (1975) examined the role of heredity in the formation of behavior and found that differences in temperament between rats persist when the animals are all raised in the same environment.

Measuring Fear-Based Behaviors

One method of testing fearfulness is the open field test (Hall, 1934). Sudden placement of an animal in an open field test arena is used to measure differences in fearfulness. Open field testing has shown differences in fearfulness between different genetic lines of animals. The test arena floor is usually marked in a grid to measure how much the animals walk around and

explore. Huck and Price (1975) showed that domestic rats are less fearful and will walk round the open field more than wild rats. Price and Loomis (1973) explained that some genetic strains of rats are less fearful and explore an open field arena more than others. Eysenck and Broadhurst (1964) found that rodents with high emotional reactivity are more fearful and explore the open field less compared to placid genetic lines.

In their study of genetic effects on behavior, Fuller and Thompson (1978) found that "simply providing the same defined controlled environment for each genetic group is not enough. Conditions must not only be uniform for all groups, but also favorable to the development of the behavior of interest." For example, in wartime Russia, Krushinski (1960) investigated the ability of dogs to be trained for the antitank service or as trail dogs trained to track human scent. The dogs were tied to a spike driven into the ground, and the person who regularly looked after them would let them lick from a bowl of food and then summon the dog to follow the man as he retreated 10 to 15 meters. The dog's activity was measured with a pedometer for the next 2 minutes. The most active dogs were found to be the best antitank dogs. They were also fearless. In the antitank service, dogs were trained to run up to a tank and either run along side of it or penetrate under the caterpillars of the tank. In order to do this, the dogs had to overcome their natural fear of a tank moving toward them at high speed. The less active dogs (as measured by the pedometer) were found to make the best trailer dogs. They slowly followed a trail and kept their noses carefully to the scent while negotiating the corners and turns on the trail. The more active dogs trailed at too high a speed and often jumped the corners and turns in the trail, which sometimes resulted in switching to another trail.

Mahut (1958) demonstrated an example of differences in fear responses between beagles and terriers. When frightened, beagles freeze and terriers run around frantically. In domestic livestock, measuring fear reactions during restraint or in an open field test has revealed differences in temperament both between breeds and between individuals within a breed (Grandin, 1993a; Tulloh, 1961; Dantzer and Mormede, 1983; Murphey *et al.*, 1980b, 1981). The fearful, flighty animals become more agitated and struggle more violently when restrained for vaccinations and other procedures (Fordyce *et al.*, 1988; Grandin, 1993a). Fear is likely to be the main cause of agitation during restraint in cattle, horses, pigs, and chickens. Genetic effects on behavior during transport, handling, and restraint of these animals are further discussed in Chapter 4.

Species Differences in Fear Reactions

In an open field test, frightened rodents often stay close to the arena walls, whereas frightened cattle may run around wildly and attempt to escape. Rodents stay close to the walls because they naturally fear open spaces, whereas cattle run around wildly because they fear separation from the herd. This is an example of differences between species in their response to a similar fear-provoking situation. Fear can be manifested in many different ways. For example, a frightened animal may run around frantically and try to escape in one situation, while in another situation the same animal may freeze or limit its movement. Chickens often freeze when handled by humans. Jones (1984) called this "tonic immobility." The chickens become so frightened that they cannot move. Forceful capture of wild animals can sometimes inflict fatal

heart damage. Wildlife biologists call this capture myopathy. In summary, much is known about the complex phenomenon of fear, but many questions still remain.

BIOLOGICAL BASIS OF FEAR

Genetics influences the intensity of fear reactions. Genetic factors can also greatly reduce or increase fear reaction in domestic animals (Price, 1984; Parsons, 1988; Flint *et al.*, 1995). Research in humans has clearly revealed some of the genetic mechanisms which govern the inheritance of anxiety (Lesch *et al.*, 1996). LeDoux (1992) and Rogan and LeDoux (1996) state that all vertebrates can be fear-conditioned. Davis (1992) recently reviewed studies on the biological basis of fear. Overwhelming evidence points to the amygdala as the fear center in the brain. A small bilateral structure located in the limbic system, the amygdala is where the triggers for flight or fight" are located. Electrical stimulation of the amygdala is known to increase stress hormones in rats and cats (Matheson *et al.*, 1971; Setckleiv *et al.*, 1961); destroying the amygdala can make a wild rat tame and reduce its emotionality (Kemble *et al.*, 1984). Destroying the amygdala also makes it impossible to provoke a fear response in animals (Davis, 1992). Blanchard and Blanchard (1972) showed that rats lose all of their fear of cats when the amygdala is lesioned. Furthermore, when a rat learns that a signal light means an impending electric shock, a normal response is to freeze. Destroying the amygdala will eliminate this response (Blanchard and Blanchard, 1972; LeDoux *et al.*, 1988, 1990). Finally, electrical stimulation of the amygdala makes humans feel fearful (Gloor *et al.*, 1981). Animal studies also show that stimulation of the amygdala triggers a pattern of responses from the autonomic nervous system similar to that found in humans when they feel fear (Davis, 1992).

Heart rate, blood pressure, and respiration also change in animals when the flight or fight response is activated (Manuck and Schaefer, 1978). All these autonomic functions have neural circuits to the amygdala. Fear can be measured in animals by recording changes in autonomic activity. In humans, Manuck and Schaefer (1978) found tremendous differences in cardiovascular reactivity in response to stress, reflecting a stable genetic characteristic of individuals.

Fearfulness and Instinct

Fearfulness and instinct can conflict. This principle was observed firsthand by the second author during his experience raising Queensland Blue Heeler dogs. Annie's first litter was a completely novel experience because she had never observed another dog giving birth or nursing pups. She was clearly frightened when the first pup was born and it was obvious that she did not know what the pup was; however, as soon as she smelled it her maternal instinct took over and a constant uncontrollable licking began. Two years later, Annie's daughter Kay had her first litter. Kay was more fearful than her mother and her highly nervous temperament overrode her innate licking program. When each pup was born Kay ran wildly around the room and would not go near them. The second author had to intervene and place the pups under Kay's nose; otherwise, they may have died. Kay's nervous temperament and fearfulness were a stronger motivation than her motherly instinct.

NERVOUS SYSTEM REACTIVITY CHANGED BY THE ENVIRONMENT

Raising young animals in barren environments devoid of variety and sensory stimulation will have an effect on development of the nervous system. It can cause an animal to be more reactive and excitable when it becomes an adult. This is a long-lasting, environmentally induced change in how the nervous system reacts to various stimuli. Effects of deprivation during early development are also relatively permanent. Melzak and Burns (1965) found that puppies raised in barren kennels developed into hyperexcitable adults. In one experiment the deprived dogs reacted with "diffuse excitement" and ran around a room more than control dogs raised in homes by people. Presenting novel objects to the deprived dogs also resulted in diffuse excitement." Furthermore, the EEGs of the kennel-raised dogs remained abnormal even after they were removed from the kennel (Melzak and Burns, 1965). Simons and Land (1987) showed that the somatosensory cortex in the brains of baby rats will not develop normally if sensory input was eliminated by trimming their whiskers. A lack of sensory input made the brain hypersensitive to stimulation. The effects persisted even after the whiskers had grown back.

Development of emotional reactivity of the nervous system begins during early gestation. Denenberg and Whimbey (1968) showed that handling a pregnant rat can cause her offspring to be more emotional and explore less in an Open field compared to control animals. This experiment is significant because it shows that handling the pregnant mother had the opposite effect on the behavior of the infant pups. Handling and possibly stressing the pregnant mothers changed the hormonal environment of the fetus which resulted in nervous offspring. However, handling newborn rats by briefly picking them up and setting them in a container reduced emotional reactivity when the rats became adults (Denenberg and Whimbey 1968). The handled rats developed a calmer temperament.

The adrenal glands are known to have an effect on behavior (Fuller and Thompson, 1978). The inner portions of the adrenals secrete the hormones adrenaline and noradrenaline, while the outer cortex secretes the gender hormones androgens and oestrogens (reproductive hormones), and various corticosteroids (stress hormones). Yeakel and Rhoades (1941) found that Hall's (1938) emotional rats had larger adrenals and thyroids compared to the nonemotional rats. Richter (1952, 1954) found a decrease in the size of the adrenal glands in Norway rats accompanied by domestication. Several line and strain differences have been found since these early reports. Furthermore, Levine (1968) and Levine *et al.* (1967) showed that brief handling of baby rats reduces the response of the adrenal gland to stress. Denenberg *et al.* (1967) concluded that early handling may lead to major changes in the neuroendocrine system.

Changing Reactivity versus Taming

Adult wild rats can be tamed and become accustomed to handling by people (Galef, 1970). This is strictly learned behavior. Taming full-grown wild animals to become accustomed to handling by people will not diminish their response to a sudden novel stimulus. This principle was demonstrated by Grandin *et al.* (1994) in training wild antelope at the Denver Zoo for low- stress blood testing. Nyala are African antelope with a hair-trigger flight response used to escape from predators. During handling in zoos for veterinary treatments, nyala are often highly stressed and sometimes panic and injure themselves. Over a period of 3 months, Grandin *et al.* (1995) trained nyala to enter a box and stand quietly for blood tests while being fed treats. Each new

step in the training had to be done slowly and carefully Ten days were required to habituate the nyala to the sound of the doors on the box being closed.

All the training and petting by zoo keepers did not change the nyala's response to a sudden, novel stimulus. When the nyala saw repairman on the barn roof they suddenly reacted with a powerful fear response and crashed into a fence. They had become accustomed to seeing people standing at the perimeter of the exhibit, but people on the roof was novel and very frightening. Sudden movements such as raising a camera up for a picture also caused the nyala to flee.

Domestic versus Wild

Wild herding species show much stronger fear responses to sudden novelty compared to domestic ruminants such as cattle and sheep. Domestic ruminants have attenuated flight responses due to years of selective breeding (Price, 1984). Wild ruminants will learn to adapt in captivity and associate people with food, but when frightened by some novel stimulus they are more likely to panic and injure themselves (Grandin, 1993b, 1997). This is especially likely if they are prevented from fleeing by a fence or other barrier. Principles for training and handling all herding animals are basically similar. Training procedures used on flighty antelope or placid domestic sheep are the same. The only difference is the amount of time required. Grandin (1989c) demonstrated this by training placid Suffolk sheep to voluntarily enter a tilting restraining device in one afternoon, but it took 3 months to train the nyala.

In summary, experience can affect behavior in two basic ways: by conventional learning or by changing nervous system reactivity Most importantly, environmental conditions (enriched versus barren) have the greatest effect on the nervous systems of young animals.

NEOTENY

Neoteny is the retention of the juvenile features in an adult animal. Genetic factors influence the degree of neoteny in individuals. Neoteny is manifested both behaviorally and physically In the forward to "The Wild Canids" (Fox, 1975), Conrad Lorenz adds a few of his observations on neoteny and the problems of domestication:

The problems of domestication have been an obsession with me for many years.

On the one hand I am convinced that man owes the life-long persistence of his constitutive curiosity and explorative playfulness to a partial neoteny which is indubitably a consequence of domestication In a curiously analogous manner does the domestic dog owe its permanent attachment to its master to a behavioral neoteny that prevents it from ever wanting to be a pack leader On the other hand, domestication is apt to cause an equally alarming disintegration of valuable behavioral traits and an equally alarming exaggeration of less desirable ones.

Infantile characteristics in domestic animals are discussed by Price (1984), Lambooi and van Putten (1993), Coppinger and Coppinger (1993), Coppinger and Scheider (1993), and Coppinger *et al.* (1987). The shortened muzzle in dogs and pigs is an example. Domestic animals have been selected for a juvenile head shape, shortened muzzles, and other features

(Coppinger and Smith, 1983). Furthermore, retaining juvenile traits makes animals more tractable and easy to handle. The physical changes are also related to changes in behavior.

Genetic studies point to the wolf as the ancestor of domestic dogs (Isaac, 1970). During domestication, domestic dogs have retained many of the infant wolf behaviors. For example, wolf pups bark and yap a lot but adult wolves rarely bark; domestic dogs bark a lot (Fox, 1975; Scott and Fuller, 1965). Wolves have hard-wired instinctive behavior patterns that determine dominance or submission in social relationships. In domestic dogs, the ancestral social behavior patterns of the wolf are fragmented and incomplete. Frank and Frank (1982) observed that the rigid social behavior of the wolf has disintegrated into "an assortment of independent behavioral fragments." Malamutes raised with wolf pups fail to read the social behavior signals of the wolf pups. Further comparisons found that the physical development of motor skills is slower in the malamute. Goodwin *et al.* (1997) studied 10 different dog breeds which ranged from German shepherds and Siberian huskies to bulldogs, cocker spaniels, and terriers. They found that the breeds which retained the greatest repertoire of wolf-like social behaviors were the breeds that physically resembled wolves, such as German shepherds and huskies. Barnett *et al.* (1979) and Price (1985) both conclude that experience can also cause an animal to retain juvenile traits. Gould (1977) also considered the effects of neoteny and stated that neoteny is determined by changes in a few genes that determine the timing of different developmental stages.

OVERSELECTION FOR SPECIFIC TRAITS

Countless examples of serious problems caused by continuous selection for a single trait can be found in the medical literature (Steinberg *et al.*, 1994; Dykman *et al.*, 1969). People with experience in animal husbandry know that overselection for single traits can ruin animals. Good dog breeders know this. Sometimes traits that appear to be unrelated are in fact linked. Wright (1922, 1978) demonstrated this clearly by continuous selection for hair color and hair patterns in inbred strains of guinea pigs. Depressed reproduction resulted in all the strains. Furthermore, differences in temperament, body conformation, and the size and shape of internal organs were found. Belyaev (1979) further showed that continuous selection for a calm temperament in foxes resulted in negative effects on maternal behavior and neurological problems. The fox experiments also found graded changes in many traits over several years of continuous selection for tame behavior. Physiological and behavioral problems increased with each successive generation. In fact, some of the tamest foxes developed abnormal maternal behavior and cannibalized their pups. Belyaev *et al.* (1981) called this "destabilizing selection," in contrast to "stabilizing selection" found in nature (Dobzhansky 1970; Gould, 1977).

There are also countless examples in the veterinary medical literature of abnormal bone structure and other physiological defects caused by overselecting for appearance traits in dog breeds (Ott, 1996). The abnormalities range from bulldogs with breathing problems to German shepherds with hip problems. Scott and Fuller (1965) reported the negative effects of continuous selection for a certain head shape in cocker spaniels:

In our experiments we began with what were considered good breeding stocks, with a fair number of champions in their ancestry. When we bred these animals to their

close relatives for even one or two generations, we uncovered serious defects in every breed. . .Cocker spaniels are selected for a broad forehead with prominent eyes and a pronounced "stop," or angle, between the nose and forehead. When we examined the brains of some of these animals during autopsy, we found that they showed a mild degree of hydroencephaly; that is, in selecting for skull shape, the breeders accidentally selected for a brain defect in some individuals. Besides all this, in most of our strains only about 50 percent of the females were capable of rearing normal, healthy litters, even under nearly ideal conditions of care.

Overselection in Livestock

Single-minded selection for production traits such as rapid gain and leanness resulted in pigs and cattle with more excitable temperaments (Grandin, 1994). Compared to the older genetic lines with more hack fat, observations by the first author on thousands of pigs indicate that lean hybrids are more excitable and difficult to drive through races. Lean hybrid pigs also have a greater startle response. Separating a single animal from the group is more difficult. Recent research conducted in our laboratory has shown that cattle with an excitable temperament have lower weight gains and more meat quality problems (Voisinet *et al.*, 1997a,b). This research illustrates that selection away from a very excitable temperament would be beneficial. However, overselection for an excessively calm temperament could possibly result in some unknown detrimental trait.

Links between Different Traits

Casual observations by the first author also indicate that the most excitable, flighty pigs and cattle have a long, slender body with fine bones. Some of the lean hybrid pigs have weak legs and a few of the normally brown-eyed pigs now have blue eyes. Blue eyes are often associated with neurological problems (Bergsma and Brown, 1971; Schaible, 1963). Furthermore, pigs and cattle with large, bulging muscles often have a calmer temperament than lean animals with less muscle definition. However, animals with the muscle hypertrophy trait (double muscling) have a more excitable temperament (Holmes *et al.*, 1972). Double muscling is extreme abnormal muscling and it might have the opposite effect on temperament compared to normal muscling.

Another example of apparently unrelated traits being linked is deafness in dogs of the pointer breed selected for nervousness (Kllen *et al.*, 1987, 1988). There appears to be a relationship between thermoregulation and aggressiveness. Wild mice selected for aggressiveness used larger amounts of cotton to build their nests than mice selected for low aggression (Sinyter *et al.*, 1995). This effect occurred in both laboratory and wild Strains of mice.

Researchers using high-tech "knockout" gene procedures have been frustrated by the complexity of genetic interactions. In this procedure, genes are knocked out in a gene-targeting procedure whereby a gene is prevented from performing its normal function. The knockout experiments have shown that blocking different genes can have unexpected effects on behavior. In one experiment, superaggressive mice were created when genes involved with learning were inactivated (Chen *et al.*, 1994). The mutant mice had little or no fear and fought until they broke their backs. In another experiment the knockout mutants demonstrated normal behavior until they had pups, and failed to care for them (Brown *et al.*, 1996). In still another experiment,

Konig *et al.* (1996) disabled the gene that produces enkephalin (a brain opioid substance) and found unexpected results. Enkephalin is a substance normally involved in pain perception; however, the mice that were deficient in this substance were very nervous and anxious. They ran frantically around their cages in response to noise. The bottom line conclusion from several different knockout experiments is that changing one gene has unexpected effects on other systems. Traits are linked, and it may be impossible to completely isolate single gene effects. Researchers warn that one must be careful not to jump to a conclusion that they have found an "aggression gene" or a "maternal gene" or an "anxiety gene." To use an engineering analogy, one would not conclude that they had found the "picture center" in a television set after they cut one circuit inside the set that ruined the picture. Gerlai (1996) and Crawley (1996) also warn that knocking out the same gene in two different species may have different effects on behavior. This is due to the complex interactions between many different genes.

Twenty years ago behavioral geneticists concluded that the inheritance of behavior is complex. Fuller and Thompson (1978) concluded, "It has been found repeatedly that no one genetic mechanism accounts exclusively for a particular kind of behavior.

Random Factors

Behavioral geneticists have discovered that it is impossible to completely control variation in some traits. Gartner (1990) found that breeding genetically similar inbred lines of rats failed to stop weight fluctuations. Even under highly standardized laboratory conditions, body weights continued to fluctuate between animals. Pig breeders have also observed that commercially bred hybrid lines of pigs do not gain weight at the same rate. Random unknown factors affect variability even in genetically identical animals. Factors in utero may be one cause; the other causes are unknown. Darrel Tatum and his students at Colorado State University found both body conformation and meat quality variation in cattle which were 50% English (*Bos taurus*) and 50% Brahman (*Bos indicus*). Some animals had more Brahman characteristics, with larger humps and longer ears than others; the body conformation of many of the animals was not half English and half Brahman. The characteristics of the meat varied as well; animals that looked more Brahman had tougher meat. The animals had about 10% variation from the body shape and meat characteristics of Brahman half-bloods.

Gartner (1990) concluded that up to 90% of the cause of random variability cannot be explained by differences in the animals' physical environment. In both mice and cattle, random factors affected body weights. Gartner (1990) believes that the random factors may have their influence either before or shortly after fertilization.

The interactions between environmental and genetic factors are complex. Both an animal's genetic makeup and its environment determine how it will behave. In subsequent chapters in this book the interactions of genetics and environment will be discussed in greater detail. Genetics has profound effects on an animal's behavior.

CONCLUSIONS

There is a complex interaction between genetic and environmental factors which determines how an animal will behave. The animal's temperament is influenced by both genetics and learning. Another principle is that changes in one trait, such as temperament, can have unexpected effects on other apparently unrelated traits. Overselection for a single trait may result in undesirable changes in other behavioral and physical traits.

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