Animal Communication

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Chapter 1

Animal Communication

Metacommunications: signals that modify the meaning of subsequent signals. The best known example is the *play face* and tail signals in dogs, which indicate that a subsequent aggressive signal is part of a play fight rather than a serious aggressive episode.

Animal communication is any behavior on the part of one animal that has an effect on the current or future behaviour of another animal. The study of animal communication,

sometimes called **Zoosemiotics** (defined as the study of sign communication or semiosis in animals; distinguishable from anthroposemiotics, the study of human communication) has played an important part in the methodology of ethology, sociobiology, and the study of animal cognition.

Animal communication, and indeed the understanding of the animal world in general, is a rapidly growing field, and even in the 21st century so far, many prior understandings related to diverse fields such as personal symbolic name use, animal emotions, animal culture and learning, and even sexual conduct, long thought to be well understood, have been revolutionized.

Validation

A lamb investigates a rabbit, an example of interspecific communication through body language and scent.

Forms of communication

- Gestures: The best known form of communication involves the display of distinctive body parts, or distinctive bodily movements; often these occur in combination, so a distinctive movement acts to reveal or emphasize a distinctive body part. For example, the presentation of a parent Herring Gull's bill to its chick signals feeding time. Like many gulls, the Herring Gull has a brightly coloured bill, yellow with a red spot on the lower mandible near the tip. When it returns to the nest with food, the parent stands over its chick and taps the bill on

the ground in front of it; this elicits a begging response from a hungry chick (pecking at the red spot), which stimulates the parent to regurgitate food in front of it. The complete signal therefore involves a distinctive morphological feature (body part), the red-spotted bill, and a distinctive movement (tapping towards the ground) which makes the red spot highly visible to the chick. Congruently, some cephalopods, such as the octopus, have specialized skin cells that can change the apparent colour, opacity, and reflectiveness of their skin. In addition to being used for camouflage, rapid changes in skin colour are used while hunting and in courtship rituals. While all primates use some form of gesture, Frans de Waal came to the conclusion that apes and humans are unique in that only they are able use intentional gestures to communicate. He tested the hypothesis of gesture evolving into language by studying the gestures of bonobos and chimps.

- Facial Expression: Facial gestures play an important role in animal communication. Dogs for example express anger through a snarling and showing their teeth. In alarm their ears will perk up. When fearful a dog will pull back their ears, expose teeth slightly and squint eyes. Jeffery Mogil studied the facial expressions of mice during increments of increasing pain. What they found were five recognizable facial expressions; orbital tightening, nose and check bulge, and changes in ear and whisker carriage.

- Gaze Following: Coordination among social animals is facilitated by monitoring of each others' head and eye orientation. Long recognized in human developmental studies as an important component of communication, there has recently begun to be much more attention on the abilities of animals to follow the gaze of those they interact with, whether members of their own species or humans. Studies have been conducted on apes, monkeys, dogs, birds, and tortoises, and have focused on two different tasks: "follow[ing] another's gaze into distant space" and "follow[ing] another's gaze geometrically around a visual barrier e.g. by repositioning themselves to follow a gaze cue when faced with a barrier blocking their view". The first ability has been found among a broad range of animals, while the second has been demonstrated only for apes, dogs (and wolves), and corvids (ravens), and attempts to demonstrate this "geometric gaze following" in marmosets and ibis gave negative results. Researchers do not yet have a clear picture of the cognitive basis of gaze following abilities, but developmental evidence indicates that "simple" gaze following and "geometric" gaze following are likely to rely on distinct cognitive foundations.

- Vocalization: Many animals communicate through vocalizations. Communication through vocalization is essential for many tasks including mating rituals, warning calls, conveying location of food sources, and social learning. Male mating calls are used to signal the female and to beat competitors in species such as hammer-headed bats, red deers, humpback whales and elephant seals . In whale species Whale song has been found to have different dialects based on location. Other instances of communication include the warning cries of the Campbell monkey ,

the territorial calls of gibbons, the use of frequency in Greater Spear-nosed bats to to distinguish between groups .

- Olafactory communication: Less obvious (except in a few cases) is olfactory communication. Many mammals, in particular, have glands that generate distinctive and long-lasting smells, and have corresponding behaviours that leave these smells in places where they have been. Often the scented substance is introduced into urine or feces. Sometimes it is distributed through sweat, though this does not leave a semi-permanent mark as scents deposited on the ground do. Some animals have glands on their bodies whose sole function appears to be to deposit scent marks: for example Mongolian gerbils have a scent gland on their stomachs, and a characteristic ventral rubbing action that deposits scent from it. Golden hamsters and cats have scent glands on their flanks, and deposit scent by rubbing their sides against objects; cats also have scent glands on their foreheads. Bees carry with them a pouch of material from the hive which they release as they reenter, the smell of which indicates that they are a part of the hive and grants their safe entry. Ants use pheromones to create scent trails to food as well as for alarm calls, mate attraction and to distinguish between colonies. Additionally, they have pheromones that are used to confuse an enemy and manipulate them into fighting with themselves.

- Electro Communication: A rarer form of animal communication is electrocommunication. It is seen primarily in aquatic life, though some mammals, notably the platypus and echidnas are capable of electroreception and thus theoretically of electrocommunication.

Functions of communication

While there are as many kinds of communication as there are kinds of social behaviour, a number of functions have been studied in particular detail. They include:

- agonistic interaction: everything to do with contests and aggression between individuals. Many species have distinctive threat displays that are made during competition over food, mates or territory; much bird song functions in this way. Often there is a matched submission display, which the threatened individual will make if it is acknowledging the social dominance of the threatener; this has the effect of terminating the aggressive episode and allowing the dominant animal unrestricted access to the resource in dispute. Some species also have *affiliative* displays which are made to indicate that a dominant animal accepts the presence of another.
- Courtship rituals: signals made by members of one sex to attract or maintain the attention of potential mate, or to cement a pair bond. These frequently involve the display of body parts, body postures (gazelles assume characteristic poses as a signal to initiate mating), or the emission of scents or calls, that are unique to the species, thus allowing the individuals to avoid mating with members of another species which would be infertile. Animals that form lasting pair bonds often have

symmetrical displays that they make to each other: famous examples are the mutual presentation of reeds by Great Crested Grebes, studied by Julian Huxley, the *triumph displays* shown by many species of geese and penguins on their nest sites and the spectacular courtship displays by birds of paradise and manakins.
- ownership/territorial: signals used to claim or defend a territory, food, or a mate.
- Food-related signals: many animals make "food calls" that attract a mate, or offspring, or members of a social group generally to a food source. When parents are feeding offspring, the offspring often have begging responses (particularly when there are many offspring in a clutch or litter - this is well known in altricial songbirds, for example). Perhaps the most elaborate food-related signal is the dance language of honeybees studied by Karl von Frisch. Young ravens signal to older, more experienced ravens when they come across new or untested food.
- Alarm calls: signals made in the presence of a threat from a predator, allowing all members of a social group (and often members of other species) to run for cover, become immobile, or gather into a group to reduce the risk of attack.
- Metacommunications: signals that modify the meaning of subsequent signals. The best known example is the *play face* in dogs, which signals that a subsequent aggressive signal is part of a play fight rather than a serious aggressive episode.

Interpretation of animal communication

It is important to note that whilst many gestures and actions have common, stereotypical meanings, researchers regularly seem to find that animal communication is often more complex and subtle than previously believed, and that the same gesture may have multiple distinct meanings depending on context and other behaviors. So generalizations such as "X means Y" are *often*, but not *always* accurate. For example, even a simple domestic dog's tail wag may be used in subtly different ways to convey many meanings including:

- Excitement
- Anticipation
- Playfulness
- Contentment/enjoyment
- Relaxation or anxiety
- Questioning another animal or a human as to intentions
- Tentative role assessment on meeting another animal
- Reassurance ("I'm hoping to be friendly, are you?")
- Brief acknowledgement ("I hear you", or "I'm aware and responsive if you want my attention")
- Statement of interest ("I want that (food/toy/activity), if you're willing")
- Uncertainty/apprehension
- Submissive placation (if worried by a more dominant animal)

Combined with other body language, in a specific context, many gestures such as yawns, direction of vision, and so on all convey meaning. Thus statements that a particular action "means" something should always be interpreted to mean "often means" something. As

with human beings, who may smile or hug or stand a particular way for multiple reasons, many animals reuse gestures too.

Intraspecies vs. interspecies communication

The sender and receiver of a communication may be of the same species or of different species. The majority of animal communication is intraspecific (between two or more individuals of the same species). However, there are some important instances of interspecific communication. Also, the possibility of interspecific communication, and the form it takes, is an important test of some theoretical models of animal communication.

A European starling (*Sturnus vulgaris*) singing

Intraspecies communication

The majority of animal communication occurs within a single species, and this is the context in which it has been most intensively studied.

Most of the forms and functions of communication described above are relevant to intra-species communication.

Interspecies communication

Many examples of communication take place between members of different species. Animals communicate to other animals with various signs: visual, sound, echolocation, body language, and smell.

Prey to predator

If a prey animal moves or makes a noise in such a way that a predator can detect and capture it, that fits the definition of "communication" given above. This type of communication is known as interceptive eavesdropping, where a predator intercepts the message being conveyed to conspecifics.

This Chihuahua is baring his teeth to signify an attack is imminent if the photographer comes closer to take his bone.

There are however some actions of prey species that are clearly communications to actual or potential predators. A good example is warning colouration: species such as wasps that are capable of harming potential predators are often brightly coloured, and this modifies the behaviour of the predator, who either instinctively or as the result of experience will avoid attacking such an animal. Some forms of mimicry fall in the same category: for example hoverflies are coloured in the same way as wasps, and although they are unable to sting, the strong avoidance of wasps by predators gives the hoverfly some protection. There are also behavioral changes that act in a similar way to warning colouration. For example, canines such as wolves and coyotes may adopt an aggressive posture, such as growling with their teeth bared, to indicate they will fight if necessary, and rattlesnakes

use their well-known rattle to warn potential predators of their poisonous bite. Sometimes, a behavioral change and warning colouration will be combined, as in certain species of amphibians which have a brightly coloured belly, but on which the rest of their body is coloured to blend in with their surroundings. When confronted with a potential threat, they show their belly, indicating that they are poisonous in some way.

Another example of prey to predator communication, is referred to as a pursuit-deterrent signal. Pursuit-deterrent signals occur when prey indicates to a predator that pursuit would be unprofitable because the signaler is prepared to escape. Pursuit-deterrent signals provide a benefit to both the signaler and receiver; they prevent the sender from wasting time and energy fleeing, and they prevent the receiver from investing in a costly pursuit that is unlikely to result in capture. Such signals can advertise prey's ability to escape, and reflect phenotypic condition (quality advertisement), or can advertise that the prey has detected the predator (perception advertisement). Pursuit-deterrent signals have been reported for a wide variety of taxa, including fish (Godin and Davis 1995), lizards (Cooper et al. 2004), ungulates (Caro 1995), rabbits (Holley 1993), primates (Zuberbuhler et al. 1997), rodents (Shelley and Blumstein 2005, Clark 2005), and birds (Alvarez 1993, Murphy 2006, 2007). The most familiar example of quality advertisement pursuit-deterrent signal is *stotting*, a pronounced combination of running while simultaneously hopping shown by some antelopes such as Thomson's gazelle in the presence of a predator. At least 11 hypothesis for stotting have been proposed. A leading theory today is that it alerts predators that the element of surprise has been lost. Predators like cheetahs rely on surprise attacks, proven by the fact that chases are rarely successful when they stot. Predators know not to waste energy on a chase that will likely be unsuccessful (optimal foraging behavior).

Predator to prey

Some predators communicate to prey in ways that change their behaviour and make them easier to catch, in effect deceiving them. A well-known example is the angler fish, which has a fleshy growth protruding from its forehead and dangling in front of its jaws; smaller fish try to take the lure, and in so doing are perfectly placed for the angler fish to eat them.

Symbiotic species

Interspecies communication also occurs in various kinds of mutualism and symbiosis. For example, in the cleaner fish/grouper system, groupers signal their availability for cleaning by adopting a particular posture at a cleaning station.

Human/animal communication

Various ways in which humans interpret the behavior of domestic animals, or give commands to them, fit the definition of interspecies communication. Depending on the context, they might be considered to be predator to prey communication, or to reflect forms of commensalism. The recent experiments on animal language are perhaps the

most sophisticated attempt yet to establish human/animal communication, though their relation to natural animal communication is uncertain.

Lacking in the study of human-animal communication is a focus on expressive communication from animal to human specifically. Other than a few natural expressions animals (especially dogs) use to communicate to humans, scientists in general do not pursue expanding the expressive/productive communication of domesticated animals. Horses are taught to not communicate (for safety). Dogs and horses are generally not encouraged to communicate expressively, but are encouraged to develop receptive language (understanding). One scientist, Sean Senechal has pursued (since the late 1990's) developing, studying, and using the learned visible, expressive language in dogs and horses. By teaching these animals a gestural (human made) ASL-like language animals have been found to learn and use the new signs on their own to get what they need. Senechal's book Dogs Can Sign, Too documents this process.

Other aspects of animal communication

Evolution of communication

The importance of communication is clear from the fact that animals have evolved elaborate body parts to facilitate it. They include some of the most striking structures in the animal kingdom, such as the peacock's tail. Birdsong appears to have brain structures entirely devoted to its production. But even the red spot on a herring gull's bill, and the modest but characteristic bowing behaviour that displays it, require evolutionary explanation.

There are two aspects to the required explanation:

- identifying a route by which an animal that lacked the relevant feature or behaviour could acquire it;
- identifying the selective pressure that makes it adaptive for animals to develop structures that facilitate communication, emit communications, and respond to them.

Significant contributions to the first of these problems were made by Konrad Lorenz and other early ethologists. By comparing related species within groups, they showed that movements and body parts that in the primitive forms had no communicative function could be "captured" in a context where communication would be functional for one or both partners, and could evolve into a more elaborate, specialised form. For example, Desmond Morris showed in a study of grass finches that a beak-wiping response occurred in a range of species, serving a preening function, but that in some species this had been elaborated into a courtship signal.

The second problem has been more controversial. The early ethologists assumed that communication occurred for the good of the species as a whole, but this would require a process of group selection which is believed to be mathematically impossible in the

evolution of sexually reproducing animals. Altruism towards an unrelated group is not widely accepted in the scientific community, but rather can be seen as a sort of reciprocal altruism, expecting the same behavior from others, a benefit of living in a group. Sociobiologists argued that behaviours that benefited a whole group of animals might emerge as a result of selection pressures acting solely on the individual. A gene-centered view of evolution proposes that behaviors that enabled a gene to become wider established within a population would become positively selected for, even if their effect on individuals or the species as a whole was detrimental.

In the case of communication, an important discussion by John Krebs and Richard Dawkins established hypotheses for the evolution of such apparently altruistic or mutualistic communications as alarm calls and courtship signals to emerge under individual selection. This led to the realisation that communication might not always be "honest" (indeed, there are some obvious examples where it is not, as in mimicry). The possibility of evolutionarily stable dishonest communication has been the subject of much controversy, with Amotz Zahavi in particular arguing that it cannot exist in the long term. Sociobiologists have also been concerned with the evolution of apparently excessive signalling structures such as the peacock's tail; it is widely thought that these can only emerge as a result of sexual selection, which can create a positive feedback process that leads to the rapid exaggeration of a characteristic that confers an advantage in a competitive mate-selection situation.

One theory to explain the evolution of traits like a peacock's tail is 'runaway selection'. This requires two traits-a trait that exists, like the bright tail, and a prexisting bias in the female to select for that trait. Females prefer the more elaborate tails, and thus those males are able to mate successfully. Exploiting the psychology of the female, a positive feedback loop is enacted and the tail becomes bigger and brighter. Eventually, the evolution will level off because the survival costs to the male do not allow for the trait to be elaborated any further. Two theories exist to explain runaway selection. The first is the good genes hypothesis. This theory states that an elaborate display is an honest signal of fitness and truly is a better mate. The second is the handicap hypothesis. This explains that the peacock's tail is a handicap, requiring energy to keep and makes it more visible to predators. Regardless, the individual is able to survive, even though its genes are not as good per se.

Cognitive aspects

Ethologists and sociobiologists have characteristically analysed animal communication in terms of more or less automatic responses to stimuli, without raising the question of whether the animals concerned understand the meaning of the signals they emit and receive. That is a key question in animal cognition. There are some signalling systems that seem to demand a more advanced understanding. A much discussed example is the use of alarm calls by vervet monkeys. Robert Seyfarth and Dorothy Cheney showed that these animals emit different alarm calls in the presence of different predators (leopards, eagles, and snakes), and the monkeys that hear the calls respond appropriately - but that this ability develops over time, and also takes into account the experience of the

individual emitting the call. Metacommunication, discussed above, also seems to require a more sophisticated cognitive process.

A recently published paper demonstrated that bottlenose dolphins can recognize identity information from whistles even when otherwise stripped of the characteristics of the whistle; making dolphins the only animals other than humans that have been shown to transmit identity information independent of the caller's voice or location. The paper concludes that:

The fact that signature whistle shape carries identity information independent from voice features presents the possibility to use these whistles as referential signals, either addressing individuals or referring to them, similar to the use of names in humans. Given the cognitive abilities of bottlenose dolphins, their vocal learning and copying skills, and their fission–fusion social structure, this possibility is an intriguing one that demands further investigation.
—V. M. Janik, *et al.*

Animal communication and human behaviour

Another controversial issue is the extent to which humans have behaviours that resemble animal communication, or whether all such communication has disappeared as a result of our linguistic capacity. Some of our bodily features - eyebrows, beards and moustaches, deep adult male voices, perhaps female breasts - strongly resemble adaptations to producing signals. Ethologists such as Irenäus Eibl-Eibesfeldt have argued that facial gestures such as smiling, grimacing, and the *eyebrow flash* on greeting are universal human communicative signals that can be related to corresponding signals in other primates. Given the recency with which spoken language has emerged, it is very likely that human body language does include some more or less involuntary responses that have a similar origin to the communication we see in other animals.

Humans also often seek to mimic animals' communicative signals in order to interact with the animals. For example, cats have a mild affiliative response involving closing their eyes; humans often close their eyes towards a pet cat to establish a tolerant relationship. Stroking, petting and rubbing pet animals are all actions that probably work through their natural patterns of interspecific communication.

Dogs have shown an ability to understand communication from a species other than their own. They were able to use human communicative gestures such as pointing and looking to find hidden food and toys.

A new approach in the 21 century of studying animal communication uses applied behavioral analysis (ABA), specifically Functional Communication Training (FCT). This FCT previously has been used in schools and clinics with humans with special needs, such as children with autism, to help them develop language. Sean Senechal, at the AnimalSign Center has been using an approach similar to this FCT with domesticated animals, such as dogs (since 2004) and horses (since 2000) with encouraging results and

benefits to the animals and people. Functional communication training for animals, Senechal calls AnimalSign Language. This includes teaching communication through gestures (like simplified ASL), pictures (PECS), tapping, and vocalization. The process for animals includes simplified and modified techniques.

Animal communication and linguistics

For linguistics, the interest of animal communication systems lies in their similarities to and differences from human language:

1. Human languages are characterized for having a **double articulation** (in the characterization of French linguist André Martinet). It means that complex linguistic expressions can be broken down in meaningful elements (such as morphemes and words), which in turn are composed of smallest phonetic elements that affect meaning, called phonemes. Animal signals, however, do not exhibit this dual structure.
2. In general, animal utterances are responses to external stimuli, and do not refer to matters removed in time and space. Matters of relevance at a distance, such as distant food sources, tend to be indicated to other individuals by body language instead, for example wolf activity before a hunt, or the information conveyed in honeybee dance language. It is therefore unclear to what extent utterances are automatic responses and to what extent deliberate intent plays a part.
3. Human language is largely learned culturally, while animal communication systems are known largely by instinct.
4. In contrast to human language, animal communication systems are usually not able to express conceptual generalizations. (Cetaceans and some primates may be notable exceptions).
5. Human languages combine elements to produce new messages (a property known as **creativity**). One factor in this is that much human language growth is based upon conceptual ideas and hypothetical structures, both being far greater capabilities in humans than animals. This appears far less common in animal communication systems, although current research into animal culture is still an ongoing process with many new discoveries.

A recent and interesting area of development is the discovery that the use of syntax in language, and the ability to produce "sentences", is not limited to humans either. The first good evidence of syntax in non-humans, reported in 2006, is from the greater spot-nosed monkey (*Cercopithecus Nictitans*) of Nigeria. This is the first evidence that some animals can take discrete units of communication, and build them up into a sequence which then carries a different meaning from the individual "words":

The putty-nosed monkeys have two main alarm sounds. A sound known onomatopoeiacally as the 'pyow' warns against a lurking leopard, and a coughing sound that scientists call a 'hack' is used when an eagle is hovering nearby.
"Observationally and experimentally we have demonstrated that this sequence [of up to three 'pyows' followed by up to four 'hacks'] serves to elicit group movement... the 'pyow-

hack' sequence means something like "let's go!" [a command telling others to move]... The implications are that primates at least may be able to ignore the usual relationship between an individual alarm call, and the meaning it might convey under certain circumstances... To our knowledge this is the first good evidence of a syntax-like natural communication system in a non-human species."

Chapter 2

Animal Training

Animal trainer

Early 20th Century animal trainer and a leopard.

	Occupation
Names	animal trainer
Type	performing arts
Activity sectors	social science, busking, circus, show business
	Description
Competencies	skills, manual dexterity
Education required	
Fields of employment	police, education, entertainment

Animal training refers to teaching animals specific responses to specific conditions or stimuli. Training may be for the purpose of companionship, detection, protection, entertainment or all of the above.

An **animal trainer** may use reinforcement or punishment to condition an animal's responses. Some animal trainers may have a knowledge of the principles of behavior analysis and operant conditioning, but there are many ways to train animals and no legal requirements or certifications are required.

Formation

The certification bodies that do exist (in some, not all, countries) do not share consistent goals or requirements so it can be difficult to tell what kind of training a trainer has had to do his or her job. The United States does not require animal trainers to have any kind of certification or psychological screening.

The type of training is often determined by the trainer's motivation, background, and psychological make-up. An individual training a seeing eye dog, for example, will have a different approach and end-goal than an individual training a wild animal to do tricks in a circus.

Ideally, animal trainers will try to use positive reinforcement (follow a desired behavior with something worthwhile to the animal and the behavior will increase) and negative punishment (withdraw something the animal wants when he performs undesirable behaviors). Traditional trainers often rely on positive punishment (follow an undesirable behavior with a punishment to reduce the rate of the behavior) and negative reinforcement (withdraw an undesirable stimulus when the animal performs the desirable behavior).

Service animals

Morphy, an Orangutan with his toy, a horse, on a walk with his keeper in a traveling circus.

Service animals, such as assistance dogs, capuchin monkeys and horses, are trained to utilize their sensory and social skills to bond with a human and help that person to offset a disability in daily life. The use of service animals, especially dogs, is an ever-growing field, with a wide range of special adaptations.

In the United States, selected inmates in prisons are used to train service dogs. In addition to adding to the short-supply of service animals, such programs have produced benefits in improved socialization skills and behavior of inmates.

Film and television

Organizations such as the American Humane Association monitor the use of animals such as those used in the entertainment industry, but they do not monitor their training. The Patsy Award (Picture Animal Top Star of the Year) was originated by the Hollywood office in 1939. They decided to honor animal performers after a horse was killed in an on-set accident during the filming of the Tyrone Power film *Jesse James*.

The award now covers both film and television and is separated into four categories: canine, equine, wild and special. The special category encompasses everything from goats to cats to pigs. One famous animal trainer, Frank Inn, received over 40 Patsy awards.

Patience and repetition are critical components of successful animal training. Inn's most famous animal was Higgins, who came from the Burbank, California Animal Shelter. Inn began training animals while incapacitated due to an automobile accident. Higgins starred in the *Petticoat Junction* sitcom in the 1960s and the first two *Benji* films in 1974 and 1977.

Lifetime bonds are often made between trainers and animals. The ashes of Higgins were buried with trainer Inn when he died in 2002.

Companion animals

Dogs

A trained dog competing in dog agility.

Basic obedience training tasks for dogs include walking on a leash, attention, housebreaking, nonaggression, and socialization with humans or other pets. Dogs are also trained for many other activities, such as dog sports, service dogs, and other working dog tasks.

Positive reinforcement for dogs can include primary reinforcers such as food, or social reinforcers such as vocal ("good boy") or tactile (stroking) ones. Positive punishment, if used at all, can be physical, such as pulling on a leash or spanking, or may be vocal ("bad

dog"). Bridges to positive reinforcement include vocal cues, whistling, and dog whistles, as well as clickers used in clicker training, a method popularized by Karen Pryor. Negative reinforcement may also be used. Punishment is also a tool, including withholding of food or physical discipline.

Horses

The primary purpose of training horses is to socialize them to be around humans, teach them to behave in a manner that makes them safe for humans to handle, and, as adults to carry a rider under saddle or to be driven in order to pull a vehicle. As prey animals, much effort must be put into training horses to overcome its natural flight or fight instinct and accept handling that would not be natural for a wild animal, such as willingly going into a confined space, or having a predator (a human being) sit on its back. As training advances, some horses are prepared for competitive sports, up to the Olympic games, where horses are the only animal athlete that is used at the Olympics. All equestrian disciplines from horse racing to draft horse showing require the horse to have specialized training.

A human with a trained horse and a trained Peregrine Falcon

Unlike dogs, horses are not motivated as strongly by positive reinforcement rewards as they are motivated by other operant conditioning methods such as the release of pressure as a reward for the correct behavior, called negative reinforcement. Positive reinforcement techniques such as petting, kind words, rewarding of treats, and clicker training have some benefit, but not to the degree seen in dogs and other predator species. Punishment of horses is effective only to a very limited degree, usually a sharp command or brief physical punishment given within a few seconds of a disobedient act. Horses do not correlate punishment to a specific behavior unless it occurs immediately. They do, however, have a remarkably long memory, and once a task is learned, it will be retained for a very long time. For this reason, poor training or allowing bad habits to be learned can be very difficult to remedy at a later date.

Birds

Typical training tasks for companion birds include perching, non-aggression, halting feather-picking, controlling excessive vocalizations, socialization with household members and other pets, and socialization with strangers. The large parrot species frequently have lifespans that exceed that of their human owners, and they are closely bonded to their owners. In general, parrot companions usually have clipped wings, which facilitates socialization and controlling aggression and vocalizations. Some birds of prey are trained to hunt, an ancient art known as falconry or hawking. In China the practice of training Cormorants to catch fish has gone on for over 1,200 years.

Chickens

Chicken on a skateboard

Training chickens has become a way for trainers of other animals (primarily dogs) to perfect their training technique. Bob Bailey, formerly of Animal Behavior Enterprises and the IQ Zoo, teaches chicken training seminars where trainers teach poultry to discriminate between shapes, to navigate an obstacle course and to chain behaviors together. Chicken training is done using operant conditioning, using a clicker and chicken feed for reinforcement. The training of chickens has become a popular event for dog trainers. Trained chickens may be confined to a fiberglas box where they play Tic-Tac-Toe against humans for a fee.

Fish

Fish can also be trained. For example, a goldfish may swim toward its owner and follow him as he walks through the room, but will not follow anyone else. The fish may swim up and down, signaling the owner to turn on its aquarium light when it is off, and it will skim the surface until its owner feeds it. Pet goldfish have also been taught to perform more complicated tasks, such as doing the limbo and pushing a miniature soccer ball into a net.

Wild animals

Wild animal training

Wild animals may also be trained, such as bears, lions, tigers, leopards, or other big cats. The Ursari Romani people were specialized in bear training, although they sometimes also used Old World monkeys. Later on, the German animal merchant Carl Hagenbeck, used brown bears and lions in his shows.

Zoological parks

Animals in public display are sometimes trained for educational, entertainment, management, and husbandry behaviors. Educational behaviors may include species-typical behaviors under stimulus control such as vocalizations. Entertainment may include display behaviors to show the animal, or simply arbitrary behaviors. Management includes movement, such as following the trainer, entering crates, or moving from pen to pen, or tank-to-tank through gates. Husbandry behaviors facilitate veterinary care, and can include desensitization to various physical examinations or procedures (such as cleaning, nail clipping, or simply stepping onto a scale voluntarily), or the collection of samples (e.g. biopsy, urine). Such voluntary training is important for minimizing the frequency with which zoo collection animals must be anesthetized or physically restrained.

Marine mammal parks

Many marine mammals are trained for entertainment such as bottlenose dolphins, killer whales, belugas, sea lions, and others. In a public display situation, the audience's attention is focused on the animal, rather than the trainer; therefore the discriminative stimulus is generally gestural (a hand sign) and sparse in nature. Unobtrusive dog whistles are used as bridges, and positive reinforcers are either primary (food) or tactile (rub downs), and not vocal. However, pinnipeds and mustelids (sea lions, seals, walruses, and otters) can hear in our frequency, so most of the time they will receive vocal reinforcers during shows and performances. The shows are turned into more of a play production because of this, instead of just a run through of behaviors like cetaceans generally do in their shows. Guests can often hear these vocal reinforcers when attending a Sea World show. During the Clyde and Seamore show, the trainers may say something like: "Good grief, Clyde!" or "Good job, Seamore". The trainers substitute the word "good" in the place of food or rubdowns when teaching a specific behavior to the animals so that the animals no longer need constant feeding as praise for achieving the appropriate behavior.

Methods

The Ursar, drawing by Theodor Aman

Animal training is generally performed in adherence to the theory of operant conditioning, although modern training methods frequently utilize tools not included in the original Skinnerian conception.

Two primary types of training philosophies are those that emphasize *positive reinforcement*, and those that use *negative reinforcement*, which is not to be confused with punishment. Certain subfields of animal training tend to also have certain philosophies and styles, for example fields such as companion bird training, hunting bird training, companion dog training, show dog training, dressage horse training, mahout elephant training, circus elephant training, zoo elephant training, zoo exotic animal training, marine mammal training. The degree of trainer protection from the animal may also vary. The variety of tasks trained may also vary, and can range from entertainment, husbandry (veterinary) behaviors, physical labor or athleticism, habituation to averse stimuli, interaction (or non-interaction) with other humans, or even research (sensory, physiological, cognitive).

Training also may take into consideration the natural social tendencies of the animal species (or even breed), such as predilections for attention span, food-motivation, dominance hierarchies, aggression, or bonding to individuals (conspecifics as well as humans). Consideration must also be given to practical aspects on the human side such as the ratio of the number of trainers to each animal. In some circumstances one animal may have multiple trainers, in others, a trainer might attend simultaneously to many animals in

a training session. Sometimes training is accomplished with a single trainer working individually with a single animal.

Other important issues related to the methods of animal training are: operant conditioning, stimulus control, SD (discriminative stimulus), desensitization, chaining, bridge, and the s-delta.

List of notable animal trainers

Known for their influence on the circus:

- Nadezhda Durova (1783–1866) founded the Durov family of performers in the Russian circus.
- Anatoly Durov (1887–1928) Russian circus animal trainer and founder of the Durov Animal Theater in Moscow.
- Carl Hagenbeck (1844–1913) a merchant of wild animals who introduced "natural" animal enclosures.
- Gunther Gebel-Williams (1934–2001) trained animals for the Ringling Bros. and Barnum & Bailey Circus.
- Mike Baray, (born 1938) animal trainer, performed with Sarrasani, Jean Richard, Bouglione, occasional performer with E. Raluy's Circus Williams.
- Martin Lacey, (born 1947), animal trainer, owner of the Great British Circus, trained most of the tigers used in the ESSO TV advertisements in the 1970s.
- Martin Lacey, Jr., (born 1977), son of Martin, an animal trainer and performer with Circus Krone in Munich.
- Alex Lacey, also son of Martin, animal trainer and performer.

Known for scientific research:

- Ivan Pavlov (1849–1946) studied the psychology of animal training and described the phenomenon of classical conditioning.
- Karen Pryor (1932–), used applied operant conditioning with marine mammals and dog clicker training

Known for work in television and film:

- Nell Shipman (1892–1970) a Canadian film maker in early Hollywood.
- Frank Inn (1916–2002) trained dogs used in the Benji series.
- Brothers Frank Weatherwax and Rudd Weatherwax trained the collie Pal who portrayed the first Lassie.
- Ralph Helfer
- Dr. Bhagavan Antle, trained exotic animals for movies including Jungle Book, Dr. Dolittle and Mighty Joe Young
- Mathilde DeCagny trained Moose, best known as Eddie Crane on the television sitcom Frasier.

Other:

- Felix Ho, professional dog behaviorist, international dog sport championship competitor and judge
- Warren Eckstein, animal trainer, author and radio personality.
- Victoria Stilwell, dog trainer, author and television presenter.
- Dave Salmoni, animal trainer, entertainer, and producer.

Chapter 3

Animal Language

Animal language is the modeling of human language in non human animal systems. While the term is widely used, researchers agree that animal languages are not as complex or expressive as human language.

Some researchers including the linguist Charles Hockett, who proposed a list of design features of Human Language, argue that there are significant differences separating human language from animal communication even at its most complex, and that the underlying principles are not related. Accordingly, Thomas A. Sebeok has proposed not to use the term 'language' in case of animal sign systems.

Others argue that an evolutionary continuum exists between the communication methods these animals use and human language. Examining this continuum could help explain how humanity evolved its incredibly sophisticated proficiency for language.

Aspects of human language

Human and ape, in this case Claudine Andre with a bonobo.

The following properties of human language have been argued to separate it from animal communication:

- *Arbitrariness:* There is no rational relationship between a sound or sign and its meaning. (There is nothing intrinsically "housy" about the word "house". i.e. *symbolism*)
- *Cultural transmission:* Language is passed from one language user to the next, consciously or unconsciously.
- *Discreteness:* Language is composed of discrete units that are used in combination to create meaning.
- *Displacement:* Languages can be used to communicate ideas about things that are not in the immediate vicinity either spatially or temporally, or both.
- *Duality:* Language works on two levels at once, a surface level and a semantic (meaningful) level.
- *Metalinguistics:* Ability to discuss language itself.
- *Productivity:* A finite number of units can be used to create an indefinitely large number of utterances.

Research with apes, like that of Francine Patterson with Koko or Herbert Terrace with Nim Chimpsky, suggested that apes are capable of using language that meets some of

these requirements. However, no experiment has shown a non-human being to be proficient in all of these areas.

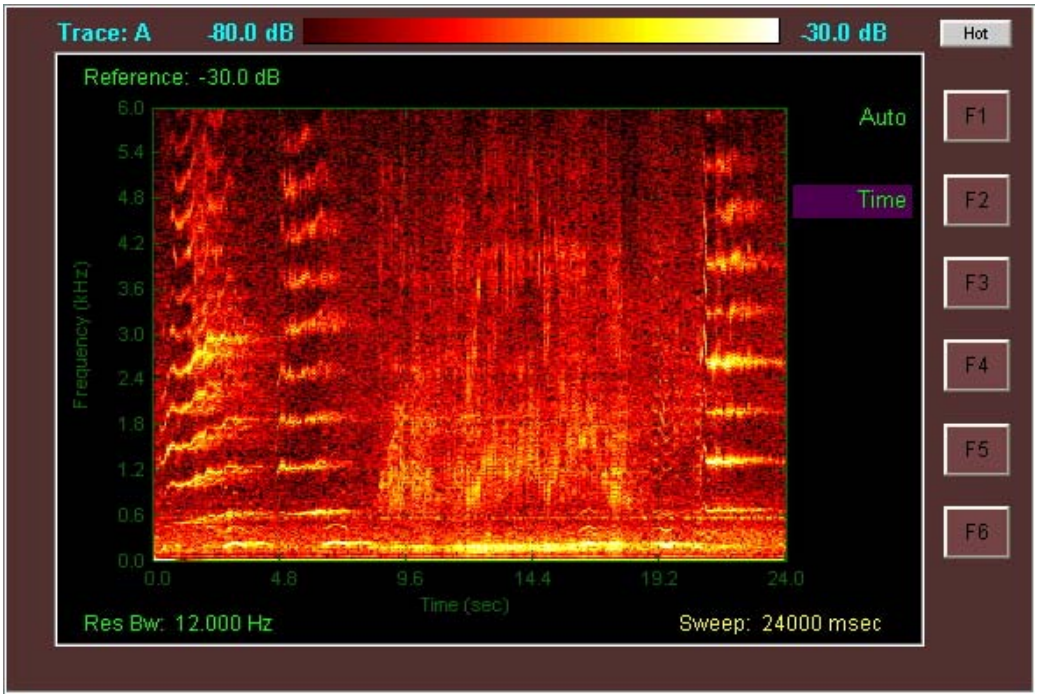
In the wild chimpanzees have been seen "talking" to each other, when warning about approaching danger. For example, if one chimpanzee sees a snake, he makes a low, rumbling noise, signalling for all the other chimps to climb into nearby trees. In this case, the chimpanzees' communication is entirely contained to an observable event, demonstrating a lack of displacement.

Arbitrariness has been noted in meerkat calls; bee dances show elements of spatial displacement; and cultural transmission has possibly occurred between the celebrated bonobos Kanzi and Panbanisha.

Human language may not be completely "arbitrary". Some research has shown that almost all humans naturally demonstrate limited crossmodal perception (e.g. synesthesia), as illustrated by the Kiki and Booba study.

Claims that animals have language skills akin to humans however, are extremely controversial. As Pinker illustrates in his book the "The Language Instinct", claims that chimpanzees can acquire language are exaggerated and rest on very limited or specious data.

Non-Primates: Studied examples



Spectrogram of Humpback Whale vocalizations. Detail is shown for the first 24 seconds of the 37 second recording Humpback Whale "Song".

The most studied examples of animal languages are:

- Bee dance - used to communicate direction and distance of food source in many species of bees.
- Bird songs - songbirds can be very articulate. African Grey Parrots are famous for their ability to mimic human language, and at least one specimen, Alex, appeared able to answer a number of simple questions about objects he is presented with. Parrots, hummingbirds and songbirds- display vocal learning patterns.
- Whale songs - Two groups of whales, the Humpback Whale and the subspecies of Blue Whale found in the Indian Ocean, are known to produce the repetitious sounds at varying frequencies known as whale song. Male Humpback Whales perform these vocalizations only during the mating season, and so it is surmised the purpose of songs is to aid sexual selection. Humpbacks also make a sound called the feeding call. This is a long sound (5 to 10 s duration) of near constant frequency. Humpbacks generally feed cooperatively by gathering in groups, swimming underneath shoals of fish and all lunging up vertically through the fish and out of the water together. Prior to these lunges, whales make their feeding call. The exact purpose of the call is not known, but research suggests that fish react to it. When the sound was played back to them, a group of herring responded to the sound by moving away from the call, even though no whale was present.
- Prairie dog language: Dr. Slobodchikoff studied prairie dog communication and made the following discoveries. His current findings are that prairie dogs have:
    - different alarm calls for different species of predators;
    - different escape behaviors for different species of predators;
    - transmission of semantic information, in that playbacks of alarm calls in the absence of predators lead to escape behaviors that are appropriate to the type of predator which elicited the alarm calls;
    - alarm calls containing descriptive information about the general size, color, and speed of travel of the predator.
- Caribbean Reef Squid have been shown to communicate using a variety of color, shape, and texture changes. Squid are capable of rapid changes in skin color and pattern through nervous control of chromatophores. In addition to camoflauge and appearing larger in the face of a threat, squids use color, patterns, and flashing to communicate with one another in various courtship rituals. Caribbean Reef Squid can send one message via color patterns to a squid on their right, while they send another message to a squid on their left.

Comparison of the term with "animal communication"

It is worth distinguishing "animal language" from "animal communication", no matter how complex the latter may be. In general the term "animal language" is reserved for the modeling of human language in animal systems; though there is some comparative interchange in certain cases (e.g. Cheney & Seyfarth's vervet monkey call studies). Thus "animal language" typically does not include bee dancing, bird song, whale song, dolphin signature whistles, prairie dogs, nor the communicative systems found in most social

mammals. The features of language as listed above are a dated formulation by Hockett in 1960. Through this formulation Hockett made one of the earliest attempts to break down features of human language for the purpose of applying Darwinian gradualism. Although an influence on early animal language efforts (see below), is today not considered the key architecture at the core of "animal language" research.

"Clever Hans", an Orlov Trotter horse that was claimed to have been able to perform arithmetic and other intellectual tasks.

Animal Language results are controversial for several reasons. In the 1970s John Lilly was attempting to "break the code": to fully communicate ideas and concepts with wild populations of dolphins so that we could "speak" to them, and share our cultures, histories, and more. This effort failed. The very early [chimpanzee] work was with chimpanzee infants raised as if they were human; a test of the nature vs. nurture hypothesis. Chimpanzees have a laryngeal structure very different from that of humans, as well as no voluntary control of their breathing. This combination made it very difficult for the chimpanzees to reproduce the vocal intonations required for human language. Researchers eventually moved towards a gestural (sign language) modality, as well as "keyboard" devices laden with buttons adorned with symbols (known as "lexigrams") that the animals could press to produce artificial language. Other chimpanzees learned by observing human subjects performing the task. This latter group of researchers studying chimpanzee communication through symbol recognition (keyboard) as well as through the use of sign language (gestural), are on the forefront of communicative breakthroughs

in the study of animal language, and they are familiar with their subjects on a first name basis: Sarah, Lana, Kanzi, Koko, Sherman, Austin and Chantek.

Perhaps the best known critic of "Animal Language" is Herbert Terrace. Terrace's 1979 criticism using his own research with the chimpanzee Nim Chimpsky was scathing and basically spelled the end of animal language research in that era, most of which emphasized the production of language by animals. In short, he accused researchers of over-interpreting their results, especially as it is rarely parsimonious to ascribe true intentional "language production" when other simpler explanations for the behaviors (gestural hand signs) could be put forth. Also, his animals failed to show generalization of the concept of reference between the modalities of comprehension and production; this generalization is one of many fundamental ones that are trivial for human language use. The simpler explanation according to Terrace was that the animals had learned a sophisticated series of context-based behavioral strategies to obtain either primary (food) or social reinforcement, behaviors that could be over-interpreted as language use.

In 1985 during this anti-Animal Language backlash, Louis Herman published an account of artificial language in the bottlenosed dolphin in the journal Cognition. A major difference between Herman's work and previous research was his emphasis on a method of studying language comprehension only (rather than language comprehension and production by the animal(s)), which enabled rigorous controls and statistical tests, largely because he was limiting his researchers to evaluating the animals' physical behaviors (in response to sentences) with blinded observers, rather than attempting to interpret possible language utterances or productions. The dolphins' names here were Akeakamai and Phoenix. Irene Pepperberg used the vocal modality for language production and comprehension in an African Grey Parrot named Alex in the verbal mode, and Sue Savage-Rumbaugh continues to study Bonobos such as Kanzi and Panbanisha. R. Schusterman duplicated many of the dolphin results in his California Sea Lions ("Rocky"), and came from a more behaviorist tradition than Herman's cognitive approach. Schusterman's emphasis is on the importance on a learning structure known as "equivalence classes."

However, overall, there has not been any meaningful dialog between the linguistics and animal language spheres, despite capturing the public's imagination in the popular press. Also, the growing field of language evolution is another source of future interchange between these disciplines. Most primate researchers tend to show a bias toward a shared pre-linguistic ability between humans and chimpanzees, dating back to a common ancestor, while dolphin and parrot researchers stress the general cognitive principles underlying these abilities. More recent related controversies regarding animal abilities include the closely linked areas of Theory of mind, Imitation (e.g. Nehaniv & Dautenhahn, 2002), Animal Culture (e.g. Rendell & Whitehead, 2001), and Language Evolution (e.g. Christiansen & Kirby, 2003).

Chapter 4

Talking Animal

A **talking animal** or **speaking animal** refers to any form of non-human animal which can produce sounds (or gestures) resembling those of a human language. Many species or groups of animals have developed forms of Animal Communication Systems which, to some, can look like a non-verbal language although it is not due to a lack of grammar, syntax, recursion, and displacement. Studies in animal cognition have been arguably successful in teaching some animals speech or sign, similar to but not actually sign language with Koko the gorilla. Koko was unable, however, to break-away from the here-and-now (displacement) which is just one of the many hallmarks of language Koko was unable to achieve.

A very similar perspective of study is talking animals in fiction.

On imitation and understanding

Clever Hans performs

The term may have a nearly literal meaning, by referring to animals which can imitate human speech, though not necessarily possessing an understanding of what they may be mimicking. The most common example of this would be parrots, many of which repeat many things nonsensically through exposure. It is an anthropomorphism to call this human speech, as it has no semantic grounding.

Clever Hans was a horse that was claimed to have been able to perform arithmetic and other intellectual tasks. After formal investigation in 1907, psychologist Oskar Pfungst demonstrated that the horse was not actually performing these mental tasks, but was watching the reaction of his human observers. The horse was responding directly to involuntary cues in the body language of the human trainer, who had the faculties to solve each problem, with the trainer unaware that he was providing such cues.

On formality of animal language

A "formal language" requires a communication with a syntax as well as semantics. It is not simply sufficient for one to communicate information, or even use symbology to communicate ideas. It has yet to be demonstrated that any animal species has developed a formal language, or been able to learn a formal language.

Researchers have attempted to teach great apes (Gorillas, Chimpanzees, and Bonobos) spoken language with poor results, and sign language with significantly better results. However, even the best communicating great ape has shown an inability to grasp the idea of syntax and grammar, instead communicating at best at the same level as a pidgin language in Humans. They are expressive and communicative, but lack the formality that remains such a rarity in human speech.

Reported cases by species

Birds

Research done by Dr. Irene Pepperberg strongly suggests that parrots are capable of speaking in context and with intentional meaning. Pepperberg's star pupil, Alex the African Grey Parrot, had demonstrated the ability to assemble words out of letters—in other words, to read and spell.

Dogs

- Odie, the talking pug that will say a convincing "I love you" on demand has made appearances on Letterman and on The Montel Show and on AOL's "T.V. top 5".
- Paranormal researcher Charles Fort wrote in his book *Wild Talents* (1932) of several alleged cases of dogs that could speak English. Fort took the stories from contemporary newspaper counts, but they are unverifiable at this late date.
- Internet phenomenon, Mishka the talking Husky, has been trained to say certain phrases, most notably "I love you", and has videos of her saying phrases like "Hello", "NOOOOO", and also has learned to sing through the help of an iPad.

Cats

- A talking cat called Cingene (Gypsy) made Turkish television news on March 20, 1993. The two year old black cat managed to say at least seven words on television.

- A more recent Internet phenomenon is the case of a cat who was videotaped speaking recognizable human words and phrases such as "Oh my dog," "Oh Don piano", and "All the live long day." Footage of this cat, nicknamed "Oh Long Johnson" from one of the phrases spoken, was featured on *America's Funniest Home Videos* in 1998, and a longer version of the clip (which revealed the animal was speaking to another cat) was later aired in the UK. Clips from this video are prevalent on YouTube.

Tiggy the talking cat at home

- Another recent Internet phenomenon is the cat named Tiggy. Tiggy the Talking Cat (1990 - June 23rd 2010) was a unique cat who made a unique talking like noise. Tiggy is from Grimsby, England and was born in 1990; she died on Wednesday 23rd June 2010 at the age of 20.

Tiggy started making this strange noise at around the age of 8 and would only make it when she was alone and out of sight. After years of hearing the noise and never seeing it being made, in May 2007 out of curiosity as to what Tiggy looked like when making this noise (and also to show it to friends who didn't believe the cat could talk) her owners set up a video camera and left it on record in a spot where Tiggy regularly "spoke", eventually footage was captured of Tiggy sitting in the hallway making the noise which sounded like "Hello" four times. This video was uploaded to youtube and was the first ever Tiggy video. In the first Tiggy video she was quite a distance from the camera so the owners tried again, the second attempt was a great success with Tiggy walking up to the camera and talking for around 20 seconds. The video captured the second time was also uploaded to YouTube along with the first video and it became a huge hit acquiring millions of views on YouTube turning Tiggy into an internet celebrity. A further video was then filmed in the same house and uploaded to Youtube in June, no more videos of tiggy appeared on YouTube until August 2009 when videos of Tiggy playing and talking were uploaded. Footage of Tiggy has made its way on to several TV Shows in Both the USA and the U.K. Tiggy's first T.V appearance was in the U.K. on channel 4's Richard and Judy show during the "funny five" segment of the show which consisted of 5 funny

videos from the internet being nominated by a different celebrity guest each week, viewers then voted for their favorite online. Tiggy won the Funny Five competition for the 2007 series of the show and the crew visited Tiggy in her home and presented her with a plaque signed by presenters Richard and Judy, it was Tiggys appearance on this show which helped to make her popularity on YouTube so large with her being featured on the main YouTube page due to the huge amount of views the TV appearances caused. Tiggy has then gone on to appear on a number of shows all over the world including: CBBC's Chute, BBC's Lenny Henry.tv, America's County Fried Home Videos, The Ellen DeGeneres and various shows on Animal Planet.

- Miles v. City Council of Augusta, Georgia

Other

- Hoover, a harbor seal that would vocally repeat common phrases he heard around his exhibit at the New England Aquarium, including his name. He appeared in publications like *Reader's Digest* and *The New Yorker* and television programs like *Good Morning America*.

- Gef the talking mongoose was an alleged talking animal who inhabited a small house on the Isle of Man, off the coast of Great Britain. Opinion is divided on whether Gef was a poltergeist, a strange animal or cryptid, a hoax, or something else. Most doubt the case happened at all as told.

- Batyr (1969–1993), an elephant from Kazakhstan, was widely published as having a vocabulary of more than 20 phrases. Recordings of Batyr saying "Batyr is good","Batyr is hungry" and using words such as "drink" and "give" was played on Kazakh state radio in 1980.

- Kosik (1990—), an elephant able to imitate some Korean words

Chapter 5

Human-Animal Communication

Human-animal communication is easily observed in everyday life. The interactions between pets and their owners, for example, reflect a form of spoken, while not necessarily verbal, dialogue. A dog being scolded does not need to understand every word of its admonishment, but is able to grasp the message by interpreting cues such as the owner's stance, tone of voice, and body language. This communication is two-way, as owners can learn to discern the subtle differences between barks and meows … one hardly has to be a professional animal trainer to tell the difference between the bark of an angry dog defending its home and the happy bark of the same animal while playing. Communication (often nonverbal) is also significant in equestrian activities such as dressage.

Word repetition in birds

Although the word repetition skills observed in some birds (most famously parrots) should not be mistaken for lingual communication, this tendency has nonetheless influenced fictional portrayals of animal communication, as sentient talking parrots and similar birds are common in children's fiction, such as the talking, loud-mouth parrot Iago of Disney's *Aladdin*. Bruce Thomas Boehner's book *Parrot Culture: Our 2,500-Year-Long Fascination with the World's Most Talkative Bird* explores this issue thoroughly.

The next level: language

Achieving a deeper level of communication between animals and humans has long been a goal of science. Perhaps the most famous example of recent decades has been Koko, a gorilla who is supposedly able to communicate with humans using a system based on American Sign Language with a "vocabulary" of over 1000 words.

John Lilly and Cetacean Communication

In the 1960s, John Lilly, M.D., prolific writer and explorer of consciousness via the isolation tank (his invention) and LSD, and contemporary and associate of Timothy

Leary, began experiments in the Virgin Islands aiming to establish meaningful communication between humans and the bottlenose dolphin (*Tursiops truncatus*). Lilly financed, mostly personally, a human-dolphin cohabitat, a house on the ocean's shore that contained an area that was partially flooded and allowed a human and dolphin to live together in the same space, sharing meals, play, language lessons, and even sleep.

Two experiments of this sort are explained in detail in Lilly's popular books. The first experiment was more of a test run to check psychological and other strains on the human and cetacean participants, determining the extent of the need for other human contact, dry clothing, time alone, and so on. Despite tensions after several weeks, the experimenter, Margaret C. Howe, agreed to a two-and-a-half month experiment, living isolated with 'Peter' dolphin.

A basic outline of Peter dolphin's linguistic progress is as follows: early lessons involved mostly noise and interruptions from Peter during English lessons, and a food reward of fish was necessary for him to 'attend class.' After several weeks, a concerted effort by Peter to imitate the instructor's speech was evident, and human-like sounds were apparent, and recorded. More interesting was the dolphin's immediate grasp of basic semantics, such as the different aural indicators for 'ball' and 'doll' and other toys present in the aquarium. Peter was able to perform tasks such as retrieval on the (aurally) indicated object without fail. Later in the project the dolphin's ability to process linguistic syntax was made apparent, in that Peter could distinguish between the commands (e.g., only) "Bring the ball to the doll," and "Bring the doll to the ball." This ability not only demonstrates the bottlenose dolphin's grasp of basic grammar, but also implies the dolphins' own language must include some such syntactical rules. The correlation between length and 'syllables' (bursts of the dolphin's sound) with the instructor's speech also went from essentially zero at the beginning of the session to almost a perfect correlation by its completion. I.e., a sentence spoken by the instructor involving 35 syllables and lasting 8 seconds would be met with an 8-second burst of sound from Peter dolphin involving 35 easily-discernible 'syllables' or bursts of sound.

Much later, experiments by Louis Herman, a former collaborator and student of Lilly's, demonstrated the crossmodal perceptual ability of dolphins. Dolphins typically perceive their environment through sound waves generated in the melon of their skulls, through a process known as echolocation (similar to that seen in bats, though the mechanism of production is different). The dolphin's eyesight however is also fairly good, even by human standards, and Herman's research found that any object, even of complex and arbitrary shape, identified either by sight or sound by the dolphin, could later be correctly identified by the dolphin with the alternate sense modality with almost 100 per cent accuracy, in what is classically known in psychology and behaviorism as a match-to-sample test. The only errors noted were presumed to have been a misunderstanding of the task during the first few trials, and not an inability of the dolphin's perceptual apparatus. This capacity is strong evidence for abstract and conceptual thought in the dolphin's brain, wherein an idea of the object is stored and understood not merely by its sensory properties; such abstraction may be argued to be of the same kind as complex language, mathematics, and art, and implies a potentially very great intelligence and conceptual

understanding within the brains of tursiops and possibly many other cetaceans. Accordingly, Lilly's interest later shifted to whale song and the possibility of high intelligence in the brains of large whales, and Louis Herman's research at the now misnomered Dolphin Institute in Honolulu, Hawaii, focuses exclusively on the Humpback whale.

Animal communication as entertainment

Though animal communication has always been a topic of public comment and attention, for a period in history it surpassed this and became sensational popular entertainment. From the late 18th century through the mid 19th century, a succession of "learned pigs" and various other animals were displayed to the public in for-profit performances, boasting the ability to communicate with their owners (often in more than one language), write, solve math problems, and the like. One poster dated 1817 shows a group of "Java sparrows" who are advertised as knowing *seven languages*, including Chinese and Russian. One pig of the era was so famous that it performed for royalty, and an obituary upon its death claimed that it made more money than any actor or actress of the same time; a fact that, whether strictly true, was at least believable to contemporary readers. By the late 1840s the fad had died down considerably. While the occasional appearance by a "learned" animal continued into the radio and television eras, it was by then generally understood that feats such as using cards to spell words, barking or tapping a hoof to solve equations, and the like were the products of training rather than actual *communication*. Though the tradition continues to this day on the "Stupid Pet Tricks" segment of Late Night with David Letterman, it seems likely that the era of trained pigs entertaining the crowned heads of Europe are over.

BowLingual

One real-world example of a technological means of one-way human-animal communication is BowLingual, a Japanese device which claims to translate barks from dozens of different breeds of dogs, including mixed-breeds. Based largely on Dr. Matsumi Suzuki's Animal Emotion Analysis System developed at Japan Acoustic Laboratory, the device outputs one of 200 phrases (grouped into six different moods), supposedly reflecting "meaning" of the dog's bark. The device was apparently successful enough in Japan to be brought to the American market, and was even named one of 2002's best inventions by Time Magazine. However, reports of the BowLingual's accuracy have been mixed at best, with popular product-review website Epinions giving it a low 1.5 stars average.

Human-animal communication in culture

The concept of human-animal communication has existed in culture for longer than recorded history, being an element of many myths and folk tales of numerous cultures, and continues in modern popular entertainment. Here we, lists some examples of this, divided by the method of communication (magical/supernatural, innate natural ability, technological, and unspecified/misc).

Magic and supernatural

- In many fantasy role playing games, Druid characters are able to speak with animals through the use of a spell. The Dungeons & Dragons version of this spell is called "Speak with Animals".
- Eliza Thornberry of Nickelodeon's animated TV series The Wild Thornberrys can speak with animals after a spell is placed on her by an African tribal shaman.
- In the Harry Potter series of books, Harry is a parselmouth (able to speak with snakes in their own language, parseltongue, which sounds like hissing and spitting to the ears of those without this (apparently hereditary) skill).
- In The Immortals series of books, Veralidaine Sarrasri (Daine) has "wild magic" which enables her to communicate with animals. After being trained in the use of her wild magic, she learns to enter the minds of animals and shapeshift.

Innate ability

- Cypher, real name Douglas Ramsey, of Marvel Comics' The New Mutants, has a "mutant" ability to instantly translate any language he hears or sees, including animal languages.
- Doctor Dolittle, subject of a series of children's books by Hugh Lofting as well as various film and stage adaptions, is a doctor whose ability to speak with animals makes him successful in dealing with animals but closes him off from most humans.

Technological

- In Star Trek, the communicator badges worn by Starfleet crew members allow direct translation between humans and various sentient and semi-sentient aliens and creatures, though it is undetermined whether they work with "dumb" animals. It is presumed that this is not possible, as the relatively few domesticated animals seen on the show do not appear to converse with their owners (Data's cat, and Archer's beagle, for example). The council-chamber of the Xindi accommodates her Aquatic members in a water-tank.
- In issue 285 of DC's Detective Comics, Martian Manhunter fights a brigade of "Martian mandrills" which were being manipulated by villains through the use of a communicator device stolen from the mandrills' rocket.
- On the television cartoon Krypto the Superdog, Krypto has an "intergalactic communicator" device in his dog tag, which allows Kevin Whitney to communicate with him. The device is technology from Krypton, Superman's homeworld.

Unspecified and miscellaneous

- In Hergé's *Tintin* comics, Tintin's dog Snowy is sentient and able to "think". Although his thoughts are written in word bubbles rather than thought bubbles, it is generally assumed that the human characters cannot understand him. Once, in

the early volume *Tintin in America*, Tintin was able to directly understand Snowy. Hergé did not elaborate on why this was so; presumably it was used simply to advance the plot and not to bog down the story with a "talking dog" element.

- The American television show Mr. Ed centers around a horse's ability to communicate with his owner, Wilbur. The plot of this television series was inspired by the movie character Francis the Talking Mule.

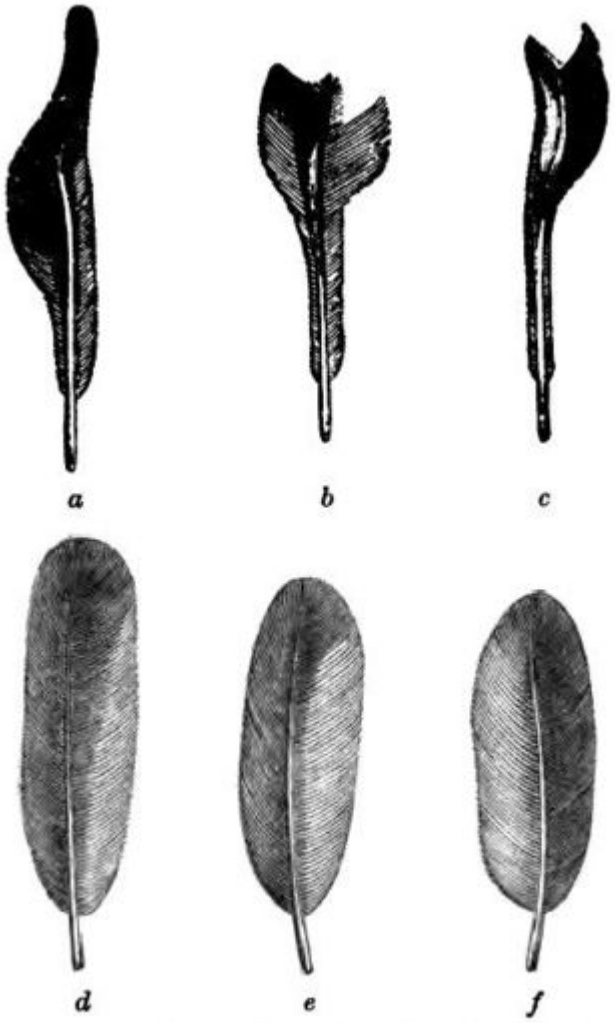
Chapter 6

Bird Vocalization

A male Blackbird (*Turdus merula*) singing. Bogense havn, Funen, Denmark.

Bird vocalization includes both bird calls and bird songs. In non-technical use, bird songs are the bird sounds that are melodious to the human ear. In ornithology and birding, (relatively complex) songs are distinguished by function from (relatively simple) calls.

Definition



Secondary wing-feathers of *Pipra deliciosa* (from Mr. Sclater, in Proc. Zool. Soc. 1860). The three upper feathers, *a*, *b*, *c*, from the male; the three lower corresponding feathers, *d*, *e*, *f*, from the female.

a. and *d*. Fifth secondary wing-feather of male and female, upper surface. *b* and *e*. Sixth secondary, upper surface. *c* and *f*. Seventh secondary, lower surface.

Wing feathers of a male Club-winged Manakin, with the modifications noted noted by P L Sclater in 1860 and discussed by Charles Darwin in 1871

The distinction between songs and calls is based upon complexity, length, and context. Songs are longer and more complex and are associated with courtship and mating, while calls tend to serve such functions as alarms or keeping members of a flock in contact. Other authorities such as Howell and Webb (1995) make the distinction based on function, so that short vocalizations such as those of pigeons and even non-vocal sounds such as the drumming of woodpeckers and the "winnowing" of snipes' wings in display flight are considered songs. Still others require song to have syllabic diversity and temporal regularity akin to the repetitive and transformative patterns which define music.

It is generally agreed upon in birding and ornithology which sounds are songs and which are calls, and a good field guide will differentiate between the two.

Bird song is best developed in the order Passeriformes. Most song is emitted by male rather than female birds. Song is usually delivered from prominent perches although some species may sing when flying. Some groups are nearly voiceless, producing only percussive and rhythmic sounds, such as the storks, which clatter their bills. In some manakins (Pipridae), the males have evolved several mechanisms for mechanical sound production, including mechanisms for stridulation not unlike those found in some insects.

The production of sounds by mechanical means as opposed to the use of the syrinx has been termed variously *instrumental music* by Charles Darwin, *mechanical sounds* and more recently *sonation*. The term *sonate* has been defined as the act of producing non-vocal sounds that are intentionally modulated communicative signals, produced using non-syringeal structures such as the bill, wings, tail, feet and body feathers.

Anatomy

The avian vocal organ is called the syrinx; it is a bony structure at the bottom of the trachea (unlike the larynx at the top of the mammalian trachea). The syrinx and sometimes a surrounding air sac resonate to sound waves that are made by membranes past which the bird forces air. The bird controls the pitch by changing the tension on the membranes and controls both pitch and volume by changing the force of exhalation. It can control the two sides of the trachea independently, which is how some species can produce two notes at once.

Function

Scientists hypothesize that bird song has evolved through sexual selection, and experiments suggest that the quality of bird song may be a good indicator of fitness. Experiments also suggest that parasites and diseases may directly affect song characteristics such as song rate, which thereby act as reliable indicators of health. The song repertoire also appears to indicate fitness in some species. The ability of male birds to hold and advertise territories using song also demonstrates their fitness.

Communication through bird calls can be between individuals of the same species or even across species. Birds communicate alarm through vocalizations and movements that are specific to the threat, and bird alarms can be understood by other animal species, including other birds, in order to identify and protect against the specific threat. Mobbing calls are used to recruit individuals in an area where an owl or other predator may be present. These calls are characterized by wide frequency spectra, sharp onset and termination, and repetitiveness which are common across species and are believed to be helpful to other potential "mobbers" by being easy to locate. The alarm calls of most species, on the other hand, are characteristically high-pitched making the caller difficult to locate.

Individual birds may be sensitive enough to identify each other through their calls. Many birds that nest in colonies can locate their chicks using their calls. Calls are sometimes distinctive enough for individual identification even by human researchers in ecological studies.

Many birds engage in duet calls. In some cases the duets are so perfectly timed as to appear almost as one call. This kind of calling is termed antiphonal duetting. Such duetting is noted in a wide range of families including quails, bushshrikes, babblers such as the scimitar babblers, some owls and parrots. In territorial songbirds, birds are more likely to countersing when they have been aroused by simulated intrusion into their territory. This implies a role in intraspecies aggressive competition.

Some birds are excellent vocal mimics. In some tropical species, mimics such as the drongos may have a role in the formation of mixed-species foraging flocks. Vocal mimicry can include conspecifics, other species or even man-made sounds. Many hypotheses have been made on the functions of vocal mimicry including suggestions that they may be involved in sexual selection by acting as an indicator of fitness, help brood parasites, protect against predation but strong support is lacking for any function. Many birds, and especially those that nest in cavities, are known to produce a snake like hissing sound that may help deter predators at close range.

Some cave-dwelling species, including Oilbird and Swiftlets (*Collocalia* and *Aerodramus* spp.), use audible sound (with the majority of sonic location occurring between 2 and 5 kHz) to echolocate in the darkness of caves. The only bird known to make use of infrasound (at about 20 Hz) is the western capercaillie.

The hearing range of birds is from below 50 Hz (infrasound) to above 20 kHz (ultrasound) with maximum sensitivity between 1 and 5 kHz. The range of frequencies at which birds call in an environment varies with the quality of habitat and the ambient sounds. It has been suggested that narrow bandwidths, low frequencies, low-frequency modulations, and long elements and inter-element intervals should be found in habitats with complex vegetation structures (which would absorb and muffle sounds) while high frequencies, broad bandwidth, high-frequency modulations (trills), and short elements and inter-elements may be expected in habitats with herbaceous cover. It has been hypothesized that the available frequency range is partitioned and birds call so that overlap between different species in frequency and time is reduced. This idea has been termed the "acoustic niche". Birds sing louder and at a higher pitch in urban areas, where there is ambient low-frequency noise.

Bird Language

The language of the birds has long been a topic for anecdote and speculation. That calls have meanings that are interpreted by their listeners has been well demonstrated. Domestic chickens have distinctive alarm calls for aerial and ground predators, and they respond to these alarm calls appropriately. However a language has, in addition to words, structures and rules. Studies to demonstrate the existence of language have been difficult

due to the range of possible interpretations. Research on parrots by Irene Pepperberg is claimed to demonstrate the innate ability for grammatical structures, including the existence of concepts such as nouns, adjectives and verbs. Studies on starling vocalizations have also suggested that they may have recursive structures.

The term "bird language" may also more informally refer to patterns in bird vocalizations that communicate information to other birds or other animals in general. Wilderness Awareness School groups bird vocalizations into 5 different classes, sometimes called "voices," each of which communicates different information. Companion calling is a short vocalization made between mates, parent and young, or members of a flock to maintain contact when out of visual range. Juvenile begging is a strident, loud vocalization often made by young to a parent when begging for food. Intraspecific aggression can consist of loud, alarmed-sounding vocalizations or of energetic song, and may be heard when members of the same species behave aggressively toward each other. Alarm may be heard when birds are startled, frightened, or terrified for their lives, and can take many forms. Mobbing is one example of alarm, while a high-pitched alarm call is another.

Of the 5 voices of the birds, four of them communicate the message that the bird feels safe. Birds that engage in song, companion calling, juvenile begging, and intraspecific aggression all display what Jon Young calls "baseline" behavior, or a relaxed state free of the fear of predation. Alarm communicates the presence of a predator, or an influence that the bird may see as predatory such as a human hiker. Alarms have distinct sounds and shapes, each of which is specific to the source of the disturbance. For example, ravens mobbing a hawk or owl in a tree will clump around the predator in a loose ball, calling and diving. If the ravens rise off the tree and fly higher, the predator was a hawk and has flown up to escape, as is typical of hawks. If the ravens drop out of the tree and fly low and away, the predator was an owl and has dropped low off its perch to escape, as is typical of owls.

Neurophysiology

The main brain areas involved in bird song are:

- Anterior forebrain pathway (vocal learning): composed of the lateral part of the magnocellular nucleus of anterior neostriatum (LMAN), which is a homologue to mammalian basal ganglia); Area X, which is part of the basal ganglia; and the Dorso-Lateral division of the Medial thalamus (DLM).
- Song production pathway: composed of the HVC (sometimes, inaccurately, called the Hyperstriatum Ventralis pars Caudalis); robust nucleus of the arcopallium (RA); and the tracheosyringeal part of the hypoglossal nucleus (nXIIts).

Both pathways show sexual dimorphism, with the male producing song most of the time. It has been noted that injecting testosterone in non-singing female birds can induce growth of the HVC and thus production of song.

Birdsong production is generally thought to start at the nucleus uvaeformis of the thalamus with signals emanating along a pathway that terminates at the syrinx. The pathway from the thalamus leads to the interfacial nucleus of the nidopallium to the HVC, and then to RA, the dorso-lateral division of the medial thalamus and to the tracheosyringeal nerve.

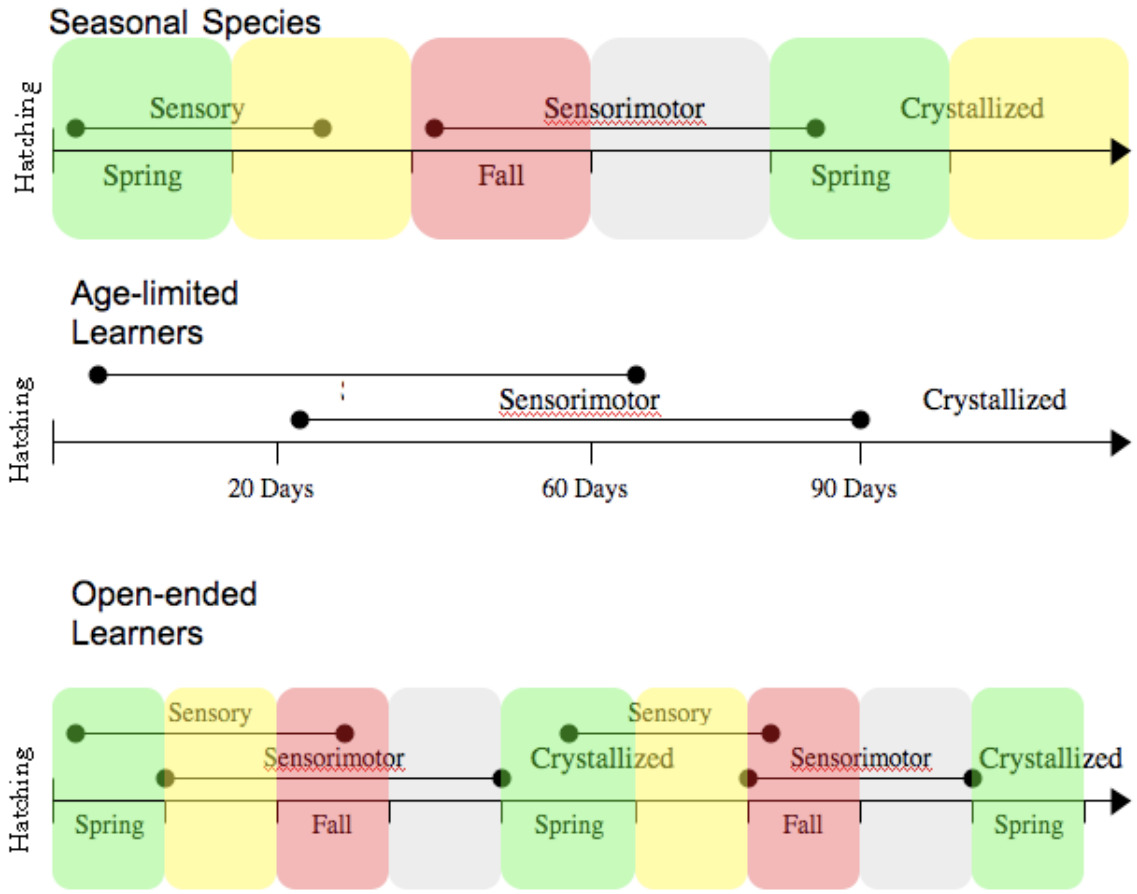
The gene FOXP2, defects of which affect both speech and comprehension of language in humans, becomes more active in the striatal region of songbirds during the time of song learning.

Recent research in birdsong learning has focused on the Ventral Tegmental Area (VTA), which sends a dopamine input to the para-olfactory lobe and Area X, LMAN and the ventrolateral medulla. Other researchers have explored the possibility that HVc is responsible for syllable production, while the robust nucleus of the arcopallium, the primary song output nucleus, may be responsible for syllable sequencing and production of notes within a syllable.

Learning

The songs of different species of birds vary, and are more or less characteristic of the species. In modern-day biology, bird song is typically analysed using acoustic spectroscopy. Species vary greatly in the complexity of their songs and in the number of distinct kinds of song they sing (up to 3000 in the Brown Thrasher); in some species, individuals vary in the same way. In a few species such as starlings and mockingbirds, songs imbed arbitrary elements learned in the individual's lifetime, a form of mimicry (though maybe better called "appropriation" [Ehrlich *et al.*], as the bird does not pass for another species). As early as 1773 it was established that birds learnt calls and cross-fostering experiments were able to force a Linnet *Acanthis cannabina* to learn the song of a skylark *Alauda arvensis*. In many species it appears that although the basic song is the same for all members of the species, young birds learn some details of their songs from their fathers, and these variations build up over generations to form dialects.

Birds learn songs early in life with sub-vocalizations that develop into renditions of adult songs. Zebra Finches, the most popular species for birdsong research, develop a version of a familiar adult's song after 20 or more days from hatch. By around 35 days, the chick will have learned the adult song. The early song is "plastic" or variable and it takes the young bird two or three months to perfect the "crystallized" song (which is less variable) of sexually mature birds.



Timeline for song learning in different species. Diagram adapted from Brainard & Doupe, 2002.

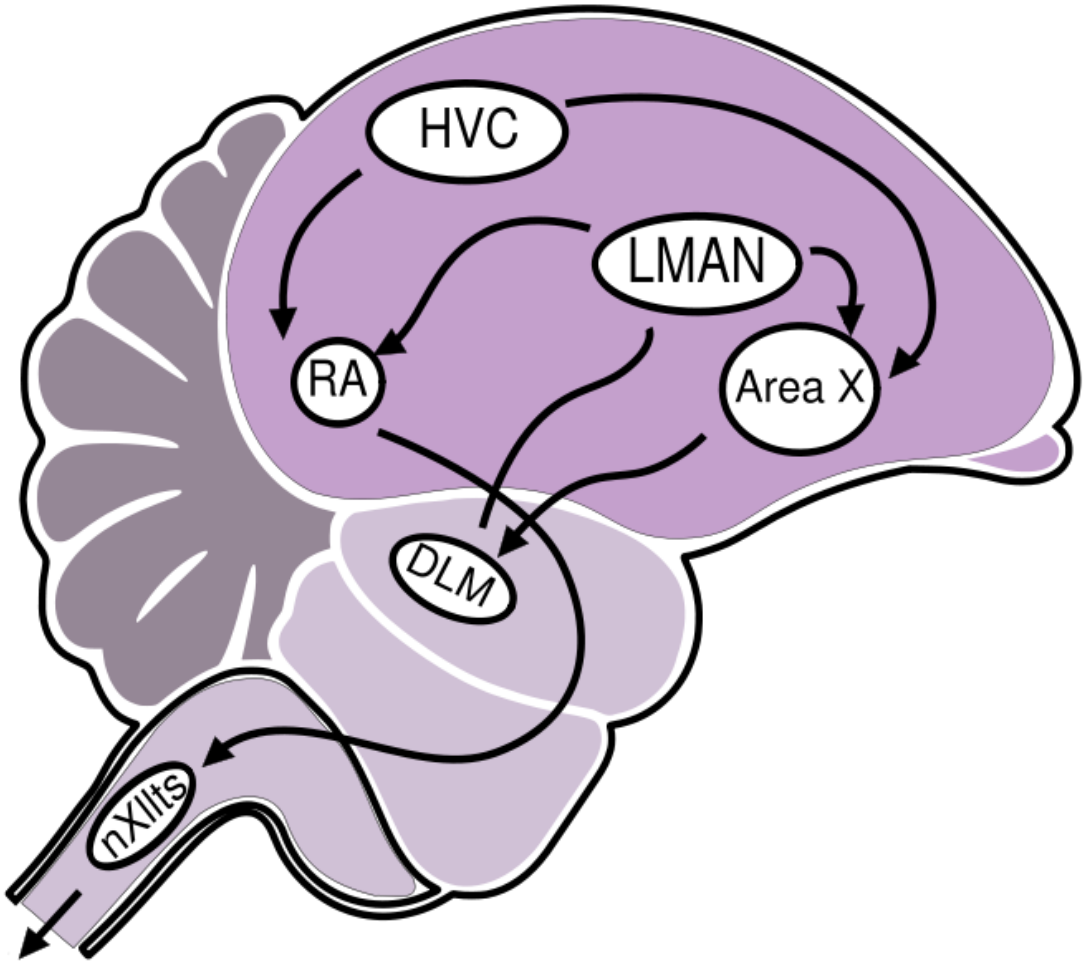
Research indicates birds' acquisition of song is a form of motor learning that involves regions of the basal ganglia. Models of bird-song motor learning are sometimes used as models for how humans learn speech. In some species such as zebra finches, learning of song is limited to the first year; they are termed 'age-limited' or 'close-ended' learners. Other species such as the canaries can develop new songs even as sexually mature adults; these are termed 'open-ended' learners.

Researchers have hypothesized that learned songs allow the development of more complex songs through cultural interaction, thus allowing intraspecies dialects that help birds stay with their own kind within a species, and it allows birds to adapt their songs to different acoustic environments.

Auditory feedback in bird song learning

Early experiments by Thorpe in 1954 showed the importance of a bird being able to hear a tutor's song. When birds are raised in isolation, away from the influence of conspecific males, they still sing. While the song they produce resembles the song of a wild bird, it

lacks the complexity and sounds distinctly different. The importance of the bird being able to hear himself sing in the sensorimotor period was later discovered by Konishi. Birds deafened before the song crystallization period went on to produce very different songs from the wild type. These findings led scientists to believe there could be a specific part of the brain dedicated to this specific type of learning.



Song learning pathway in birds (Based on Nottebohm, 2005)

The main focus in the search for the neuronal aspect of bird song learning was guided by the song template hypothesis. This hypothesis is the idea that when a bird is young he memorizes the song of his tutor. Later, during the development phase as an adult, he matches his own trial vocalizations using auditory feedback to an acoustic template in the brain. Based on this information, he adjusts his song if needed. To find this "song template," experimenters lesioned certain parts of the brain and observed the effects.

- Lesioning the song production pathway (RA, xXII or HVc) in the brain creates serious effects on song production in all birds.

- Lesions parts of the anterior forebrain pathway, or vocal learning pathway, DLM and area X, result in deficits in learning in all birds.
- Lesioning LMAN, located in the anterior forebrain pathway in young birds disrupts song production.
- Lesioning LMAN on an adult bird shows no effect.
- Lesioning LMAN on an adult canary (an "open-ended learner" species, which can learn songs later in life) shows a progressive deterioration of song.

These results show that the area known as LMAN is the only brain area in the pathway that shows some plasticity and further studies have shown that this area of the brain responds best to the bird's own song. This neuroplasticity is vital for a bird being able to learn a song. The ability to make small adjustments based on auditory feedback is needed for the complexity of these beautiful songs. Just like any musician, birds need to practice and be able to evaluate what their song sounds like and what it's supposed to sound like in order to get it right.

To complete the picture on bird song learning, experimenters needed to discover the true plasticity of the brain. While deafening and creating auditory isolation were good techniques for discovering basic characteristics about the brain, a reversible procedure was needed to investigate further. The solution was found in disruption of the auditory feedback, or what a bird hears. A computer is able to capture the song of a singing bird and play back portions of its song, or selectively play back a certain syllable while the bird is singing. The computer is basically playing the age old trick of repeating whatever the bird sings, the "stop copying me" game. This creates such a disruption that an adult bird will start to decrystallize its song, which includes a loss of spectral and temporal rigidity characteristic of adult song. It reverts back to the song it started singing with, before any learning took place. Furthermore, when the feedback was stopped, the birds slowly recovered their original song, something that was unheard of. These results show that there is a fair amount of plasticity retained in the brain, even for close-ended learners. This new found plasticity in adult birds and the results on the plasticity of LMAN (shown above) combine into a model for bird song learning (diagram coming soon).

Mirror neurons and vocal learning

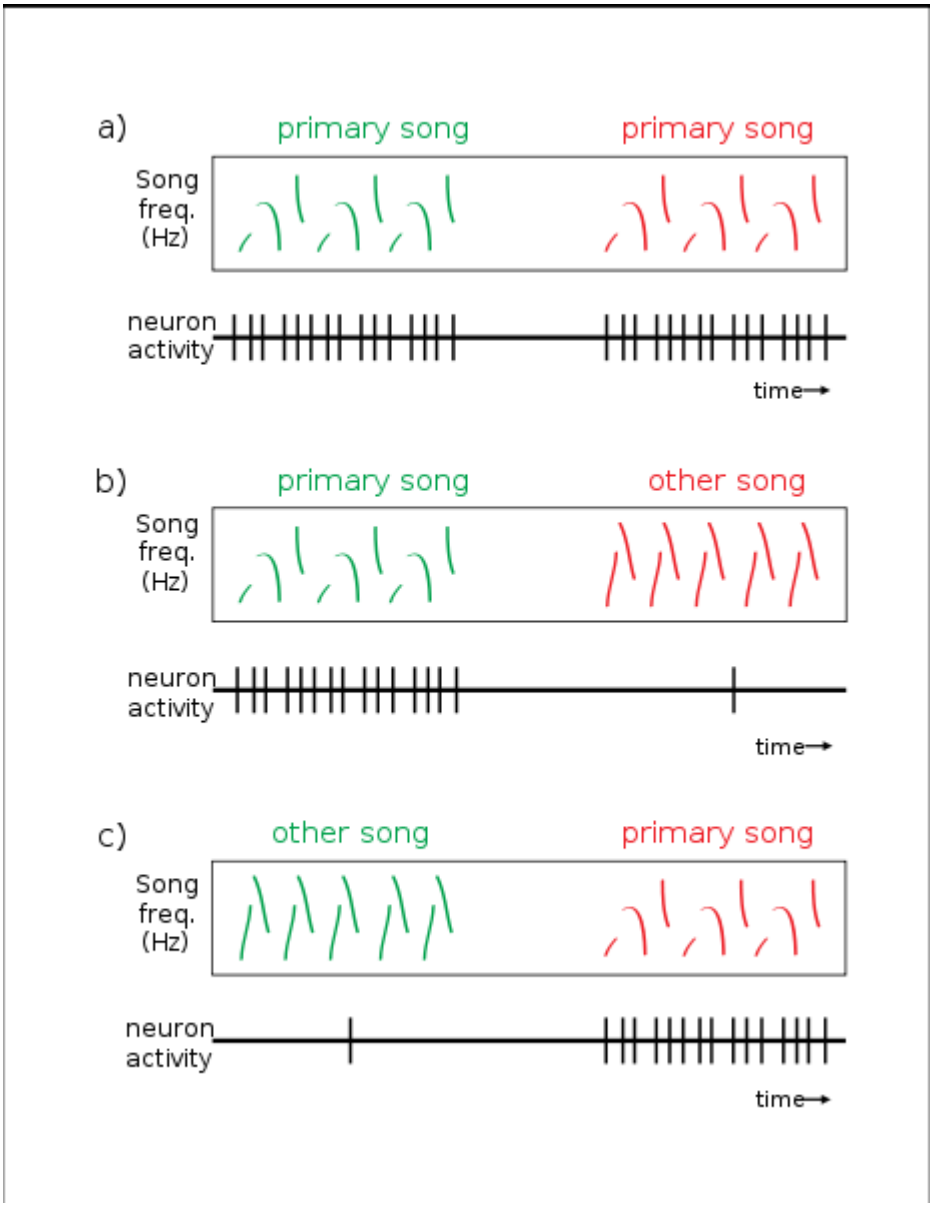
A mirror neuron is a neuron that discharges both when an individual performs an action, and when he perceives that same action being performed by another. These neurons were first discovered in macaque monkeys, but recent research suggests that mirror neuron systems may be present in other animals including humans.

Mirror neurons have the following characteristics:

- They are located the premotor cortex
- They exhibit both sensory and motor properties

- They are action-specific – mirror neurons are only active when an individual is performing or observing a certain type of action (e.g.: grasping an object).

Because mirror neurons exhibit both sensory and motor activity, some researchers have suggested that mirror neurons may serve to map sensory experience onto motor structures. This has implications for birdsong learning– many birds rely on auditory feedback to acquire and maintain their songs. Mirror neurons may be mediating this comparison of what the bird hears and what he produces.



Song selectivity in HVCx neurons: neuron activity in response to calls heard (green) and calls produced (red). **a.** Neurons fire when the primary song type is either heard or

sung. **b,c.** Neurons do not fire in response to the other song type, regardless of whether it is heard or sung. Sketch based on figure from Prather et al. (2008)

In search of these auditory-motor neurons, Jonathan Prather and other researchers at Duke University recorded the activity of single neurons in the HVCs of swamp sparrows. They discovered that the neurons that project from the HVC to Area X (HVC_X neurons) are highly responsive when the bird is hearing a playback of his own song. These neurons also fire in similar patterns when the bird is singing that same song. Swamp sparrows employ 3-5 different song types, and the neural activity differs depending on which song is heard or sung. The HVC_X neurons only fire in response to the presentation (or singing) of one of the songs, the primary song type. They are also temporally selective, firing at a precise phase in the song syllable.

Because the timing of the neural response is identical regardless of whether the bird was listening or singing, how can we be sure that the bird isn't just hearing himself? Prather et al. found that during the short period of time before and after the bird sings, his HVC_X neurons become insensitive to auditory input. In other words, the bird becomes "deaf" to his own song. This suggests that these neurons are producing a corollary discharge, which would allow for direct comparison of motor output and auditory input. This may be the mechanism underlying learning via auditory feedback.

Overall, the HVC_X auditory-motor neurons in swamp sparrows are very similar to the visual-motor mirror neurons discovered in primates. Like mirror neurons, the HVC_X neurons:

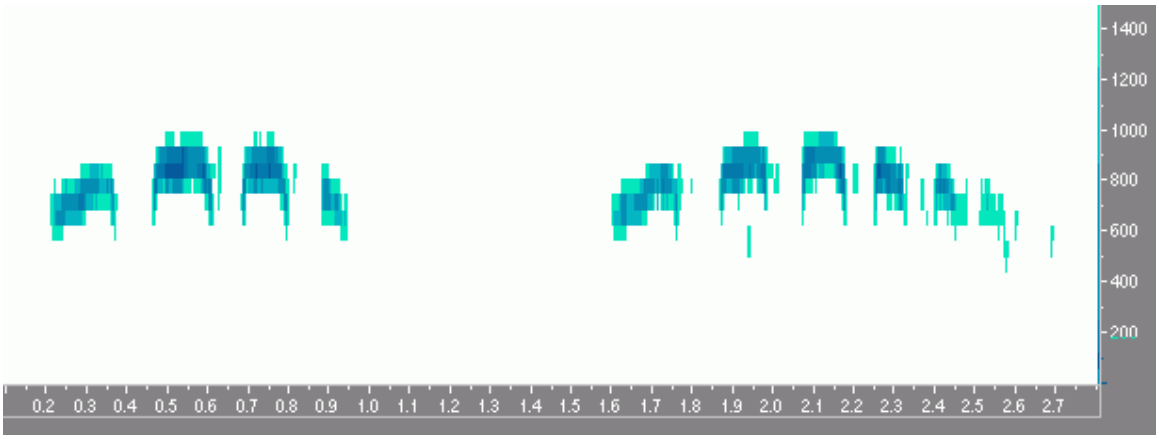
- Are located in a premotor brain area
- Exhibit both sensory and motor properties
- Are action-specific – a response is only triggered by the 'primary song type'

The function of the mirror neuron system is still unclear. Some scientists speculate that mirror neurons may play a role in understanding the actions of others, imitation, theory of mind and language acquisition, though there is currently insufficient neurophysiological evidence in support of these theories. Specifically regarding birds, it is possible that the mirror neuron system serves as a general mechanism underlying vocal learning, but further research is needed. In addition to the implications for song learning, the mirror neuron system could also play a role in territorial behaviors such as song-type matching and countersinging.

Identification and systematics

The specificity of bird calls has been used extensively for species identification. The calls of birds have been described using words or nonsense syllables, or line diagrams. Common terms in English include words such as *quack*, *chirp* and *chirrup*. These are

subject to imagination and vary greatly; a well-known example is the White-throated Sparrow's song, given in Canada as *O sweet Canada Canada Canada* and in New England as *Old Sam Peabody Peabody Peabody* (also *Where are you Frederick Frederick Frederick?*). In addition to nonsense words, grammatically correct phrases have been constructed as likenesses of the vocalizations of birds. For example, the Barred Owl produces a motif which some bird guides describe as *Who cooks for you? Who cooks for you all?* with the emphasis placed on *you*.



Sonogram of the call of a Laughing Dove.

The use of spectrograms to visualize bird song was first introduced by W. H. Thorpe. These visual representations are also called sonograms or sonagrams. Some recent field guides for birds use sonograms to document the calls and songs of birds. The sonogram is objective, unlike descriptive phrases, but proper interpretation requires experience. Sonograms can also be roughly converted back into sound.

Bird song is an integral part of bird courtship and is a pre-zygotic isolation mechanism involved in the process of speciation. Many allopatric sub-species show differences in calls. These differences are sometimes minute, often detectable only in the sonograms. Song differences in addition to other taxonomic attributes have been used in the identification of new species. The use of calls has led to proposals for splitting of species complexes such as those of the *Mirafra* Bushlarks.

Bird song and music

Some musicologists believe that birdsong has had a large influence on the development of music. Although the extent of this influence is impossible to gauge, it is sometimes easy to see some of the specific ways composers have integrated birdsong with music.

There seem to be three general ways musicians or composers can be affected by birdsong: they can be influenced or inspired (consciously or unconsciously) by birdsong, they can include intentional imitations of bird song in a composition, or they can incorporate recordings of birds into their works.

One early example of a composition that imitates birdsong is Janequin's "Le Chant Des Oiseaux", written in the 16th century. Other composers who have quoted birds or have used birdsong as a compositional springboard include Vivaldi (*Spring* from the *Four Seasons*)), Biber (*Sonata Representativa*), Beethoven (*Sixth Symphony*), Wagner (*Siegfried*) and the jazz musicians Paul Winter (*Flyway*) and Jeff Silverbush (*Grandma Mickey*).

The twentieth-century French composer Olivier Messiaen composed with birdsong extensively. His Catalogue d'Oiseaux is a seven-book set of solo piano pieces based upon birdsong. His orchestral piece *Réveil des Oiseaux* is composed almost entirely of birdsong. Many of his other compositions, including *Quatuor pour la fin du temps*, similarly integrate birdsong.

The Italian composer Ottorino Respighi, with his *The Pines of Rome* (1923–1924), may have been the first to compose a piece of music that calls for pre-recorded birdsong. A few years later, Respighi wrote *Gli Uccelli* ("The birds"), based on Baroque pieces imitating birds.

The Finnish composer Einojuhani Rautavaara in 1972 wrote an orchestral piece of music called *Cantus Arcticus* (Opus 61, dubbed *Concerto for Birds and Orchestra*) making extensive use of pre-recorded birdsongs from Arctic regions, such as migrating swans.

The American jazz musician Eric Dolphy sometimes listened to birds while he practiced flute. He claimed to have incorporated bird song into some of his improvisational music.

In the psychedelic era of the 1960s and 1970s, many rock bands included sound effects in their recordings. Birds were a popular choice. The English band Pink Floyd included bird sound effects in many of the songs from their 1969 albums *Soundtrack from the Film More* and *Ummagumma* (for example, Grantchester Meadows). Similarly, the English singer Kate Bush incorporated bird sound effects into much of the music on her 2005 album, Aerial.

The Music hall artist Ronnie Ronalde has gained notoriety for his whistling imitations of birds and for integrating birdsong with human song. His songs 'In A Monastery Garden' and 'If I Were A Blackbird' include imitations of the blackbird, his "signature bird."

The French composer François-Bernard Mâche has been credited with the creation of zoomusicology, the study of the music of animals. His essay *Musique, mythe, nature, ou les Dauphins d'Arion* (1983) includes a study of "ornitho-musicology", in which he speaks of "animal musics" and a longing to connect with nature.

The German DJ, techno music producer and naturalist Dominik Eulberg is an avid bird watcher, and several tracks by him prominently feature sampled bird sounds and even are titled after his favourite specimens.

The productions of The Jewelled Antler Collective often use field recordings featuring birdsong.

In 2007, The CT Collective issed two free albums devoted to music made using bird songs (one with human interaction, one without). The project was co-ordinated by looping musician Nick Robinson

Bird song and poetry

Bird song is a popular subject in poetry. Famous poems inspired by bird song include Percy Bysshe Shelley's To a Skylark ("Hail to thee, blithe Spirit!/Bird thou never wert") and Gerard Manley Hopkins' Sea and Skylark. Birdsongs and their relations to Middle-earth inhabitants are a common motif in J. R. R. Tolkien's literary work. The Grateful Dead performed a song called "Bird Song" that Jerry Garcia wrote and dedicated to Janis Joplin.

Chapter 7

Talking Bird

A caged Orange-winged Amazon saying "Hello" having been prompted by visitors.

Talking birds are birds that can mimic human speech. Talking birds have varying degrees of intelligence and communication capabilities: some, like the crow, a highly intelligent bird, are only able to mimic a few words and phrases, whilst some budgerigars have been observed to have a vocabulary of almost two thousand words. The Hill Myna is a commonly kept pet, well known for its talking ability – whilst its relative, the European Starling, is also adept at mimicry.

Budgerigars

Puck

In 1995 a budgerigar named Puck was credited by Guinness World Records as having the largest vocabulary of any bird, at 1,728 words.

African Grey Parrots

The African Grey Parrots are particularly noted for their cognitive abilities. Some of the most notable African Grey Parrots are Alex, Prudle, N'kisi and a new rising star, Einstein.

Alex

Alex had a vocabulary of about 100 words, but he was one of the most famous birds because of his cognitive abilities. In 2005, World Science reported that Alex understood the concept of zero. Alex died on September 6, 2007.

Prudle

Prudle held the Guinness world record for bird with biggest vocabulary for many years with a documented vocabulary of 800 words.

N'kisi

N'kisi is noted for his impressive English usage skills and other abilities. As of January 2004, he had a documented vocabulary of 950 words and shows signs of a sense of humor. N'kisi is believed to be one of the most advanced users of human language in the animal world.

Einstein

Einstein appeared on many television shows and became famous for her ability to recreate sounds as well as voice. Video clips show her making the sound of a laser beam and an evil laugh. She has been trained by Stephanie White.

Sparky

African Grey Sparky is popular on YouTube for copying one liners from the sitcom *Still Game* in a broad Scottish accent.

Bibi

Bibi, a Congo African Grey Parrot, is best known for her ability to use greetings from 20 different languages, earning her the nickname "The Polyglot Parrot." At only three years of age, Bibi has already developed a vocabulary of about 300 words, and she understands the concepts of color and shape.

Amazon parrots

Many species of Amazona (particularly the yellow-head variety) are outstanding talkers. Yellow-napes, Double Yellow-headed, Yellow-crowned, and Panama Amazons are highly regarded as talking parrots.

Other parrots

Most parrot species are capable of imitating human words. Many can learn to use phrases in context; they can also be trained to imitate any words.

Hill Mynas

Hill Mynas are renowned for their ability to mimic the human voice. Many have claimed that the Hill Myna is the best talking bird and the best mimic in the world.

Chapter 8

Dog Communication

It is important to look at the dog's whole body and not just the mouth or tail before deciding what the dog is trying to communicate. What appears initially as aggression might be an invitation to play.

Dog communication refers to body movements and sounds dogs use to send signals to other dogs, and other animals (usually humans). Dog communication comes in a variety

of forms, and is part of the foundation of dog social behavior. Dogs use certain movements of their bodies and body parts and different vocalizations to express their emotions. There are a number of basic ways a dog can communicate its feelings. These are movements of the ears, eyes, eyebrows, mouth, head, tail, and entire body, as well as barks, growls, whines and whimpers, and howls.

Interpreting animal body language

A dog might stretch after taking a nap, just as people do, or might drop into a stretch to lead into a play bow or to calm a person or other dog.

It is important to note that while many gestures and actions may have common, stereotypical meanings, researchers regularly find that animal communication is often more complex and subtle than previously believed, and that the same gesture may have multiple distinct meanings depending on context and other behaviors. So, generalizations such as "X means Y" are *often*, but not *always* accurate. For example, even a simple tail wag may (depending on context) convey many meanings including:

- Excitement
- Anticipation
- Playfulness
- Contentment/enjoyment
- Happiness, self-confidence

But also:

- Anxiety
- Uncertainty/apprehension

Combined with other body language, in a specific context, many gestures such as yawns and direction of vision all convey the dog's emotions or feeling states. Thus statements that a particular action "means" something, or that the dog is using its body language with the intent to report information to others, should be avoided. In *Consciousness Explained*, Daniel C. Dennett of Tufts University, tells us that there are two basic forms of communication: the unconscious expression of a mental or emotional state, and the intentional act of reporting information. He goes on to say that there are many ways of expressing a mental or emotional state, “but only one way of reporting information, and that is through the use of language, written, spoken, or signed.” It's also important to note that most of the body language exhibited by human beings isn't done consciously, with the intent to communicate, so it could be mistake to believe that dogs intentionally use their body language to report information to others.

Canine nose-to-anus greeting

Descriptions here are therefore best viewed as common generalizations, to which a more experienced observer will be able to add further detail or understanding.

Ethology is a science which studies animal behavior.

Greeting Ritual

One of the first forms of communication that will be observed is the greeting ritual. When a dog first encounters another dog, a brief assessment of aggression or friendliness is made. If one dog growls or barks, for instance, the encounter will usually end quickly, either by the other dog avoiding the encounter, or by a fight ensuing. If this test is passed, the dogs usually attempt to greet each other. This is done first by sniffing each other's odors. Dogs often sniff each other's rear-ends simultaneously, and this is the clearest indication of what some in the field believe to be a greeting ritual. This so-called greeting ritual is said to establish the identities of the dogs by scent, and is the dogs' way of saying 'hello' to each other. However, most people miss an important observation: even dogs who know each other very well will sniff one another when they first run into each other on the street. Dogs who live in multiple dog households will also sniff each other from time to time (for instance, if one dog gets up to get a drink of water while another dog is asleep, that dog might go over and sniff his housemate on his way to the water bowl). Dogs who are playing will sometimes get too wound up, stop, shake themselves off, then sniff each other before resuming their play session. So the idea that sniffing is just a greeting ritual is probably a misunderstanding.

If the dogs are satisfied with the encounter (it is not unusual for dogs to take a sudden dislike to each other at this stage), then they may either move on in disinterest, or proceed further in the greeting ritual by showing affection. Affection is shown by some or all of the following: Wagging the tail, licking the face, playful barking, panting, or jumping (including playful jumping on the other dog). Dogs that show affection in this way will usually get along fairly well, and this display can be considered a display of friendship.

Hand-sniff Greeting

Humans can also participate in a greeting ritual with a newly met dog, by bending down in front of (not looming over) or kneeling down to the dog, and slowly but confidently extending the hand to be sniffed in front of and just below the dog's snout. If the dog is timid or has a habit of snapping at strangers, it is best to allow the dog to come sniff your hand, rather than extending it into the dog's space (this can make the dog nervous) while using words of praise in a calm, soothing voice. To limit the chance of getting bitten, keep the hand palm-down with fingers cupped downward or the hand fully closed in a loose fist, making it difficult for the dog to grab hold of a finger in a bite. Be watchful of the dog's demeanor. If the dog makes a sudden snap at your hand, try not to pull it away as that will only reinforce and increase the dog's desire to bite you. Any object moving away from a dog triggers an instinctive urge to bite. However, if you continue praising the dog in a soothing voice, even if it's just snapped at you, the dog is much less likely to get frightened and will more than likely sniff your hand in a friendly manner.

After the dog has completed the hand-sniff, it is possible to proceed to making physical contact by gently petting the dog on its chest or shoulders. Attempting to pet the top of the head can create a nervous response because the movement of the hand toward the head may interrupt the dog's ability to see your eyes, thereby assessing your emotional

state. Again, it is possible to get snapped at, so care should be taken not to block the dog's ability to see your eyes. If the dog does snap, the best course of action is not pull your hand away suddenly, but to keep praising the dog in a soothing tone. If the dog completes the sniff without snapping or barking, another attempt to pet the dog can be made.

Once the dog allows the affectionate petting, it will more likely only take a quick hand-sniff on the next meeting for the person to attempt petting the dog. Petting can at this time become more playful without risking the dog snapping at the person.

The dog is showing signs of fear aggression. Notice the lowered head, body down, foot pointing, raised back hair, ready to pounce hind legs and focused attention.

For timid or mildly aggressive dogs, it may not be possible to establish friendship in one greeting ritual. Friendship cannot be forced, and may require repeated attempts over time.

Caution against aggression during the greeting ritual

Some breeds of dog have a more suspicious or aggressive temperament by nature and are more difficult or dangerous to approach with the greeting ritual. Dogs that have been physically abused tend to be much more timid and defensive than a well-treated dog, so great care should be taken before trying to perform the greeting ritual with such a dog, as these dogs are more prone to react aggressively. Some dogs are also trained to be

aggressive, such as guard dogs. A safer route to gaining the dog's trust would be to provide it with food, and to slowly acclimatise the dog to your presence. The best might be to avoid aggressive dogs altogether.

Dominance and submission

Dominance and submission are often mistaken to be part of normal social behaviors for dogs. They are not. Wild canines form packs specifically for the purpose of hunting large prey. Evolutionary biologist Raymond Coppinger has noted that wolves that live near garbage dumps, and therefore don't need to hunt large prey, don't form packs. He also states that coyotes, which are more solitary than wolves, sometimes form packs, but only when they need to hunt large prey. In Dog Language, biologist Roger Abrantes has noted that it's easier for a group of wolves to hunt large prey by working together. So pack formation in canines seems to be a function of prey size more than dominance and submission.

The idea that dogs exhibit dominant and submissive behaviors is based partly on behaviors seen in captive wolves that were culled from various sources, didn't know one another, and weren't able to hunt together. David Mech of the University of Minnesota has been studying wild wolf packs since the 1960s. Mech states that in wild packs "dominance" displays are so rare as to be totally nonexistent. The only time they seem to take place is when a conflict emerges between the pack parents over how to disburse food to the young. The female invariably wins these encounters by acting as "non-threatening" (or submissive) as possible. Rudolph Schenkel was the first biologist to ask the question, if the "submissive" wolf always wins, who's really dominant? Also, since "dominance aggression" in dogs can be treated with anti-anxietal medications, it's more likely that this behavior is an expression of stress or anxiety, and is not a natural part of the canine social instincts. (Mech (1999) asserted that the significance of dominance relationships within pack society has been overrated, and he argued that wolf packs are best understood as family groups in which a breeding pair "shares leadership in a division of labor system in which the breeding female initiates pup care and the breeding male leads in foraging and food provisioning". INTRODUCTION: "Leadership behavior in relation to dominance and reproductive status in gray wolves, Canis lupus," Rolf O. Peterson, Amy K. Jacobs, Thomas D. Drummer, L. David Mech, and Douglas W. Smith, *Canadian Journal of Zoology*, Vol. 80, 2002, p. 1406)

Body movements

Tail

How high or low the tail is held, in relation to how the dog's breed naturally carries its tail, and how it is moved can signify the dog's mood. When the tail is held high, it shows that the dog is alert; tail between the legs means that the dog is afraid. If the fur on the tail is also bristled, the dog is saying it is willing to defend.

Small, slow wags of the tail say the dog is questioning things around it. Either it is not sure whether the target dog or person is friendly, or it is not sure what is going on or what is expected of it.

Large, fast wags of the tail may be a sign of a happy or excited dog, but can also signal aggression. A large percentage of the victims of dog bites are bitten while the dog is wagging its tail.

Dogs are said to exhibit a left-right asymmetry of the tail when interacting with strangers, and will show the opposite, right-left motion with people and dogs they know.

Aggressive/ violent

These dogs are showing the major signs of aggression, but they are not fighting, so body language should not be inferred on isolated signs

This dog is not "smiling" but feeling defensive about its bone.

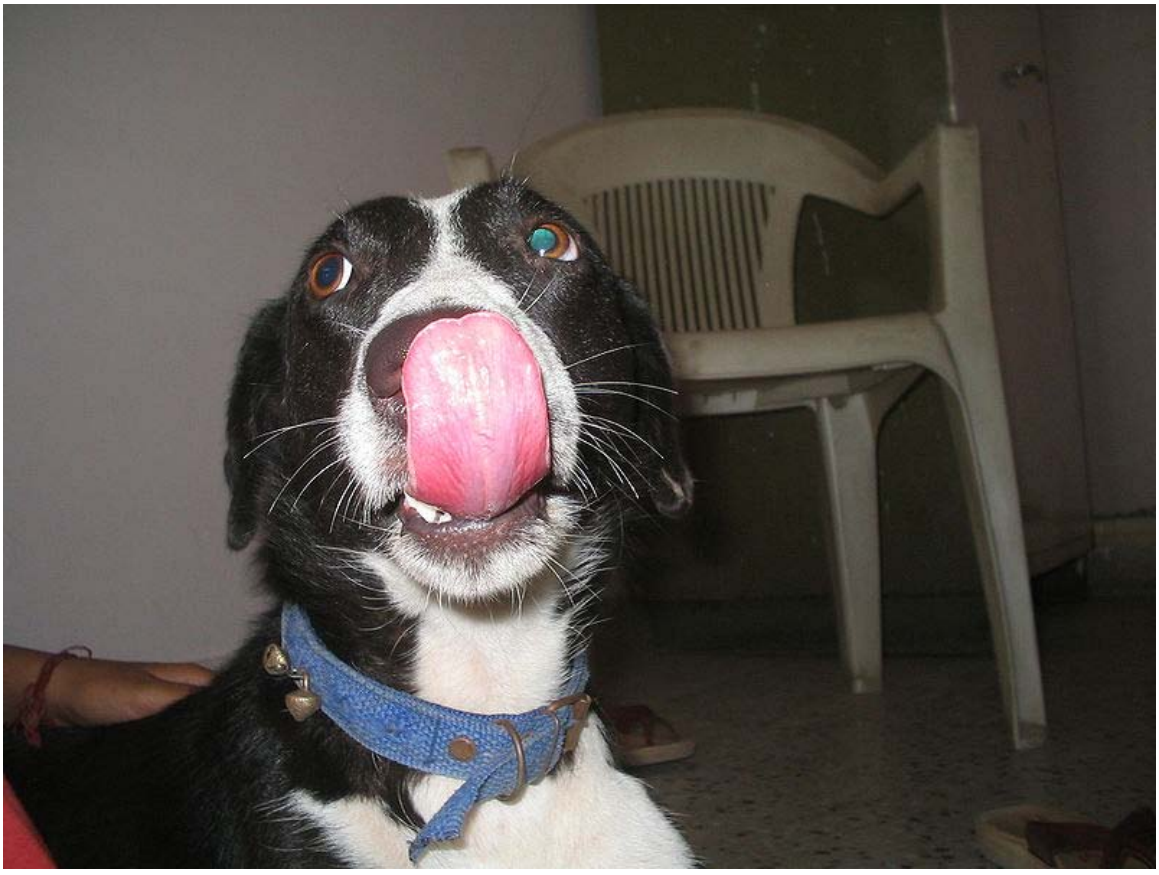
When a dog's lips curl back this shows that the dog has a strong urge to bite. This is an unconscious reflex, designed to get the soft flesh of the lips away from the teeth before the dog bites, and is often misinterpreted as a way of communicating aggressive intent. For example, many dogs will curl their lips back into a "snarl" when they take a cookie or bone.

Ears

Ear position relates the dog's level of attention, and reaction, to a situation or animal. Erect ears facing forward means the dog is very attentive, while ears laid back suggests a

negative, usually fearful or a timid reaction. They also lay their ears back for the sounds surrounding them. Dogs with drop ears, like Beagles, can't use these signals very well, as the signals first developed in wolves, whose ears are pricked. Wolf-like dogs (such as the Samoyed or Husky) will, when content and happy, often hold their ears in a horizontal position but still forward. This has been referred to as the "wolf smile".

Mouth



A dog showing all signs of being anxious - white half moon eyes, nose licking, sideways glance etc

Mouth expressions can provide information about the dog's mood. When a dog wants to be left alone, it might yawn (although yawning also might indicate sleepiness, confusion, or stress) or start licking its mouth without the presence of any food. When a dog is happy or wants to play, it might pant with lips relaxed, covering the teeth and with what sometimes appears to be a happy expression (it might appear as a smile to some observers) or with the mouth open. Mouth expressions that indicate aggression include the snarl, with lips retracting to expose the teeth, although some dogs also use this during play. However, some dogs will pull back their "top lips" in what looks like an aggressive way, when they are excited or happy. For example a dog prone to "smiling" may do so in greeting to a much loved owner and this should not be punished lest the dog become less affectionate and more withdrawn.

It's important to look at the dog's whole body and not just the mouth or tail before deciding what the dog is feeling. What appears initially as aggression might be an invitation to play, or vice-versa.

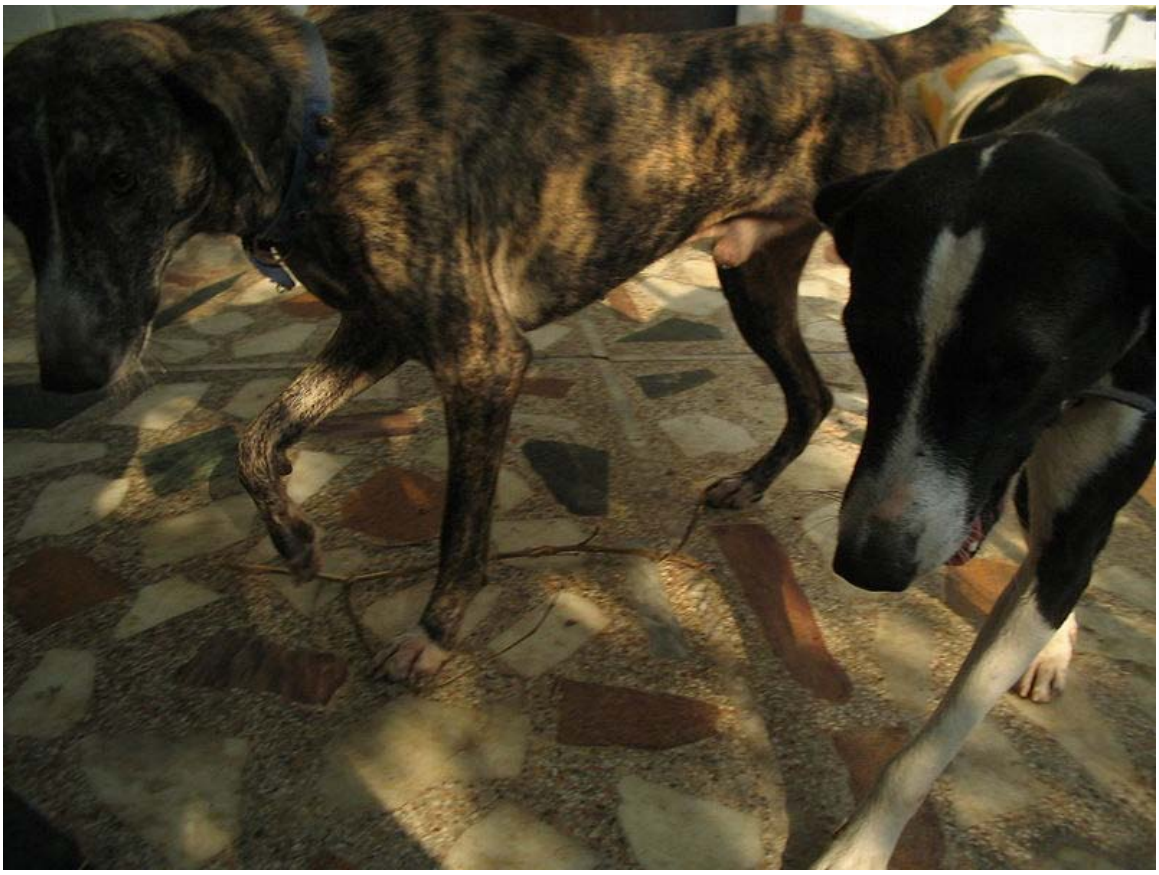
Tongue (Licking)

A very common form of communication is for a dog to lick another dog, or a person. Dogs lick other dogs' faces and mouths when they greet each other to indicate friendliness. Dogs like to lick human skin not only for the salt from the sweat, but also as a form of greeting, such as by briefly licking a person's hand after sniffing it. Licking is also used as a social bonding analogous to primate social grooming and stroking. This can indicate intimacy. Such licking is longer and slower, as compared to the brief licking of faces during a greeting.

Eyes and eyebrows

While dogs don't have actual eyebrows, they do have a distinctive ridge above their eyes, and some breeds, like the Labrador Retriever, Rottweiler, German Shepherd, and Doberman have markings there. A dog's eyebrow movements usually express a similar emotion to that of a human's eyebrow movements. Raised eyebrows suggest interest, lowered brows suggest uncertainty or mild anger, and one eyebrow up suggests bewilderment. Eyes narrowed to slits indicate affection for the person or animal the dog is looking at.

Feet and legs



Two dogs stamping their feet, maybe to gain attention.

Although a dog's feet lack the dexterity of human hands, a dog can use them as an avenue of communication. A dog might stamp its feet, alternating its left and right front legs, while its back legs are still. This occurs when the dog is excited, wants something, or wants its owner's attention. Pointers tend to tuck one front leg up when they sense game nearby. This behavior is not communicative so much as the dog exhibiting a fixed-action pattern called "the eye stalk." It is also common for dogs to paw or scratch for objects they desire. Many dogs are trained to mimic a human handshake, offering a paw to a human stooping down and offering their own hand in exchange.

Head

Leaning of head and forward ears on hearing the shutter sound of camera for the first time

The leaning of a dog's head to the right or to the left often indicates curiosity and/or a sound it has not heard before. This, however, may also be a sign of recognition to a familiar word.

If the dog's head is held high with its neck craning forward, it is showing interest, although, it could also mean an aggressive mood if other body language is present.

Some adult dogs that were not properly raised have been known to challenge their owners for alpha position. One of the signs, though this is rarely seen in dogs, involves the dog slightly lowering its head while standing tall with its eyes fixed upward at the owner or any human beings they are about to challenge (start a fight with). This behavior is extremely rare and usually occurs with dogs that have been severely neglected or in some cases, abused. This can also be dangerous and sometimes fatal if no action is taken immediately. However, this behavior is preventable if owners avoid being neglectful or abusive to their dogs.

Vocalizations

Barks

Dogs bark for many reasons, such as when perceived intruders (humans, dogs, or other animals) approach their living space, when hearing an unfamiliar or unidentified noise, when seeing something that the dog doesn't expect to be there, or when playing. Barking also expresses different emotions for a dog, such as loneliness, fear, suspicion, stress, and pleasure. Playful or excited barks are often short and sharp, such as when a dog is attempting to get a person or another dog to play.

Dogs generally try to avoid conflict; their vocalizations are part of what allows other dogs to tune into their emotions, i.e., whether they're aggressive or are in a playful mood.

The bark of a distressed or stressed dog is high pitched and repetitive; it tends to get higher in pitch as the dog becomes more upset. For example, a dog left home alone and who has separation anxiety might bark in such a way.

Some breeds of dogs have been bred to bark when chasing, such as scent hounds whose handlers use the bark to follow the dog if it has run out of sight. Coonhounds and bloodhounds are good examples. This kind of barking is often called "singing" as the sound is longer and more tonal.

Some research has suggested that dogs have separate barks for different animals, including dog, fox, deer, human, squirrel and cat.

Growls

Growls can express aggression, a desire to play, or simply that the dog doesn't want to participate in what's about to happen next (being picked up for example). For this reason, most pet owners have been urged to treat growls with special attention. This includes always considering the context of a growl, and exercise caution.

Howls

Howling may provide long-range communication with other dogs or owners. Howling can be used to locate another pack member, to keep strangers away, or to call the pack for hunting. Some dogs howl when they have separation anxiety.

Whines

Whining is a high-pitched vocalization, often produced nasally with the mouth closed. A dog may whine when it wants something (such as food), wants to go outside (possibly to 'go to the bathroom'), wants to be let off the leash (possibly to greet another dog or a person), or just wants attention. A very insistent dog may add a bark at the end of a whine, in a whine-bark, whine-bark pattern.

Whimpers

A whimper or a yelp often indicates the dog is in pain. This is often heard when dogs play-fight if one dog bites the other dog too hard. The whimper or yelp is used only when the dog intends to communicate its distress to a pack member (or human) to whom they are submissive or friendly, and the other dog or human is expected to react positively to the communication; dogs engaged in serious fights do not whimper, as this indicates weakness. Dogs also whimper when they are physically abused or neglected by people. Whimpers are often associated with the lowering of the tail between the legs. Whimpers can also indicate strong excitement when a dog is lonely and is suddenly met with affection, such as when a dog is left alone in a house during the day and its owner comes through the door late at night. Such whimpering is often accompanied by licking, jumping, and barking. Whimpering is distinct from barking in that it is softer, higher pitched, and lower volume.

Human speech

Though the phenomenon is often undiscussed, some dogs, followed by personal curiosities through observing the vocalization of the humans around them, may try to repeat human speech sounds, or are trained to do so. This kind of vocalization is typically achieved after lengthy training with positive reinforcement techniques. It's more likely that the dog is exhibiting these behaviors not because they "want" to communicate with humans, but is rather instead a previously reinforced behavior for a reward. Recent examples have included a whimpering pug on the *Late Show with David Letterman*.

Chapter 9

Ethology

A Blue Jay cracking nuts

Ethology is the scientific study of animal behavior, and a sub-topic of zoology.

Although many naturalists have studied aspects of animal behavior throughout history, the modern discipline of ethology is generally considered to have begun during the 1930s with the work of Dutch biologist Nikolaas Tinbergen and Austrian biologists Konrad Lorenz and Karl von Frisch, joint winners of the 1973 Nobel Prize in Physiology or Medicine. Ethology is a combination of laboratory and field science, with a strong relation to certain other disciplines — e.g., neuroanatomy, ecology, evolution. Ethologists are typically interested in a behavioral process rather than in a particular animal group and often study one type of behavior (e.g. aggression) in a number of unrelated animals.

The desire to understand animals has made ethology a rapidly growing topic, and since the turn of the 21st century, many prior understandings related to diverse fields such as animal communication, personal symbolic name use, animal emotions, animal culture, learning, and even sexual conduct long thought to be well understood, have been modified, as have new fields such as neuroethology.

Etymology

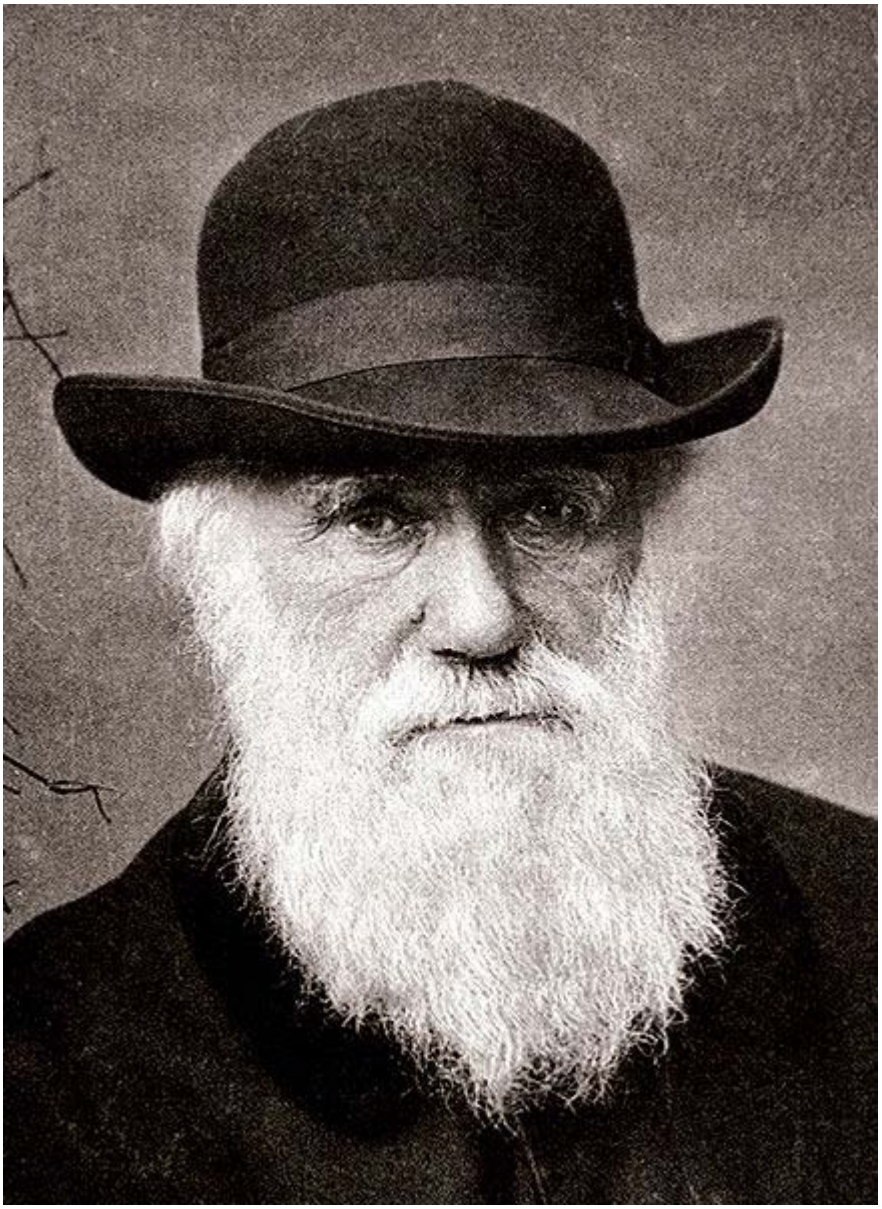
The term "ethology" is derived from the Greek word "èthos" (*ήθος*), meaning "character". Other words derived from the Greek word "ethos" include "ethics" and "ethical". The term was first popularized in English by the American myrmecologist William Morton Wheeler in 1902. (An earlier, slightly different sense of the term was proposed by John Stuart Mill in his 1843 *System of Logic*. He recommended the development of a new science, "ethology," the purpose of which would be explanation of individual and national differences in character, on the basis of associationistic psychology. This use of the word was never adopted.)

Differences and similarities with comparative psychology

Comparative psychology also studies animal behaviour, but, as opposed to ethology, is construed as a sub-topic of psychology rather than as one of biology. Historically, where comparative psychology researches animal behaviour in the context of what is known about human psychology, ethology researches animal behaviour in the context of what is known about animal anatomy, physiology, neurobiology, and phylogenetic history. This distinction is not representative of the current state of the field. Furthermore, early comparative psychologists concentrated on the study of learning and tended to research behaviour in artificial situations, whereas early ethologists concentrated on behaviour in natural situations, tending to describe it as instinctive. The two approaches are complementary rather than competitive, but they do result in different perspectives and, sometimes, in conflicts of opinion about matters of substance. In addition, for most of the twentieth century, comparative psychology developed most strongly in North America, while ethology was stronger in Europe. A practical difference is that early comparative psychologists concentrated on gaining extensive knowledge of the behaviour of very few species, while ethologists were more interested in gaining knowledge of behaviour in a wide range of species in order to be able to make principled comparisons across taxonomic groups. Ethologists have made much more use of a truly comparative method than comparative psychologists have. Despite the historical divergence, most ethologists (as opposed to behavioural ecologists), at least in North America, teach in psychology departments. It is a strong belief among scientists that the mechanisms on which behavioural processes are based are the same that cause the evolution of the living species: there is therefore a strong association between these two fields.

Scala naturae *and Lamarck's theories*

Jean-Baptiste Lamarck (1744–1829)



Charles Darwin (1809–1882)

Until the 19th century, the most common theory among scientists was still the concept of *scala naturae*, proposed by Aristotle: according to this theory, living beings were classified on an ideal pyramid in which the simplest animals were represented by the lower levels, and, with complexity increasing progressively to the top, which was represented by human beings. There was also a group of 'biologists' who refuted the Aristotelian theory for a more anthropocentric one, according to which all living beings were created by Buddha to serve mankind, and would behave accordingly. A well-radicated opinion in the common sense of the time in the Western world was that animal species were eternal and immutable, created with a specific purpose, as this seemed the only possible explanation for the incredible variety of the living beings and their surprising adaptation to their habitat.

The first biologist elaborating a complex theory of evolution was Jean-Baptiste Lamarck (1744–1829). His theory substantially comprised two statements: the first is that animal organs and behaviour can change according to the way they are being used, and second that those characteristics are capable of being transmitted from one generation to the next (well-known is the example of the giraffe whose neck becomes longer while trying to reach the upper leaves of a tree). The second statement is that each and every living organism, human beings included, tends to reach a greater level of perfection. At the time of his journey for the Galapagos Islands, Charles Darwin was well aware of Lamarck's theories and was influenced by them.

Theory of evolution by natural selection and the beginnings of ethology

Because ethology is considered a topic of biology, ethologists have been concerned particularly with the evolution of behaviour and the understanding of behaviour in terms of the theory of natural selection. In one sense, the first modern ethologist was Charles Darwin, whose book, *The Expression of the Emotions in Man and Animals*, influenced many ethologists. He pursued his interest in behaviour by encouraging his protégé George Romanes, who investigated animal learning and intelligence using an anthropomorphic method, anecdotal cognitivism, that did not gain scientific support.

Other early ethologists, such as Oskar Heinroth and Julian Huxley, instead concentrated on behaviours that can be called instinctive, or natural, in that they occur in all members of a species under specified circumstances. Their beginning for studying the behaviour of a new species was to construct an **ethogram** (a description of the main types of natural behaviour with their frequencies of occurrence). This provided an objective, cumulative base of data about behaviour, which subsequent researchers could check and supplement.

Fixed action patterns and animal communication

An important development, associated with the name of Konrad Lorenz though probably due more to his teacher, Oskar Heinroth, was the identification of fixed action patterns (FAPs). Lorenz popularized FAPs as instinctive responses that would occur reliably in the presence of identifiable stimuli (called **sign stimuli** or **releasing stimuli**). These FAPs could then be compared across species, and the similarities and differences between behaviour could be easily compared with the similarities and differences in morphology. An important and much quoted study of the Anatidae (ducks and geese) by Heinroth used this technique. Ethologists noted that the stimuli that released FAPs were commonly features of the appearance or behaviour of other members of their own species, and they were able to prove how important forms of animal communication could be mediated by a few simple FAPs. The most sophisticated investigation of this kind was the study by Karl von Frisch of the so-called "dance language" related to bee communication. Lorenz developed an interesting theory of the evolution of animal communication based on his observations of the nature of fixed action patterns and the circumstances in which animals emit them.

Instinct

Kelp Gull chicks peck at red spot on mother's beak to stimulate regurgitating reflex.

The Merriam-Webster dictionary defines instinct as a largely inheritable and unalterable tendency of an organism to make a complex and specific response to environmental stimuli without involving reason. For ethologists, instinct means a series of predictable behaviors for fixed action patterns. Such schemes are only acted when a precise stimulating signal is present. When such signals act as communication among members of the same species, they are known as releasers. Notable examples of releasers are, in many bird species, the beak movements by the newborns, which stimulates the mother's regurgitating process to feed her offspring. Another well known case is the classic experiments by Tinbergen on the Graylag Goose. Like similar waterfowl, it will roll a displaced egg near its nest back to the others with its beak. The sight of the displaced egg triggers this mechanism. If the egg is taken away, the animal continues with the behaviour, pulling its head back as if an imaginary egg is still being maneuvered by the underside of its beak. However, it will also attempt to move other egg shaped objects, such as a giant plaster egg, door knob, or even a volleyball back into the nest. Such objects, when they exaggerate the releasers found in natural objects, can elicit a stronger version of the behavior than the natural object, so that the goose will ignore its own displaced egg in favor of the giant dummy egg. These exaggerated releasers for instincts were termed supernormal stimuli by Tinbergen. Tinbergen found he could produce supernormal stimuli for most instincts in animals, such as cardboard butterflies which male butterflies preferred to mate with if their stripes were darker than a real female or dummy fish which a territorial male stickleback fish would fight more violently than a

real invading male if the dummy had a brighter colored underside. Harvard psychologist Deirdre Barrett has done research pointing out how easily humans also respond to supernormal stimuli for sexual, nurturing, feeding, and social instincts. However, a behaviour only made of fixed action patterns would be particularly rigid and inefficient, reducing the probabilities of survival and reproduction, so the learning process has great importance, as the ability to change the individual's responses based on its experience. It can be said that the more the brain is complex and the life of the individual long, the more its behaviour will be "intelligent" (in the sense of guided by experience rather than stereotyped FAPs).

Learning

Learning occurs in many ways, one of the most elementary being habituation. This process consists in ignoring persistent or useless stimuli. An example of learning by habituation is the one observed in squirrels: when one of them feels threatened, the others hear its signal and go to the nearest refuge. However, if the signal comes from an individual who has caused many false alarms, its signal will be ignored.

Another common way of learning is by association, where a stimulus is, based on the experience, linked to another one which may not have anything to do with the first one. The first studies of associative learning were made by Russian physiologist Ivan Pavlov. An example of associative behaviour is observed when a common goldfish goes close to the water surface whenever a human is going to feed it, or the excitement of a dog whenever it sees a collar as a prelude for a walk. The associative learning process is related to the necessity of developing discriminatory capacities, that is, the faculty of making meaningful choices. Being able to discriminate the members of your own species is of fundamental importance for reproductive success. Such discrimination can be based on a number of factors in many species including birds, however, this important type of learning only takes place in a very limited period of time. This kind of learning is called imprinting.

Imprinting

Example of imprinting in a moose

A second important finding of Lorenz concerned the early learning of young nidifugous birds, a process he called imprinting. Lorenz observed that the young of birds such as geese and chickens followed their mothers spontaneously from almost the first day after they were hatched, and he discovered that this response could be imitated by an arbitrary stimulus if the eggs were incubated artificially and the stimulus was presented during a **critical period** (a less temporally constrained period is called a **sensitive period**) that continued for a few days after hatching.

Imitation

Finally, imitation is often an important type of learning. A well-documented example of imitative learning is that of macaques in Hachijojima island, Japan. These primates used to live in the inland forest until the 1960s, when a group of researchers started giving them some potatoes on the beach: soon they started venturing onto the beach, picking the potatoes from the sand, and cleaning and eating them. About one year later, an individual was observed bringing a potato to the sea, putting it into the water with one hand, and cleaning it with the other. Her behaviour was soon imitated by the individuals living in contact with her; when they gave birth, they taught this practice to their young.

The National Institutes of Health recently reported that capuchin monkeys preferred the company of researchers who imitated them to that of researchers who did not imitate

them. The monkeys not only spent more time with their imitators, but also preferred to engage in a simple task with them even when provided with the option of performing the same task with a non-imitator.

Mating and the fight for supremacy

Individual reproduction is the most important phase in the proliferation of individuals or genes within a species: for this reason, we can often observe complex mating rituals, which can be very complex even if they are often regarded as fixed action patterns **(FAPs)**. The Stickleback's complex mating ritual was studied by Niko Tinbergen and is regarded as a notable example of a FAP. Often in social life, animals fight for the right of reproducing themselves as well as social supremacy.

A common example of fight for social and sexual supremacy is the so-called pecking order among poultry. A pecking order is established every time a group of poultry co-lives for a certain amount of time. In each of these groups, a chicken is dominating among the others and can peck before anyone else without being pecked. A second chicken can peck all the others but the first, and so on. The chicken in the higher levels can be easily distinguished for their well-cured aspect, as opposed to the ones in the lower levels. During the period in which the pecking order is establishing, frequent and violent fights can happen, but once it is established it is only broken when other individuals are entering the group, in which case the pecking order has to be established from scratch.

Living in groups

Several animal species, including humans, tend to live in groups. Group size is a major aspect of their social environment. Social life is probably a complex and effective survival strategy. It may be regarded as a sort of symbiosis among individuals of the same species: a society is composed of a group of individuals belonging to the same species living within well-defined rules on food management, role assignments and reciprocal dependence.

The situation is actually much more complex than it seems. When biologists interested in evolution theory first started examining social behaviour, some apparently unanswerable questions occurred. How could, for instance, the birth of sterile castes, like in bees, be explained through an evolving mechanism which emphasizes the reproductive success of as many individuals as possible? Why, among animals living in small groups like squirrels, would an individual risk its own life to save the rest of the group? These behaviours may be examples of altruism. Of course, not all behaviours are altruistic, as indicated by the table below. Notably, revengeful behaviour was at one point claimed to have been observed exclusively in *Homo sapiens*. However other species have been reported to be vengeful, including reports of vengeful camels and vengeful chimpanzees.

Classification of social behaviours

Type of behaviour	Effect on the donor	Effect on the receiver
Egoistic	Increases fitness	Decreases fitness
Cooperative	Increases fitness	Increases fitness
Altruistic	Decreases fitness	Increases fitness
Revengeful	Decreases fitness	Decreases fitness

The existence of egoism through natural selection doesn't pose any question to evolution theory and is, on the contrary, fully predicted by it, as well as for the cooperative behaviour. It is more difficult to understand the mechanism through which the altruistic behaviour initially developed.

Tinbergen's four questions for ethologists

Lorenz's collaborator, Niko Tinbergen, argued that ethology always needed to include four kinds of explanation in any instance of behaviour:

- Function — How does the behaviour affect the animal's chances of survival and reproduction? Why does the animal respond that way instead of some other way?
- Causation — What are the stimuli that elicit the response, and how has it been modified by recent learning?
- Development — How does the behaviour change with age, and what early experiences are necessary for the behaviour to be displayed?
- Evolutionary history — How does the behaviour compare with similar behaviour in related species, and how might it have begun through the process of phylogeny?

These explanations are complementary rather than mutually exclusive - all instances of behaviour require an explanation at each of these four levels. For example, the function of eating is to acquire nutrients (which ultimately aids survival and reproduction), but the immediate cause of eating is hunger (causation). Hunger and eating are evolutionarily ancient and are found in many species (evolutionary history), and develop early within an organism's lifespan (development). It is easy to confuse such questions - for example to argue that people eat because they're hungry and not to acquire nutrients - without realizing that the reason people experience hunger (causation) is because it causes them to acquire nutrients (function).

Growth of the field

By the work of Lorenz and Tinbergen, ethology developed strongly in continental Europe during the years prior to World War II. After the war, Tinbergen moved to the University of Oxford, and ethology became stronger in the UK, with the additional influence of William Thorpe, Robert Hinde, and Patrick Bateson at the Sub-department of Animal Behaviour of the University of Cambridge, located in the village of Madingley. In this period, too, ethology began to develop strongly in North America.

Lorenz, Tinbergen, and von Frisch were jointly awarded the Nobel Prize in Physiology or Medicine in 1973 for their work of developing ethology.

Ethology is now a well recognised scientific discipline, and has a number of journals covering developments in the subject, such as the Ethology Journal. In 1972, the International Society for Human Ethology was founded to promote exchange of knowledge and opinions concerning human behavior gained by applying ethological principles and methods and published in their journal, The Human Ethology Bulletin. During 2008, in a paper published in the journal Behaviour, ethologist Peter Verbeek introduced the term "Peace Ethology" as a sub-discipline of Human Ethology that is concerned with issues of human conflict, conflict resolution, reconciliation, war, peacemaking, and peacekeeping behavior.

Social ethology and recent developments

During 1970, the English ethologist John H. Crook published an important paper in which he distinguished **comparative ethology** from **social ethology**, and argued that much of the ethology that had existed so far was really comparative ethology—examining animals as individuals—whereas in the future ethologists would need to concentrate on the behaviour of social groups of animals and the social structure within them.

Also in 1970, Robert Ardrey's book *The Social Contract: A Personal Inquiry into the Evolutionary Sources of Order and Disorder* was published. The book and study investigated animal behaviour and then compared human behaviour as a similar phenomenon.

Indeed, E. O. Wilson's book *Sociobiology: The New Synthesis* appeared in 1975, and since that time the study of behaviour has been much more concerned with social aspects. It has also been driven by the stronger, but more sophisticated, Darwinism associated with Wilson, Robert Trivers and William Hamilton. The related development of behavioural ecology has also helped transform ethology. Furthermore, a substantial rapprochement with comparative psychology has occurred, so the modern scientific study of behaviour offers a more or less seamless spectrum of approaches – from animal cognition to more traditional comparative psychology, ethology, sociobiology and behavioural ecology. Sociobiology has more recently developed into evolutionary psychology.

Chapter 10

Bee Learning and Communication

Honey bees learn and communicate in order to find food sources and for other means.

Swarming bees require good communication in order to congregate all in the same spot

Learning

Learning is essential for efficient foraging. Honey bees are unlikely to make many repeat visits if a plant provides little in the way of reward. A single forager will visit different flowers in the morning and, if there is sufficient attraction and reward in a particular kind of flower, she will make visits to that type of flower for most of the day, unless the plants stop producing reward or weather conditions change. Honey bees are quite adept at associative learning, and many of the standard phenomena of classical conditioning take the same form in honey bees as they do in the vertebrates that are the more usual subjects of such experiments.

Foragers were trained to enter a simple Y-shaped maze that had been marked at the entrance with a particular color. Inside the maze was a branching point where the bee was required to choose between two paths. One path, which led to the food reward, was marked with the same color that had been used at the entrance to the maze, while the other was marked with a different color. Foragers learned to choose the correct path, and continued to do so when a different kind of marker (black and white stripes oriented in various directions) was substituted for the colored markers. When the experimental conditions were reversed, rewarding bees for choosing the inner passage marked with a symbol that was different from the entrance symbol, the bees again learned to choose the correct path. Extending the length of the tunnel to increase the time between seeing the one marker indicating the correct path and a second marker identifying the correct path show that the bees can retain the information in their visual working memory for about 5 seconds, equivalent to the short-term memory of birds.

Color Learning in Honeybees

One of the most common ways that honey bees, *Apis mellifera*, demonstrate associative learning is in the context of color recognition and discrimination tasks. Just as vertebrate species such as mice or pigeons that can be trained to perform associative learning tasks, honey bees make excellent subjects for tasks involving discrimination and color memory. Beginning in the early 1900s, scientists Karl von Frisch and later Randolf Menzel began asking questions about the existence, learning rates, memory, and timing of color vision in bees.

Color Discrimination

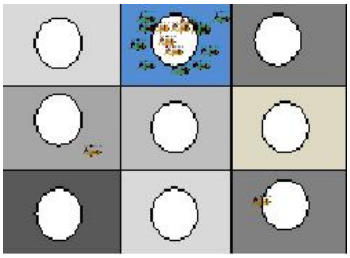


Figure 1. Testing for color vision in honey bees. The majority of bees flew directly to the dish with the blue background as they had been trained to do. Thus, they were able to

discriminate between gray and blue backgrounds, showing their capability for color vision.

The Austrian zoologist Karl von Frisch began the exploration of color vision in honey bees when he asked the first question in 1919: does color vision in bees exist? By making use of bees associative learning abilities he performed an elegant experiment to show that honey bees were in fact capable of color discrimination.

To test color vision, von Frisch first trained his honey bees to feed from a small dish filled with a nectar-like sugar water. This dish was placed over a small piece of blue colored cardboard so that the color was visible to the bees as they fed. Once the bees had become accustomed to the blue cardboard, von Frisch surrounded the blue piece of cardboard with other identically sized pieces in varying shades of gray and placed small dishes over each piece. If bees could not discriminate between colors, they would be unable to distinguish the blue piece from the many gray toned pieces. In the case that bees did not have color vision then, von Frisch predicted that the bees would visit the gray and blue pieces with equal frequency, as they would not be able to tell a difference between them.

When he allowed bees access to the dishes, however, he found that the vast majority of the bees flew directly to the blue piece of cardboard on which they had previously obtained their sugar-water reward. The bees largely ignored the gray pieces which had not been rewarded. This directed exploration and targeting of the blue cardboard showed the bees could indeed discriminate between the gray and blue shades, showing that bees do possess color vision. Von Frisch repeated this same basic experiment to show that bees produced the same results with other colors like red and yellow. Later other researchers were able to apply this excellent experimental design to other vertebrates as well, making it an invaluable insight into testing color vision in many organisms.

Color Learning Rates and Preferences

After von Frisch's initial studies, the German scientist Randolf Menzel continued the study of color vision in honey bees and performed more detailed tests. He was curious about which colors honey bees would be able to learn fastest and whether or not bees had a greater aptitude for learning certain colors.

He used lights of varying color and intensity to illuminate circles of light on a solid surface. This set up was similar to the pieces of colored cardboard employed by von Frisch, but by using light instead of cardboard, Menzel was able to change the intensity and color of light easily. He could simply adjust the projection of the light to create a wide variety of different experimental set-ups.

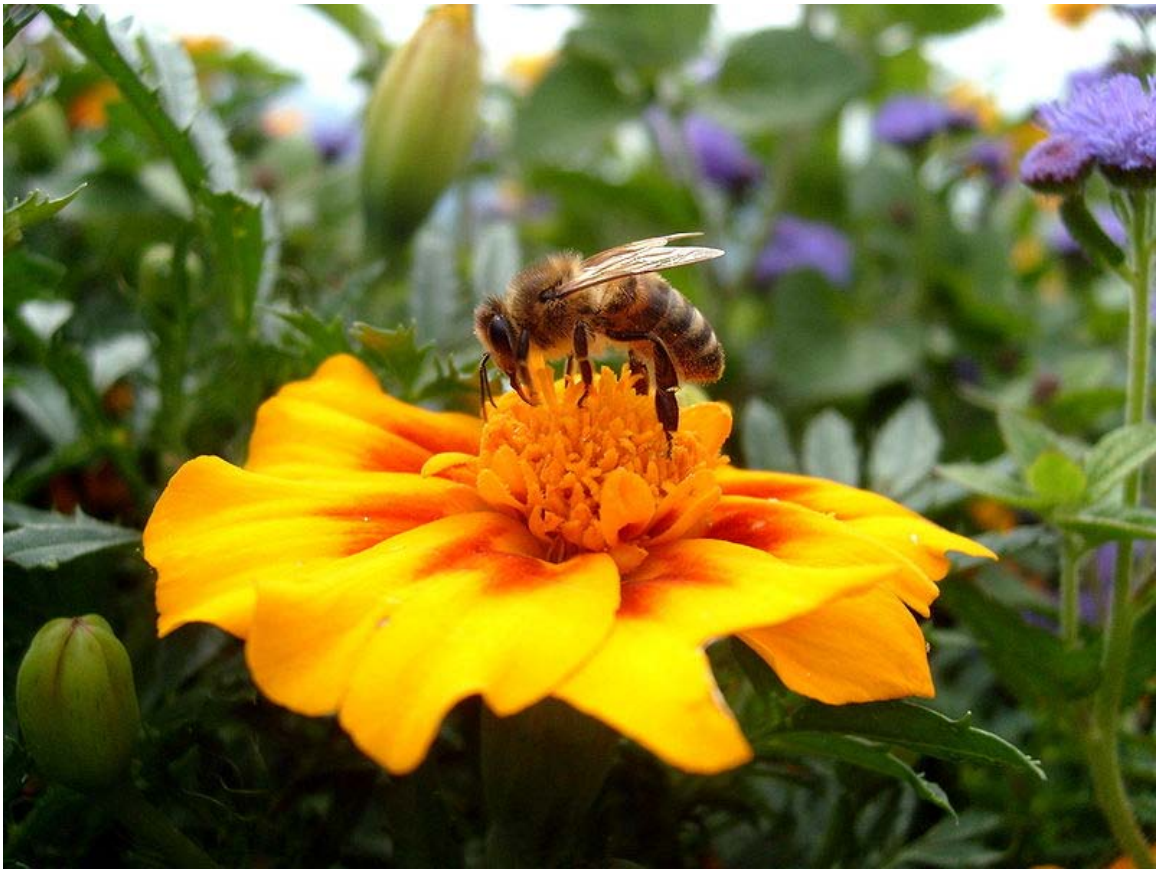


Figure 2. Honey bee collecting pollen

To test the intricacies of the bee color vision von Frisch had established, Menzel performed an experiment that aimed to test bees ability to distinguish between two different colors. To do this, Menzel used a projected circle of colored light surrounding a small dish that could hold a sugar-water reward. Menzel then projected a second circle of differently colored light surrounding a second dish some distance away from the first. Next, a single bee was placed equidistant between these two different lights and allowed to choose which dish to search for a sugar-water treat. Only one of the colored light circles surrounded a dish that contained sugar-water; the other was empty. Menzel was then able to measure how quickly the bees learned to preferentially search only the rewarded light and to ignore the dish surrounded by unrewarded light.

Interestingly, the results of the experiment showed that bees did not learn to discriminate between all color pairs equally well. The fastest rate of learning was when violet light was rewarded. The color that the bees had the most difficulty learning was green, and all other colors fell somewhere in between. This evidence of inherent bias is evolutionarily reasonable given that color vision in bees allows them to distinguish between different nectar-bearing flowers, much like the rewarded dishes. As more flowers are purple than green it makes sense that bees would be more sensitive to colors likely to result in nourishment.

Color Memory

After this work on color preferences, Menzel extended his experiments to study memory in honey bee color vision. He wanted to know how many trials were necessary for honey bees to reliably choose a previously rewarded color when presented with several choices for potential rewards and how long honey bees could retain information about which color would be rewarded.

To test these questions, Menzel performed a variety of experiments. First, he presented individual bees with a sugar reward on a colored background for just a single trial. He then kept these bees in small cages for several days without any further trials. After a few days, he presented each bee with several dishes each on a different colored background at once. One of the colors was the same as that used during the initial trial. The others were novel, unrewarded colors. Amazingly, after just one trial and several days without any exposure to the rewarded color, bees correctly chose to explore the color used in the first trial more than fifty-percent of the time.

Menzel then repeated this experiment with another group of bees, keeping all factors the same except that in the second round of testing he gave the bees three initial trials with the rewarded color instead of just one. After several days in confinement when the bees were presented with a choice of colors just as in the first experiment, they virtually always chose the color that had been used during the first three trials.

This ability to retain information about color-linked rewards over a period of several days and after only very minimal exposure to the colored background indicates the great strength of honeybees memory with respect to color vision.

Timing in Color Learning

One of von Frisch's students, Elizabeth Opfinger, observed that bees would learn color when approaching a feeder. Menzel took this question further: when do bees register and learn color? He wanted to know if bees registered color before, during, or after receiving their sugar-water reward. In order to explore this intriguing question, Menzel displayed the color beneath a rewarded dish at different stages of the honey bee feeding process: during approach, feeding and departure.

The outcome of this experiment revealed that bees register color during both the approach and feeding stages of the exposure process. In order for a bee to accurately remember a given color, it must be present for approximately five seconds in total. Although it varies slightly, Menzel and his colleagues found that bees usually remember best when the stimulus is present for about three seconds during the approach and two seconds after landing and beginning to feed.

The Neurobiology of Color Vision

Figure 3. Western Honey Bee

Color vision in honey bees can also be examined from a neurobiological perspective in terms of the structure and organization of their compound eyes.

In 1975 Menzel published a seminal paper describing the morphology and spectral sensitivity of the honey bee eye. He examined color coding the honey bee retina by using a technique to mark individual cells with a fluorescent dye and record from these cells as single units. Such fine structure analysis allowed him to determine that there are three types of receptors in the honey bee eye: 1) UV receptors, 2) blue receptors, and 3) green receptors. The three receptors are dominated by three rhodopsin-like pigments. These pigments have maximal absorbance at wavelengths corresponding to 350 nm, 440 nm, and 540 nm.

As the cells were examined in detail, certain features were distinguishable for each type of receptor cell. UV cells were found to form the longest visual fibres. These long visual fibers penetrated the lamina with arborizations, a tree-like branching of the fibers and spines. Blue and green receptor cells have more shallow fibers.

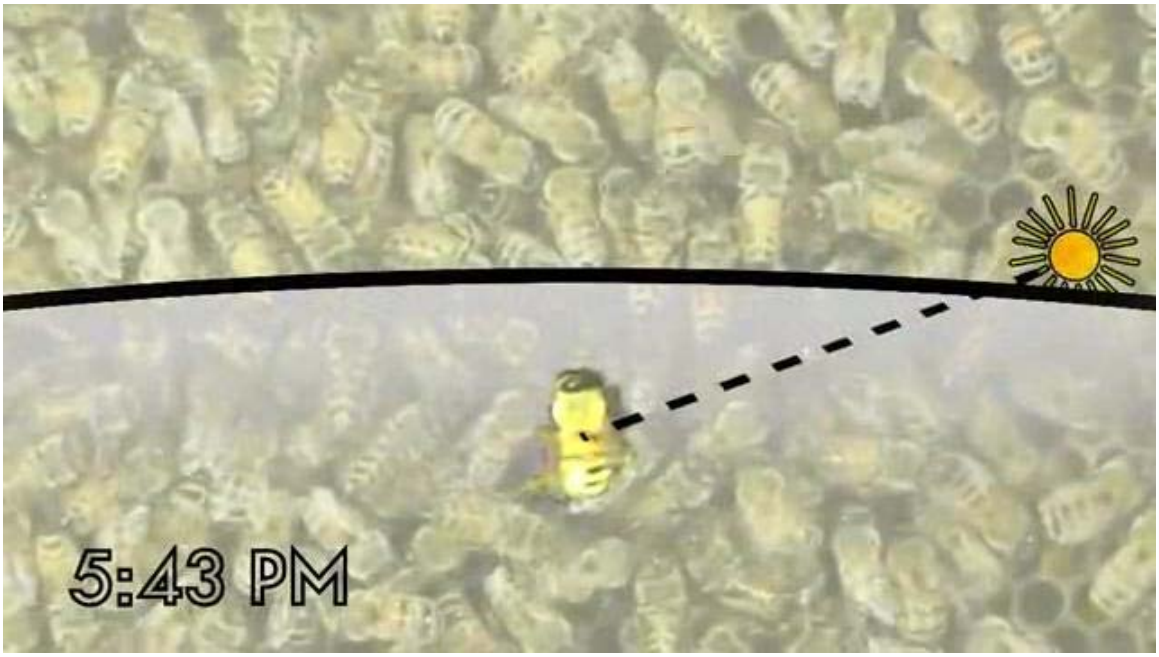
Interestingly, Menzel found that most of the cells he studied had secondary sensitivities that corresponded to wavelength regions at which the other two receptor types were

maximally active. He used spectral efficiency experiments to show that such corresponding wavelength receptivity is the result of electric coupling.

Communication

Foragers communicate their floral findings in order to recruit other worker bees of the hive to forage in the same area. The factors that determine recruiting success are not completely known but probably include evaluations of the quality of nectar and/or pollen brought in.

There are two main hypotheses to explain how foragers recruit other workers — the "waggle dance" or "dance language" theory and the "odor plume" theory. The dance language theory is far more widely accepted, and has far more empirical support. The theories also differ in that the former allows for an important role of odor in recruitment (i.e., effective recruitment relies on dance *plus* odor), while the latter claims that the dance is essentially irrelevant (recruitment relies on odor alone).



The Waggle Dance of the Honeybee

It has long been known that successfully foraging Western honey bees perform a dance on their return to the hive, known as *waggle dance*, indicating that food is farther away, while the *round dance* is a short version of the *waggle dance*, indicating that food is nearby. The laden forager dances on the comb in a circular pattern, occasionally crossing the circle in a zig-zag or waggle pattern. Aristotle described this behaviour in his Historia Animalium. It was thought to attract the attention of other bees.

In 1947, Karl von Frisch correlated the runs and turns of the dance to the distance and direction of the food source from the hive. The orientation of the dance correlates to the relative position of the sun to the food source, and the length of the waggle portion of the run is correlated to the distance from the hive. Also, the more vigorous the display is, the better the food. There is no evidence that this form of communication depends on individual learning.

Von Frisch performed a series of experiments to validate his theory. He was awarded the Nobel Prize in Physiology or Medicine in 1973 for his discoveries.

One of the most important lines of evidence on the origin and utility of the dance is that all of the known species and races of honey bees exhibit the behavior, but details of its execution vary among the different species. For example, in *Apis florea* and *Apis andreniformis* (the "dwarf honeybees") the dance is performed on the dorsal, horizontal portion of the nest, which is exposed. The runs and dances point directly toward the resource in these species. Each honey bee species has a characteristically different correlation of "waggling" to distance, as well. Such species-specific behavior suggests that this form of communication does not depend on learning but is rather determined genetically. It also suggests how the dance may have evolved.

Various experiments document that changes in the conditions under which the dance is performed lead to characteristic changes in recruitment to external resources, in a manner consistent with von Frisch's original conclusions. Researchers have also discovered other forms of honeybee dance communication, such as the tremble dance.

Odor plume

While the majority of researchers believe that bee dances give enough information to locate resources, proponents of the odor plume theory argue that the dance gives no actual guidance to a nectar source. They argue that bees instead are primarily recruited by odor. The purpose of the dance is simply to gain attention to the returning worker bee so she can share the odor of the nectar with other workers who will then follow the odor trail to the source.

The primary lines of evidence used by the odor plume advocates are

1. clinical experiments with odorless sugar sources which show that worker bees are unable to recruit to those sources and
2. logical difficulties of a small-scale dance (a few centimeters across) giving directions precise enough to hold the other bees on course during a flight that could be several kilometers long. Misreading by even a few degrees would lead the bee off course by hundreds of meters at the far end.

Neither of these points invalidate the dance theory, but simply suggest out that odor might be involved, which is indeed conceded by all proponents of dance theory. Critics of the odor plume theory counter that most natural nectar sources are relatively large -

orchards or entire fields. Precision may not be necessary or even desirable. They have also challenged the reproducibility of the odorless source experiment.

Significant to the argument are the elegant experiments of William F. Towne, of the Kutztown University in Pennsylvania, such as this pdf file, in which hives are moved to "mirror image" terrain settings, and thus fooled into both dancing about the wrong location for a nectar source, and successfully recruiting foragers to that wrong location, but only when the sun is obscured by clouds, forcing them to rely on terrain-based navigation rather than "solar ephemeris" based navigation. As the cloud cover breaks up, more and more bees correct their dances to indicate the actual location of nectar, and forager visits shift to the correct location.

The academic debate between these two theories is extremely polarized and often hostile. Adrian Wenner, a modern bee researcher, is the chief proponent of the odor plume theory (anti-dance). One supporter of Wenner's theories, Julian O'Dea, has proposed an evolutionary explanation for the "waggle dance" that does not involve communication from one bee to another, by claiming it may be a simple idiothetic movement that conveys no information . Conversely, experiments with robotic dummies were indeed able to induce some recruitment, which should not have been possible if the dance contains no information.

An article in the 18 September 2009 issue of New Scientist sets out evidence against the use by bees of the information in the dance.

The controversy persists, though it does so primarily due to an asymmetry between the two "camps"; those who study dance communication freely admit that odor is an essential component of the system, and even necessary at various stages of the recruitment process, including once a recruited forager reaches the vicinity of the resource (e.g.), while odor-plume advocates do not acknowledge that the dance contains any information whatsoever. Various experimental results demonstrate that the dance does convey information, but the use of this information may be context-dependent (e.g.), and this may explain why the results of earlier studies were inconsistent. In essence, both sides of the "controversy" agree that odor is used in recruitment to resources, but they differ strongly in opinion as to the information content of the dance.

Odor learning is usually tested by a method called the proboscis extension reflex.

Note: much of the research on the two competing hypotheses of communication has been restricted to Western honey bees. Other species of *Apis* use variants on the same theme, and other types of bees use other methods altogether.

Trophallaxis

The exchange of food, trophallaxis, is also used by means to communicate and includes information on the quality of and thus competition for a food source, temperature and water demand, and the condition of the queen (Sebeok, 1990).

Primer Pheromones

Research that was published in November 2004, by scientists under the leadership of Dr. Zachary Huang, Michigan State University indicates that so called primer pheromones play an important part in how a honey bee colony adjusts its distribution of labor most beneficially. In order to survive as a bee colony of sometimes 50,000 -100,000 individual bees, the communal structure has to be adaptable to seasonal changes and the availability of food. The division of labor has to adjust itself to the resources available from foraging. While the division of labor in a bee colony is quite complex, the work can be roughly seen as work inside the hive and outside the hive. Younger bees play a role inside the hive while older bees play a role outside the hive mostly as foragers. Huang's team found that forager bees gather and carry a chemical called ethyl oleate in the stomach. The forager bees feed this primer pheromone to the worker bees, and the chemical keeps them in a nurse bee state. The pheromone prevents the nurse bees from maturing too early to become forager bees. As forager bees die off, less of the ethyl oleate is available and nurse bees more quickly mature to become foragers. It appears that this control system is an example of decentralized decision making in the bee colony.

Cognition

Experiments by James Gould suggest that honey bees may have a cognitive map for information they have learned, and utilize it when communicating.

In one test reported in a 1983 issue of *Science News*, he moved a supply of sugar water 25% further away from a hive each day. The bees communicated to each other as usual on its location. Then he placed the sugar water on a boat anchored in the middle of a small lake. When scouts returned to the hive to communicate their find, other bees refused to go with them, not expecting to find food in the middle of a lake, even though they frequently flew over the lake to reach pollen sources on the opposite shore.

In another test related in the August 1986 issue of *Discover* ("A Honey of a Question: Are Bees Intelligent?"), Gould lured some bees to a dish of artificial nectar, then gradually moved it farther from the hive after they became accustomed to it. He marked the addicted bees, placed them in a darkened jar, and relocated them to a spot where the hive was still visible, but not the dish. When released one by one, the bees would appear disoriented for a few seconds, then fly directly for the covert dish. 73 of 75 bees reached it in about 28 seconds. They apparently accomplished this feat by devising a new flight path based on a cognitive map of visible landmarks.

Chapter 11

Cat Communication

A primary method by which cats communicate is through body language.

Cat communication is the range of methods by which cats communicate with other cats, humans, and other animals. Communication methods include postures, movement (including "quick, fine" movements not generally perceived by human beings), and auditory and chemical signals.

The communication methods used by cats have been impacted by the domestication process.

Auditory communication methods

Meowing

A cat meowing

Adult cats do not normally meow to each other, and so the meowing to human beings that domesticated cats exhibit is likely partly an extension of the use of this plaintive signal. When communicating with human beings, adult cats express variations of this tone to demand food or attention, register complaints, and convey bewilderment. An alteration in tone, pace, or punctuation changes the meaning, however slight.

While cats occasionally vocalize to one another with purrs, growls, and screeches, they generally communicate with one another through body language. When preparing to fight an adversary or to frighten one away, cats can emit long, articulated meows. Most vocalizations recognized as "meow" are specifically for human interaction.

The word *meow* is itself an onomatopoeia with various spellings including meow, miaow, miaou, mrow, mau, me-ow, and myow, and sometimes other sounds such as reow, or booreow.

Purring

A purr is a sound made by all species of felids. A tonal buzzing can characterize differently between cats. Domestic cats purr in a frequency of 25 to 150 vibrations per second. Purring is often understood as signifying happiness; however, cats sometimes purr when they are ill, or during tense, traumatic, or painful moments.

Although purring is a universally recognized phenomenon, the mechanism by which cats purr is elusive. This is partly because the cat has no unique anatomical feature that is clearly responsible for the sound.

Other noises

A cat hissing and arching its back to make itself appear larger to ward off a threat.

Most cats growl or hiss when angered or feeling threatened, which serves as a warning to the offending party. If the warning is not heeded, a more or less serious attack may follow. Some may engage in nipping behavior or batting with their paws, with claws either extended or retracted.

Most cats make chirping or chattering noises when observing prey. Proposed explanations for this behavior include that it is a threatening sound, an expression of

excitement or frustration, or an attempt to replicate a bird-call (or replicate the call of a bird's prey, for example a cicada). Recent animal behaviourists have theorized that it is a "rehearsal behaviour" in which the cat anticipates or practices the killing of prey, because the sound usually accompanies a biting movement similar to the one they use to kill their prey (the "killing bite", which saws through the victim's neck vertebrae).

Some cats will snort (exhale sharply) after a determined effort to catch something has fallen short.

Some cats (including tigers) will chirrup or chudder as a form of greeting.

Some cats grunt while purring when given physical attention. Contented sleeping cats make soft humming sounds, similar to sighs, when petted. The cry of a cat in heat is called a caterwaul.

Cats in close contact with human beings use vocalization more frequently than cats that live in the wild, the reason being that owners respond strongly to cat vocalizations, reinforcing the behavior. Adult cats in the wild rarely vocalize; they use mostly body language and scent to communicate.

Body language

A surprised cat

Cats communicate a variety of messages using body language. Examples include arching their backs as a signal of fear or aggression, and slowly blinking to signal relaxation. A cat that chooses to lie with its stomach and chest exposed conveys happiness, trust, and comfort (this is also typical of overweight cats, as it is more comfortable for them); however, a cat may also roll on its side or back to be able to defend itself with all four sets of claws. Usually other signs (like ears and whiskers folded backwards) give an indication of the cat's overall humour. Flattened ears mean that the cat feels threatened, and may attack. Mouth open and no teeth exposed suggests a feeling of playfulness.

A mackerel tabby cat kneading a blanket before a nap. Note the forward position of the whiskers, indicating happiness or curiosity.

A young black cat, showing relaxation and happiness.

As is the case with dogs, the tail is often used as a signaling mechanism. A tail held high suggests confidence or happiness, or can be used as a greeting towards human beings or other cats (usually close relatives), while a half-raised tail shows less pleasure, and unhappiness is indicated with a tail held low. In addition, a cat's tail may "wag" or move rapidly to express a state of conflict. A cat with tail held high and twitching shows excitement, but this is often mistaken for anger. Cats will twitch the tips of their tails when hunting or when irritated, while larger twitching indicates displeasure. They may also twitch their tails when playing. A scared or surprised cat may puff up its tail, and the hair along its back may stand straight up and the cat will turn its body sideways to a threat, in order to increase its apparent size. Tailless cats, such as the Manx, which possess only a small stub of a tail, move the stub around as though they possess a full tail.

Touching noses is a friendly greeting for cats, while a lowered head is a sign of submission. Some cats will rub their faces along their guardian's cheek, hands, or ankles as a friendly greeting or sign of affection. This action is also sometimes a way of "marking their territory", leaving a scent from the scent glands located in the cat's cheeks. More commonly, cats do something called a "head bonk", or "bunting", where they literally bump someone with the front part of their heads to express affection.

A Tortoiseshell Cat yawning

Cats also lick each other and people (e.g. their owners). Cats lick each other to groom one other and to bond (this grooming is usually done between cats that know each other very well). They will also sometimes lick people for similar reasons. These reasons include wanting to "groom" people and to show them care and affection.

When cats are happy, they are known to paw their human companions, or a soft object on which they may be sitting, with a kneading motion also called "padding", "pitter-patting", "pacing", "kneading dough", "happy feet", "treading", "needle paws" and "marching in place". Cats often use this action alongside purring to show contentment and affection for their companions. This can also indicate curiosity. A cat may also do this when in pain or dying, as a method of comforting itself. It is instinctive to cats, and they use it when they

are young to stimulate the mother cat's breast to release milk during nursing. As a result, cats hand-raised by human beings may not exhibit this behaviour. Pawing is also a way for cats to mark their territory. The scent glands on the underside of their paws release small amounts of scent onto the person or object being pawed, marking it as "theirs" the same way they would urinate to mark their territory. Since the nature of the activity is an instinctive response related to the mother's care for the kitten, it may be an expression of need, indicating an empty water bowl, hunger, an unappealing litter box, or the need for some attention from the caregiver.

Biting

A bite accompanied by hissing or growling is not a demonstration of playful behavior. When cats mate, the male tom bites the scruff of the female's neck as she assumes a position conducive to mating. However, cats familiar with their owners will bite someone else suddenly and painfully in response to uncomfortable petting.

Scent

Cats can communicate through scent via urine, feces, and chemicals in skin glands located around the mouth, tail, and paws. They also use scent in order to mark their territory. If another animal tries to get in the cat's territory, it will fight for the territory, or the cat will scare the animal off. Urine spraying is also a territorial marking. Cats rub up against furniture or doorways to mark the items as "theirs". When cats rub people, they are marking them with their scent, claiming them as "theirs". In addition, they are picking up the peoples' scents.

Chapter 12

Mobbing (Animal Behavior)

Crows mobbing a Red-tailed Hawk.

Mobbing in animals is an antipredator behavior which occurs when individuals of a certain species mob a predator by cooperatively attacking or harassing it, usually to protect their offspring. A simple definition of mobbing is an assemblage of individuals around a potentially dangerous predator. This is most frequently seen in avian species, though it is also known to occur in many other animals such as the Meerkat. While mobbing has evolved independently in many species, it only tends to be present in those whose young are frequently preyed upon. This behavior may complement cryptic

adaptations in the offspring themselves, such as camouflage and hiding. **Mobbing calls** may be used to summon nearby individuals to cooperate in the attack.

Konrad Lorenz, in his book entitled On Aggression (1966), first described mobbing among birds and animals, attributing it to instincts rooted in the Darwinian struggle to survive. In his view, we humans are subject to similar innate impulses but capable of bringing them under rational control.

Mobbing in birds

A Great Kiskadee (right) mobs a hawk.

Crow mobbing perched Bald Eagle

"Dive-bombing"

Birds that breed in colonies such as gulls are widely seen to attack intruders, including encroaching humans. Through mobbing, mockingbirds can effectively force a cat or dog to seek something less troublesome. One mockingbird might fly in front of the cat or dog, enticing a common predator upon birds to lunge, while another pecks at the cat or dog from behind to inflict a sharp pain that forces the predator to hesitate when it encounters mockingbirds. Behavior includes flying about the intruder, dive bombing, loud squawking and defecating on the predator. Costs of mobbing behavior include the risk of engaging with predators, as well as energy expended in the process. Black-headed Gulls are one species which aggressively engages intruding predators, such as Carrion Crows. Classic experiments on this species by Hans Kruuk involved placing hen eggs at intervals from a nesting colony, and recording the percentage of successful predation events as well as the probability of the crow being subjected to mobbing. The results showed decreasing mobbing with increased distance from the nest, which was correlated with increased predation success. Mobbing may function by reducing the predator's ability to locate nests (as a distraction) since predators cannot focus on locating eggs while they are under attack.

Besides the ability to drive the predator away, mobbing also draws attention to the predator, making stealth attacks impossible. Mobbing plays a critical role in the identification of predators and inter-generational learning about predator identification. Reintroduction of species is often unsuccessful, because the established population lacks this cultural knowledge of how to identify local predators. Scientists are exploring ways to train populations to identify and respond to predators before releasing them into the wild.

Adaptationist hypotheses regarding why an organism should engage in such risky behavior have been suggested by Eberhard Curio, including advertising their physical fitness and hence uncatchability (much like stotting behavior in gazelles), distracting predators from finding their offspring, warning their offspring, luring the predator away, allowing offspring to learn to recognize the predator species, directly injuring the predator or attracting a predator of the predator itself. The much lower frequency of attacks between nesting seasons suggests such behavior may have evolved due to its benefit for the mobber's young. Niko Tinbergen argued that the mobbing was a source of confusion to gull chick predators, distracting them from searching for prey . Indeed, an intruding carrion crow can only avoid incoming attacks by facing its attackers, which prevents it from locating its target.

Besides experimental research, the comparative method can also be employed to investigate hypotheses such as those given by Curio above. For example, closely related species such as the Kittiwake do not show mobbing behavior. The kittiwake's cliff nests are almost completely inaccessible to possible predators due to gusty winds and sheer cliffs, meaning its young are not at risk to predation like the Black-headed Gull. This is an example of an evolutionary pattern known as divergent evolution.

Mobbing is thought to carry risks to roosting predators, including potential harm from the mobbing birds, or attracting larger, more dangerous predators. Birds at risk of mobbing such as owls have cryptic plumage and hidden roosts to reduce this danger.

In other animals

The occurrence of mobbing behavior across widely different taxa, including California Ground Squirrels, is evidence of convergent evolution.

Another way the comparative method can be used here is by comparing gulls with distantly related organisms. This approach relies on the existence of convergent evolution, where distantly related organisms evolve the same trait due to similar selection pressures. As mentioned, many bird species such as the swallows also show mobbing of predators, however even more distantly related species including mammals have been known to engage in this behavior. One example is California ground squirrels, which are known to distract predators such as the rattlesnake and gopher snake from locating their nest burrows by kicking sand into their eyes. This social species also uses alarm calls.

Mobbing has also been observed in fish. For example, bluegills have been seen to attack snapping turtles. Bluegills, which form large nesting colonies, were seen to attack both released and naturally occurring turtles, which may function to advertise their presence, drive the predator from the area, or aid in cultural transmission of predator recognition.

Mobbing calls

The Great Tit, a passerine bird, employs both mobbing behavior and alarm calls.

Mobbing calls are signals made by the mobbing species while harassing a predator. These differ from alarm calls, which allow con-specifics to *escape* from the predator. The Great Tit, a European songbird uses such a signal to call on nearby birds to harass a perched bird of prey, such as an owl. This call occurs in the 4.5kHz range, and is effective in traveling long distances. However, when their prey are in flight, they employ an alarm signal in the 7–8 kHz range. This call is less effective at travelling great distances, but is much more difficult for both owls and hawks to hear (and detect the direction from which the call came). In the case of the alarm call, it is disadvantageous to the sender if the predator picks up on the signal, hence selection has favored those birds able to hear and employ calls in this higher frequency range.

Mobbing calls may also be part of an animal's arsenal in harassing the predator. Studies of *Phainopepla* mobbing calls indicate it may serve to enhance the swooping attack on the predators, including Scrub Jays. In this species, the mobbing call is smoothly upsweeping, and is made when swooping down in an arc beside the predator. This call

was also heard during agonistic interactions with conspecifics, and may serve additionally or alternatively as an alarm call to their mate.

Evolution

The evolution of mobbing behavior is explained using evolutionarily stable strategies, which are in turn based on game theory.

Mobbing involves risks (costs) to the individual and benefits (payoffs) to the individual and others. The individuals themselves are often genetically related, and mobbing is increasingly studied with the gene-centered view of evolution by considering inclusive fitness (the carrying on of one's genes through one's family members), rather than merely benefit to the individual.

By cooperating to successfully drive away predators all individuals involved increase their chances of survival and reproduction. An individual stands little chance against a larger predator, but when a large group is involved, the risk to each group member is minimized. By being in a large group, the risk for a particular individual is reduced or diluted. This so-called dilution effect proposed by W. D. Hamilton is another way of explaining the benefits of cooperation by selfish individuals. Lanchester's laws also provide an insight into the advantages of attacking in a large group rather than individually.

Another interpretation involves the use of the handicap principle. Here the idea is that a mobbing bird, by apparently putting itself at risk, displays its status and health so as to be preferred by potential partners.