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CANINE COMMUNICATION

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ANIMAL COMMUNICATION

Communication occurs when the actions of one individual, the sender, provide a signal that changes the behavior of another individual, the receiver.[48] In canine communication, the sender is a dog communicating information to a receiver, another dog. The signal is the information transmitted from the sender to the receiver. In studies of communication, this information is measured by a neutral observer, noting the behavioral interactions between individuals but not participating in the communication process.

In general, because of their social relationships, the signals used by dogs in interactions with other dogs also are used to communicate with humans.[18, 37] These signals include visual behaviors such as a stare, auditory behaviors such as a growl, or olfactory signals such as a perianal gland secretion. For example, a veterinarian approaches a canine patient. The dog acts as a sender by producing a signal, a stare, that is perceived by the receiver, the veterinarian. The purpose of the communication signal is to influence the behavior of the receiver; in this case, the purpose of the dog's behavior is to threaten the veterinarian so that he or she will retreat. The outcome of the sequence is dependent on the veterinarian's behavior.

The Signal

The information communicated in a signal may be one of two types: transmitted information or broadcast information.[48] Transmitted

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information occurs when a sender produces a signal that affects the behavior of a receiver. Transmitted information is measured by an increase in the predictability of the receiver's behavior after the signal is produced. The significance of the signal to the receiver has been called the *meaning*.[44] The meaning may vary from one recipient to another and according to the context of the signal.

In contrast, broadcast information is an increase in the predictability of the signaler's identity or behavior after a signal. The information about the sender encoded in a signal has been termed the *message*.[44] In the case of broadcast information, the signaler provides information about its identity or translates the state of its nervous system into external changes that produce identifiable signals. For example, a dog begins to shake when placed on an examination table, thereby expressing the state of its autonomic nervous system. Broadcast information provides a signal that can be used by a receiver, such as an attending veterinarian, to predict the signaler's future behavior.

Broadcast information also can signal species identity and individual physical features. Such information is extremely important for appropriate social interactions. In addition to species information, individual traits such as body size may be assessed to determine the suitability of an opponent for competition over resources such as food, mating opportunities, and resting places.

Manipulation and Prevarication

Communication behavior is goal-directed and functional. In the case of transmitted information, communication involves the transmission of a signal from one animal to another such that the sender benefits, on average, from the response of the receiver.[43] Although the definition does not imply benefit to the receiver, interpreted according to classic ethologic theory this transmission involves a "synergistic interplay between participants, both of which are committed to maximizing the efficiency of the interchange."[31] The receiver benefits by using the signal to perceive the motivation and internal state of the signaler and to gain information regarding the probability of its future behavior.

Recently, emphasis on communication as manipulation of the receiver by the sender has been increased.[22, 28] According to this approach, signals evolve not to "provide information," but to induce the receiver by any means possible, including deceit, to behave in a way that benefits the signaler.[48] Deceitful signals, such as mimicry or bluffing, deliberately mislead the receiver.

Theoretically, the information transfer between the sender and receiver can have one of four outcomes.[48] It can (1) benefit the sender and benefit the receiver (mutuality), (2) benefit the sender and disadvantage the receiver (manipulation or deceit), (3) disadvantage the sender and benefit the receiver (manipulation or eavesdropping), or (4) disadvantage the sender and disadvantage the receiver (spite). Except for spiteful behavior, which is maladaptive for both parties, the occurrence of these

outcomes is frequency dependent. Indeed, senders might, in some circumstances, manipulate receivers and receivers might manipulate senders. However, this can occur only if misleading signals occur rarely in relation to correct ones. When misleading signals are produced by senders, the ability of receivers to identify such signals or ignore them is selected for and improves with time. In response, receivers respond not as "manipulated" but according to their own benefit.

The Evolution of Communication Signals

For a functional communication system, signals must be produced by a sender so that they can be understood by a receiver. Mechanisms for effective signal production and recognition are shaped by natural selection according to their action on the biologic fitness of individuals. Signals produced as part of successful survival and reproduction become increasingly efficient.

Competition for food, space, resting sites, mates, and other limited resources essential for survival and reproduction provides one of the fundamental conditions under which natural selection acts. Competition is costly. It takes up time and uses energy, and, if it involves fighting, may lead to injury or death. Thus, natural selection has favored patterns of behavior that enable individuals to minimize the occurrence, duration, or severity of competitive interactions. One way that dogs do this and avoid injurious fights is to communicate, early in an encounter, their respective strength and motivation.

As part of the evolution of communication signals, certain characteristics improve unambiguous production and detection of signals and are favored. These features are especially important during the communication of unequivocal information, such as species or sexual identity, or against a high level of "background noise" over which a receiving animal may be unable to identify variant signals.[21] These signal characteristics include conspicuousness and redundancy.[49]

Conspicuousness is a feature of signals produced in "noisy" environments, where the presence of many individuals or long distances might obscure the information in the signal.[49] A howl is a conspicuous auditory signal that can be distinguished from other environmental sounds over long distances.

Redundancy reduces errors in the detection and recognition of signals. Redundancy allows a receiver to identify a signal even if it recognizes only a component of that signal. The simplest form of redundancy is repetition. For example, a growl is given by one dog to another, then repeated. This redundancy ensures that the signal is received. Redundancy also can be a function of complexity. For example, when a canine threat display is given, redundancy is provided in the duplication of information in the many display components. Thus, the body components of the display, with head, ears, and tail elevated, convey similar information.

Stereotypy is another aspect of redundancy. The need for signals to

be perceivable and unambiguous, that is, not confused with other signals, has led to the evolution of stereotypic signals. Stereotypic signals are consistent in form and intensity from one animal to the next. Some signals are so stereotyped that they appear to be relatively invariant and are referred to as "fixed action patterns" or more accurately "modal action patterns."[1] One example among canids is the play bow, which shows marked stereotypy in duration and form.[5]

Although evidence exists that some communication signals are innate, learning plays an important role in communication, especially in mammals such as dogs that live in social groups. Neural processes that facilitate cognitive abilities such as recognition of individual traits of group members and memory of these traits for later identification have been favored. Through familiarity with the appearance, odor, or vocalizations of group members, animals become able to discriminate between strangers and nonstrangers.

Displays

Displays are behavior patterns that function as signals. A display may be simple or complex, incorporating redundancy by the processes of conspicuousness, repetition, and stereotypy. The stereotypic aspect of displays improves a receiver's signal detection and recognition. Many displays have undergone ritualization, in which a behavior without communicative function evolves over time toward increased efficiency as a signal. During ritualization, signals may become more conspicuous, more repetitive, and more stereotypic.

Signals used in displays have numerous sources. One source may be behavior patterns evoked by the situation that are performed incompletely, called *intention movements*. The raised-lip display of the aggressive dog is an example of a ritualized intention movement that appears preparatory to the intention to bite. Autonomic and protective responses also may become ritualized. Piloerection is an autonomic response to arousal that has become ritualized as part of a canine aggression display.

Alternately, the display may have its source in motivational conflict. When an animal is motivated to perform more than one activity at the same time, such as attack and retreat, it may perform neither activity but instead show some other form of behavior that is interpreted as the expression of its motivational conflict.[21] This conflict can be expressed in the form of redirected movements, displacement activities, or ambivalent behaviors. Redirected movements are oriented at objects other than the evoking stimulus. Displacement activities are unrelated behaviors that appear to be functionally irrelevant in the given situation.[21, 46] Examples of displacement activities in dogs include yawning, falling asleep, grooming, or playing.[47] Ambivalent behavior is most commonly incorporated as elements from both aggressive and fearful behaviors. An example in dogs is the lifting and flexing of the foreleg in a stationary dog. These expressions of conflict may serve as signals conveying information about the animal's motivational state.

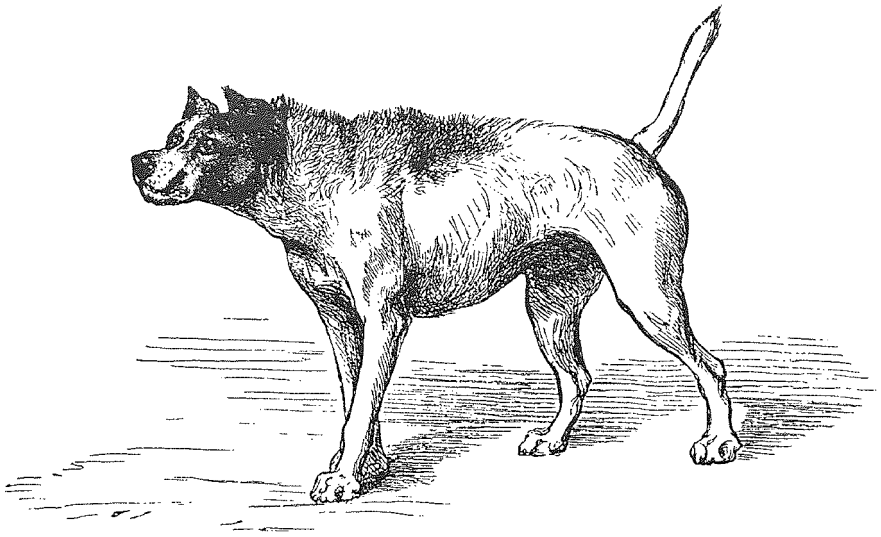

Figure 1. Canine threat display. (Figure by Reviere, in a text by Charles Darwin, 1872.)

Darwin[15] developed the "principle of antithesis," pointing out the extreme differences in posture between a "hostile" (threatening) dog (Fig. 1) and the same animal "in a humble and affectionate frame of mind" (submissive) (Fig. 2). Signals of opposite meaning often are opposite in form, to avoid ambiguity. Thus the aggressive dog appears large

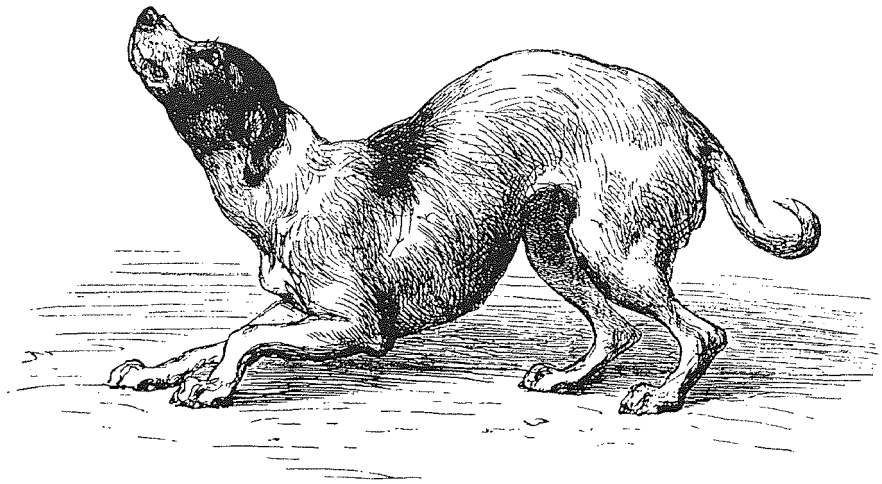

Figure 2. Submissive display. (Figure by Reviere, in a text by Charles Darwin, 1872.)

and the submissive dog appears small. Auditory signals are similarly antithetical. Harsh, low-pitched sounds such as a growl are used in hostile contexts or distance-provoking contexts; purer, higher-pitched sounds such as whines are used in friendly or care-soliciting contexts.[35] Such a system may have evolved because, mechanically, large individuals can produce harsh sounds of low frequency. Thus, because size is an important factor in success in fights, animals may avoid individuals producing lower sounds than they themselves can produce. Selection then should lead to aggressive sounds being as low and harsh as possible. In contrast to this, appeasing and friendly signals are higher sounds to make them easy to discriminate and to minimize the chance of their eliciting a hostile response.

The concept of universal principles underlying animal signals provides the mechanism for interspecies communication, as between dogs and humans.[32] Threat displays are probably similar across species because they universally involve the prominent display of weapons, an increase in apparent size, and the production of harsh, low-frequency sounds. Convergent evolution has probably led to conditions in which one species, such as humans, can "understand" the signals of another species, the dog.[21]

THE DOG AS A DOMESTIC SPECIES

Evidence from many fields of study indicates that the domestic dog *Canis domesticus* evolved from the wolf *Canis lupus*.[11] Comparative studies have shown many features of dog and wolf communication and social behavior to be remarkably similar.[19] Dogs share with wolves the ability to identify individuals and form stable relationships.[33] Feral dogs and wolves form affiliations with conspecifics with which they share food and resting sites.[19] Dominance hierarchies and competition for resources such as food, resting sites, and mating opportunities appear to be fundamental features of the social behavior of both species. Communication displays similar among dogs and wolves are critical to the establishment of social relations and the maintenance of these activities.

Communication behaviors of wolves cannot be extrapolated to those of dogs in all aspects because of certain differences in their social organization. The cooperation evident in hunting large prey and sharing in the care of young is seen in wolves[33] but not stray,[4, 14, 17] free-ranging,[7] or feral dogs.[6, 8] Possibly because they are continuously disrupted by humans, alliances formed between stray dogs do not usually develop into stable social groups as they do in wolves. In cases when stable social groups develop,[8, 17, 42] the cooperation seen in wolf packs hunting large prey is not observed, possibly because stray and feral dogs gather scavenged food, carrion, and small wildlife. Among feral dogs and unlike wolves, breeding is not restricted to a single dominant female and males do not assist with care of the young.[8, 33, 42]

Domestication of the dog by the process of selective breeding has

led to changes in certain behavior patterns. These include alterations in components of ritualized behavior sequences, an increase or decrease in response thresholds, and changes in the motivational context for certain behaviors.[9, 19] When compared with wolves, dogs appear to have a less complex repertoire of visual signals, but appear to be more vocal,[19] although many of these differences are breed specific.[10]

Dogs have been domesticated for approximately 10,000 years by artificial selection.[11] During the last 5000 years, when specialized breeds were developed, which individuals reproduced and passed their genes to subsequent generations has been dictated by human standards of esthetics and functionality. By this process, the rigor of natural selection based on differential survival and reproduction of individuals best adapted to their environment has been diluted. In spite of this, Bradshaw and Lea[9] observed 292 dyadic interactions between dogs in parks, and concluded that the observed behaviors represented a small number of stereotypic displays occurring in predictable sequences. This suggests that, in spite of intensive selective breeding, dogs have retained discernible canid communication behavior patterns that are used in establishing relationships between individuals.

Some traits of domestication physically constrain the range of communication signals available to dogs compared with wolves, particularly with respect to visual displays. These include such general physical canine characters as smaller teeth and a shorter, wider muzzle, which limit the intensity of facial displays.

Breed-specific differences affect the ability to produce certain signals.[11] Selection by humans for certain traits has led to ambiguity in certain visual cues. For example, dogs with brachycephalic faces, bred for specific phenotypic traits and protected as house pets, are unable to convey the range of expression of the lip-lift display. Corkscrew or stump tails and large pendulous ears reduce the ability to use these structures for communication signals. Excessively long hair limits the capacity for piloerection and obscures detection of cues associated with the eyes and mouth. Cosmetic surgical procedures, such as tail docking and ear trims, further increase the ambiguity of visual signals. Because of these features, the visual communication signals of dogs of certain breeds are difficult to interpret. Such confusion may lead to greater dependence on olfactory communication.

Specific breeds, as a result of selective breeding, have greater dependence on one or more modalities for communications signals. For example, the "sight" hounds use visual signals to a greater degree than the "scent" hounds.[19] Among other breeds, alerting barking occurs at a high frequency. Dogs have been selected for certain behavioral traits useful to humans, such as pointing game, herding ruminants, and fighting predators. These activities have led to artificial selection for certain communication postures beyond those used in species-typical interactions. These unique postures include the "stalk" and "eye" postures of herding dogs and the "point" of certain hunting dogs.[12]

TYPES OF SIGNALS

The communication signals used by dogs include vision, smell, and hearing. In the following sections, these modalities are discussed, with functions and motivational meanings assigned to specific canine displays. These functions and motivations are not proven. In spite of the ubiquity of dogs, few experimental data are available to confirm field observations and clinical impressions, largely because of difficulties inherent in the study of communication. Nonetheless, general agreement exists about the message and meaning associated with many of the communication signals given by dogs.

Visual Signals

Visual displays have numerous advantages to the sender and receiver. They can be instantaneously "turned on" and "turned off" to respond to alterations in the social environment. They can be graded to provide subtle information about motivation and emotional state. They are effective for communication at close and medium distances, within the range of canid vision. Unlike other modalities, visual signals do not persist in the environment, are ineffective in the absence of the sender, and are not useful in long-range communication.

Most of the communication among wolves in a pack involves visual displays made up of postures or gestures.[33] Similarly, visual displays are thought to be the primary mode of signaling in dog-dog and dog-human communication.[20, 40] Facial expressions and body postures, including ear and tail positions, form a continuum of communicative signals, incorporating levels of aggression and fear.[29] Various parts of the body can be used to assess the agonistic behavior level of dogs. The position of the head can signal aggression (see Fig. 1, head high, neck arched) or submission (see Fig. 2, lowered head, neck extended and twisted). In addition to monitoring auditory stimuli in the environment, the position of the ears can be used to indicate the emotional state of the animal, ranging from aggression (ears alert) to submission (ears laid back). The position of the eyes can indicate threat (nonwavering stare) or fear (eyes wide) or submission (gaze averted). The position of the tail can reflect the relative agonistic intent from aggression (see Fig. 1, held high) to submission (see Fig. 2, held low or tucked).

The tail is very expressive in the dog. Contrary to public perception, wagging the tail does not necessarily indicate "friendliness" or lack of aggression. A high-positioned, wagging tail is associated with a dominant dog and can be part of a threat (see Fig. 1). In contrast, playful and friendly submissive dogs exhibit wide excursions of the tail. The submissive dog carries its tail low and wags it stiffly, possibly as an appeasement signal (see Fig. 2).[37]

Wolves and dogs appear to form stable dominance hierarchies that dictate priority of access to limited resources and leadership roles. Domi-

nance hierarchies are established by threats, which are ritualized visual signals that indicate an intention or a readiness on the part of the sender to fight. The receiver acknowledges and appeases the sender using submissive displays or, less commonly, escalates the agonistic interaction by responding with a threat or an attack. Among young dogs, dominance order can be identified as early as 3 to 4 weeks of age.[10] Among adult dogs, dominance order appears to be established early in their interactions and is maintained by ritualized displays that communicate the relative dominance and subordinance of each individual in dyadic interactions. Bradshaw and Nott[10] point out an alternative explanation to dominance hierarchies: that dogs actually may be resolving conflicts, not by an underlying social structure, but simply by pairwise assessment of each dog's ability to acquire and defend resources. However, the traditional view of an underlying dominance order remains a useful construct for rapidly interpreting and responding to canine behavior, particularly for veterinarians (Table 1).

When two dogs meet, they may assess each other through ritualized displays[9] that may establish social priorities.[3] Similar displays may be given to humans. Among canine dyadic interactions, one dog, possibly the dominant, may stand and stare at the other. The subordinant dog breaks eye contact first.[37] The dogs may circle head to tail. Olfactory inspection of the head, ears, and anogenital areas of one dog by the other may occur. After an approach, a number of behaviors may follow, ranging from play to escalation of aggression.

One dog may threaten another dog or a human, presumably to establish dominance order. A canine threat display involves numerous features, with repetitive, conspicuous, and stereotypic components. Directly (perpendicularly) facing a rival and staring is a common component of the threat display. Overall motion may be slowed and the gait may be stiff. Postural changes increase the performer's apparent size as perceived by a rival. This is accomplished by raising of the general posture and piloerection of the hair, called *hackles,* along the neck and back.[21] The tail is positioned straight up in the air, the head is held high, and the ears are rotated forward. Vertical retractions of the lips and prominent exposure of the teeth, displayed as offensive weapons, may occur.

Other dominant behaviors seen in wolves and dogs include grasping the muzzle, pinning the head and neck, standing over, or placing the chin on the neck or back or shoulders of a subordinant.[34] In general, these behaviors are ritualized and do not result in injury.

In dogs used for fighting, selective breeding has reduced the usual reliance on threat displays and has favored overt fighting abilities. Such dogs may not display a threat behavior prior to attack. In the bull-baiting or dog-fighting arena, dogs that attack their foe without warning are likely to be winners and are preferentially bred. Similarly, the behavioral tendency to bite the prey and hold on has been favored and is characteristic of the attacks of dogs of certain fighting breeds, such as pit bulls.[30]

Table 1. "TYPICAL" CANINE POSTURES

State	Body	Head	Ears	Eyes	Hackles	Tail
Attentive	Weight evenly distributed	Up or horizontal	Relaxed	Moving	Down	Horizontal wagging
Dominant individual (not aggressive)	Upright, forward	Up	Upright, forward	Variable	Down	High, may wag
Offensive threat (may escalate to aggression; see Fig. 1)	Upright, immobile, or slow motion	Up, +/− lip raised, bared teeth	Upright, forward	Staring, fixed	Raised	High, may wag stiffly
Fearful (may escalate to aggression)	Withdrawn, weight to rear, attempts escape, hides	Down	Down facing back	Variable	Down	Down
Active submissive (see Fig. 2)	Low, withdrawn	Down	Down, flat, facing back	Down	Down	Down, may wag slightly
Passive submissive	Lateral recumbent, underbelly exposed	Down	Down, facing back	Down	Down	Down
Play	Play bow or paw-up, rapid, exuberant, bounding body movements	Moving, play face	Variable	Variable brief stares and exaggerated looking away are common	Down	High flagging, wide range of movement

Dogs adopt submission or appeasement displays (see Fig. 2) to reduce the level of aggression shown toward them and to communicate their relative inferiority in the dominance order. Because submission displays often are diametrically opposed to threat displays, canine submissive displays involve the concealment of the teeth and the exposure of vulnerable body parts such as the belly and neck.[15] The term *subordinant* is used to refer to a relative position lower on a dominance order; *submissive* refers to specific signals used to confirm the subordinant position. Submission is "the effort of the inferior to attain friendly or harmonic social integration"[41] or "an appeal for friendliness."[33] Two general types of submissive behaviors are recognized, active and passive.[2, 41]

When displaying active submission, a subordinant animal greets a dominant one by approaching in a low general body posture, with the hind end lowered and the back arched into a "C" posture,[19] laterally presented. Typically, the tail is carried low but wagging, the head and neck are positioned low with the muzzle up, and the ears are flattened back. The eyes are averted or may range toward and away. When a submissive dog is approached, one foreleg may be raised and flexed, suggesting conflict between approach and avoidance. Cringing and dribbling of urine may occur.

Several submissive displays are associated with the mouth. The submissive grin may be performed in which the lips are pulled back horizontally (see Fig. 2). In some dogs, this may result in exposure of the teeth, confusing human observers with the lip lift of the aggressive dog. The submissive grin always is accompanied by other submissive postures, such as the muzzle up and ears back, and the forelip is not lifted to expose the canine teeth as it is in the lip-lift display.

The subordinant may signal intention to lick by extruding its tongue and smacking its mouth, and actually may lick the muzzle of the more dominant individual. This is observed by humans when their dog greets them with licking of their face and hands.[37] Nose pokes may also occur. Because the posture is similar to the one that puppies assume when approaching the mother to stimulate regurgitation of food, facial licking may be a ritualized social gesture derived from food soliciting.[19] Active submission, among wolves, is associated with a friendly and tolerant response from the dominant wolf.[33]

Passive submission is a demonstration of low rank and helplessness.[33] If stimulated by a touch or a threat or when greeted by more than one dominant animal, the subordinant dog may become passively submissive. Passive submission is characterized by lateral recumbency with elevation of the uppermost hind limb and tail tucked (see Fig. 2). It may be accompanied by submissive urination. In such dogs, defensive aggression is strongly inhibited.

In fearful situations, dogs of any rank can exhibit either submission or defensive aggression. How or if aggressive behavior is expressed depends on features of the environment and motivation,[34] as well as breed predispositions and early experience. Fear responses can appear in the form of active or passive submission, often including trembling.

Alternately, fearful dogs may exhibit defensive aggression. Their appearance incorporates some features of submission and some of aggression. Such dogs hold their ears down and back and their heads down with the eyes wide. They attempt to flee or freeze in place, with their weight back. Often, they face what frightens them. Thus, when restrained by a leash, they exhibit jerky motions in an attempt to orient toward the fearful stimulus.

When reached for or approached by a human, such dogs are likely to bite, particularly when unable to escape.[38] Among pet dogs, the aggressive response may be more likely in the presence of the owner, possibly owing to motivation to protect the owner or because of inadvertent reinforcement of fearful behavior by the owner. Attacks by fearfully aggressive dogs are usually brief, followed by retreat. Fearful dogs are likely to exhibit such autonomic responses as trembling, defecation, and display of the perianal glands.

Another visual display, the raised-leg urination (RLU) pattern, is performed most commonly, but not exclusively,[45] by males and may be associated with dominance status. A male dog on a walk may exhibit RLU 50 to 200 times.[19] The raised leg display itself likely has communication value, signaling sexual identity and dominance status, because the RLD may be performed in the absence of actual urine deposition.[19] Among wolves, the dominant male wolf of a captive group raises its leg more frequently when urinating compared to subordinant males.[19] Leg raising may be delayed in subordinant individuals.

Scratching the ground with alternating forelimbs or hindlimbs may occur after urination or defecation. Although this appears to be a remnant intention movement to cover urine or feces, actually it is performed at a distance from the elimination product. Ground scratching is likely used to make a visual or olfactory mark.[6] Among wolves, ground scratching increases among dominant individuals when aroused by the proximity or elimination products of a stranger.[19, 33]

Play is characteristic of immature and mature dogs. It often is preceded by the *play bow,* which acts as a metacommunication signal, indicating that what follows is play.[5, 29] Thereafter, growls and face-on approaches are interpreted as play instead of aggression. In the play-bow, the dog lowers and extends its forepaws and elevates its hindquarters. The tail is wagged in a wide arc. Activity is rapid, with abrupt transitions between stationary positions and active ones. The playful dog may move rapidly back and forth in exaggerated movements in front of a potential playmate. A foreleg may be raised as part of the play solicitation. The facial expression, termed the *play face,* is characterized by an expression similar to the submissive grin.

Olfactory Signals

Dogs live in a rich olfactory world, of which humans are largely unaware. Because the effectiveness of visual communication has been limited by selective breeding, olfactory communication may have be-

come more important to domestic dogs.[37] Various body odors from glandular secretions may permit individual identification during direct interactions between individuals. In addition, dogs deposit odors in the environment in the form of feces, urine, and perianal gland secretions.[6] Such olfactory signals used by dogs persist, permitting a signal to communicate information for extended periods of time in the absence of the sender. Olfactory signals can provide information about species, sex, and individual identity but cannot reflect rapid changes in emotional states, compared with visual or acoustic signals. Olfactory signals are detectable at close range or medium range even in dense vegetation when animals cannot be seen.

The dog's sense of smell is highly sensitive. Dogs can detect many odors at low concentrations and discriminate odors in "noisy" environments full of distracting, extraneous odors. This ability has been exploited by selective breeding in bloodhounds and other "scent" hounds that demonstrate remarkable odor discrimination.

Anatomically, dogs are endowed with a large olfactory epithelium. In addition, dogs possess bilateral vomeronasal organs (VNO), two small organs located in the floor of the nasal cavity dorsal to the palatine bone. The VNO connect to the mouth via ducts located behind the upper incisors. Dogs do not exhibit flehman, a behavior that directs olfactory stimuli into the VNO in other species, but instead exhibit tongueing—a behavior in which the tongue is rapidly and repeatedly placed behind the upper incisors, presumably transferring material into the VNO. The role of the VNO in dogs has not been well studied; it may be important in the detection of estrus by male dogs or in some other aspect of sexual behavior.[23]

From an early age, all canids show an interest in urine and feces.[19] Individuals sniff the excretory products of themselves and others and may urinate or defecate over these materials. Urine and feces may contain odor cues that aid in individual identification and the presence of that individual. The marks may also indicate to a stranger the proximity of a resident and the home-range boundaries. The freshness of the mark may indicate a temporal pattern: how recently the sender left the mark. This may be one mechanism by which wolves assess population density as well as home-range boundaries.[33]

Visual displays may accompany urine or fecal marking. Males, and less frequently females, utilize the raised-leg posture concomitantly with urine marking. Raised-leg urination is used most commonly by dominant male and female wolves. Urination or defecation may be followed by a stereotypic scratching of the ground with alternate forelegs and hind legs. This may also provide an olfactory mark from interdigital scent glands.[6]

Urine deposits are used to communicate information. Females can communicate their reproductive status because sexually experienced male dogs are able to identify a female in estrus by the odor of her urine.[16] The male trait of marking numerous elevated sites each with a small amount of urine may communicate sexual and individual identity

as well as dominance status. Dogs tend to overmark the urine of other dogs, and actually may line up for the opportunity. By extrapolation from wolves, urine marks may be used to denote territories or home ranges, and to mask the odors of intruders.[10] Among wolves, all pack members recognize home-range "scent posts" and become excited when these have been marked by an unfamiliar individual. In such cases, the scent is overmarked repeatedly.[19] Among male dogs that exhibit objectionable urine marking in the house, approximately 50% are improved with castration, suggesting an endocrine basis for the behavior.[25]

Dogs show interest and sniff the feces of other dogs, but evidence for olfactory communication using feces is not clear.[10] The ability to discriminate familiar from unfamiliar feces is suggested by the behavior of wolves. Resident wolves tend to defecate at trail junctions and along home-range borders where the marks could serve as "keep-out" signals. Lone wolves tend to leave the trails to defecate, depositing their feces where it may not be detected.[39]

When greeting another dog, the initiator will commonly investigate areas of apocrine gland density.[9] These sites include the head, favored by females, and the anogenital region, favored by males.[9] When presented with life-sized paintings of conspecifics, dogs initially react as if the figure were another dog, visually orienting laterally toward the figure, then sniffing the ear, mouth, inguinal, and perianal areas.[19] Familiar dogs, when reintroduced after an absence, often spend time in concomitant oroanal sniffing. When two male wolves or dogs approach, the dominant lifts its tail to allow the subordinant to sniff its perianal region. At the same time, the dominant may try to similarly investigate the subordinant. Typically, the subordinant keeps its tail tucked to prevent sniffing.

Normally, the contents of perianal glands are discharged during defecation.[10] This may permit individual identity of the feces on the basis of odor, which may be socially significant to conspecifics. Differences exist in the biochemical contents of perianal gland secretions among classes of dogs and possibly individuals.[36] This suggests that dogs use perianal gland secretions to assess the sex, physiologic state, and individual identity of the signaler.

Like wolves, free-ranging and pet dogs may roll in unfamiliar feces, urine, or decomposing carrion. Rolling in pungent substances may reduce the novelty of the odor by habituation or may increase the amount of social investigation by conspecifics and be socially rewarding.[19] This, in turn, may reduce the likelihood of agonistic attacks by familiar individuals, although no empirical evidence for this hypothesis exists.

Auditory Signals

Numerous auditory signals are used for communication by dogs as well as by wolves.[20] These are summarized in Table 2 along with their

Table 2. SELECTED AUDITORY SIGNALS USED BY DOGS

Name of Vocalization	Proposed Function
Bark	Alert others/warning
	Territorial defense/rivalry/defense
	Individual identity
	Social facilitation
	Play solicitation
	Greeting, call for attention
Howl	Territorial maintenance
	Locate pack members
	Individual recognition
	Coordinate social activities/hunting
	Attract others
	Reactive (in response to sirens, etc)
Growl	Aggression
	Play
	Defense
	Warning
	Threat
Whine	Greeting
	Frustration, pain
	Submission
	Attention-seeking
	Defense

Data from references 10, 19, 27, and 37

common behavioral associations.[10, 20] In dogs, barking and howling are more stereotyped and louder than low-intensity vocalizations, and are used to effect communication over greater distances. Their acoustic properties allow these signals to permit localization of sound. Other vocalizations, such as growls and whines, are used in short- or medium-range communication.

Dogs produce distinguishable barks in a number of different contexts. These include territorial barking, aggressive barking, and alerting barking. Territorial barking is common to most dogs. It varies in intensity and amplitude with the decreasing distance of the intruder and the level of arousal of the sender. In response to approach by conspecific or heterospecific intruders at far distances, the bark has an alerting function. At near distances, the barks may become more rapid and be accompanied by visual signals indicating the aggression of the signal. Because of their social relationship to humans, dogs also bark territorially at humans as well as conspecifics.

Barking also can occur as a long-range signal between dogs, communicating the location and individual identity of the sender. In response to other dogs barking at a distance, a dog commonly barks, perhaps to indicate its presence and individual identity. Humans and presumably dogs can distinguish the long-range bark of one dog from another. In addition, barking can occur in play and in anxiety states, such as when

agitated dogs are frustrated by a barrier that prevents their movement or in cases of separation anxiety.

Dogs tend to bark more commonly than other canids.[10] In general, young canids bark at a higher rate than adults. Barking may be a neotenic trait, selected for in the course of domestication of the dog.[13] Indeed, when foxes were selected for breeding on the basis of tameness alone, after 20 generations, the resulting foxes vocalized more than wild types, often producing a doglike bark.[20] Certain breeds bark more than others. Barking at unusual sounds and at the approach of strangers has been a desirable trait to dog owners and has likely been favored in the course of selective breeding.

Dogs of some breeds howl during states of arousal, although the exact message is not known. Wolves howl to recruit other pack members before a hunt or to seek social contact from other wolves, for mating or other purposes.[27]

The growl generally occurs as part of an aggressive display. The low-pitched, wide frequency–band sound is usually accompanied by a visual threat such as a lip lift or stare. However, that the growl can occur during play, particularly during tug-of-war or chasing games, provides evidence that the context must be considered to interpret the meaning in a particular signal. The play-growl always is accompanied by other signs of play, such as a high-flagging tail, play bow, and exuberant motion.

The whine is used during greeting, when frustrated (such as when desired movement is prevented), when experiencing pain, and in submission situations (given by a subordinate individual to a more dominant one during the greeting ritual of active submission).

Dogs of breeds as disparate as the Chihuahua and the St. Bernard are receptive to sounds up to 47 kHz, much higher than the frequency of signals detectable by humans.[24] This ability, which allows dogs to respond to "silent" whistles, is not thought to be used in canine communication, but may be an adaptation of localizing rodents by their ultrasonic noises.[26]

HANDLING DOGS IN THE VETERINARY SETTING IN RESPONSE TO THEIR SIGNALS

The veterinarian is required to handle dogs after brief assessment and greeting, to effectively restrain them, and to perform procedures that may be odious to the dog. Handling dogs efficiently and with the minimum of resistance and distress is important from the welfare standpoint as well as the efficiency of the veterinary hospital. A positive experience by the dog and owner serves to cement their bond to the veterinary facility. Negative experiences distress the dog and owner. In addition, each negative experience conditions the animal for the future, so that subsequent visits are more and more difficult and unsettling for all.

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Table 3. USEFUL RESPONSES TO DOGS IN THE VETERINARY SETTING

Posture*	Suggested Response	Comments
Attentive	Speak to the dog Permit approach and investigation	Utilize minimal necessary restraint, as indicated by dog's breed, size, & activity level
Dominant	As above; watch for threatening behavior by the dog Avoid threatening behavior such as approaching face-on or standing over the dog	As above Establish control using obedience commands while positioned to the side of the dog
Offensive threat (see Fig. 1)	Be sure the dog is under leash control At first, place a table or distance between you and the dog to defuse the confrontation Initially ignore the aggressive display and give the dog time to habituate to the environmental stimuli Do not stare at the dog, do not reach for it or pat it on the head Do not approach face-on; approach the dog from the side or back If the dog knows obedience commands, these can be used to focus the dog's attention away from you and gain control of the situation	Avoid staring back or approaching face-on, which can escalate aggression Enter the exam room before the dog enters to reduce the incidence of face-on confrontations and gain the "home court" advantage Handling the dog away from the owner avoids any protective component of the behavior and reduces risk of injury to the owner For future visits, the client may be able to train the dog to accept a muzzle that can be placed prior to entry into the veterinary hospital For safe handling, a muzzle and trained assistant are required
Fearful (Defensively aggressive)	Do not immediately approach the dog Take time to allow the dog to habituate to your sound and smell Reduce the threat of your presentation by increasing the distance to the dog, standing behind a barrier, such as an exam table, or sitting down Try to avoid standing over the dog or approaching it in a corner or under a chair Use restraint appropriate to size, breed, and response of the dog	Fearful dogs are unpredictable Do not approach them in a corner or under a chair, where they are more apt to be defensive The temporary use of a restraining muzzle can eliminate the aggressive component in some dogs and is best placed before the defensive behavior Discuss a counterconditioning/desensitization program whereby the dog comes to the veterinary office for delectable food rewards (but no treatments) for a number of brief visits Eating and obedience exercises are incompatible with defensive aggression and can be used as counterconditioning/desensitization tools
Active submissive	Use food treats, petting, and verbal reinforcements to reward attentive behavior Do not reward (pet, talk to) the dog when it cowers or trembles, but note the circumstances so that you can reduce the impact of the stimulus	A genetic or experimental basis to this behavior may exist Minimize aversive experiences with sedatives, analgesics, or anxiolytics If accompanied by trembling and other obvious signs of fear, a desensitization/counterconditioning program may be useful
Passive submissive (see Fig. 2)	Aggression is usually inhibited Passive submission, including submissive urination, should be discouraged by taking on a less threatening posture Sitting down may be helpful	Encourage the owner not to reward this behavior by petting and cooing to the dog as it displays submissive behavior Instead, the owner should ignore the dog when it is submissive and pay attention to it when it is not submissive
Play	These dogs can be difficult to work with because they are constantly moving and wiggling Use food rewards when the dog is attentive and immobile	Basic obedience training should be encouraged The owner should be taught how to reward the dog for settling down

*See *States* outlined in Table 1.

For these reasons, techniques that lead to favorable veterinary hospital visits are important. Communication plays an important role in this process. Fearful animals must be identified early and techniques used to reduce their fear. Table 3 suggests approaches.

SUMMARY

Communication occurs when one individual, the sender, produces a signal that alters the behavior of another individual, the receiver. The signal can provide broadcast information about species and individual identity or transmitted information, in which the sender effects a change in the receiver's behavior. To reduce ambiguity, signals have evolved to be conspicuous, redundant, and stereotypic. These features allow communication signals to be produced by senders and perceived and acted upon appropriately by receivers, both conspecific and heterospecific.

The modality of the communication signal can be visual, olfactory, or acoustic. Visual signals can be adjusted rapidly for response during interactions between individuals at close or medium range. Examples include displays of relative dominance or submission. Olfactory signals can be used for individual, sex, or group identity at close range during greetings and assessments of individuals. Excretory products can be used for olfactory communication over long distances and for long periods of time. Acoustic signals can be adjusted rapidly for close- and far-range communication. They do not persist in the environment.

For dogs, communication is fundamental to maintaining affiliations, reducing competition, and identifying individuals. These factors are critical to the highly developed social behavior of dogs. In an ultimate sense, dogs have been selectively bred for positive interactions with humans; in a proximate sense, many dogs spend their lives in close social association with humans. For these reasons, many of the signals used by dogs in dog-dog communication are also used in dog-human communication.

Veterinarians act as receivers for communication signals when greeting dogs as patients. The information obtained is used to assess the state of arousal and probability of future behavior of the dog so that handling of the animal can be facilitated. The goals are to minimize stress and injury, to successfully complete the treatment program, and to promote the health of the animal.

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