

Individual Recognition in Animal Species

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No empirical evidence is required to convince even the most skeptical reader that humans use distinctive facial and vocal features as cues for recognizing other individuals, and that individual recognition provides the foundation for our social relationships. Based on our own experiences, we also know that the recognition of a particular individual, say a friend or colleague, entails a multifaceted representation, or concept, of that individual. In other words, we often possess knowledge about recognized individuals gained through previous social interactions that goes far beyond the mere characteristic appearances of their faces or sounds of their voices. This knowledge, in part, determines the conditions for our present and future social interactions.

But what can be said of the role of individual recognition in the social behavior of nonhuman animals? There is ample evidence from a range of species that other animals also base many of their social interactions on an ability to recognize other individuals, such as relatives, mates, and members of their social group. However, providing a general and concise answer to questions about 'social recognition' in animals is exceedingly difficult, given the diversity of social recognition systems found in nature, the diversity of species and behavioral contexts in which social recognition has been investigated, and the diversity of approaches and perspectives taken by animal behaviorists in their investigations of social recognition. Therefore, no short review of the subject, including this one, can be comprehensive.

In this article, the basic components common to all social recognition systems, and two general mechanisms that mediate social recognition in animals, are described, and several different perspectives on social recognition in animals are briefly discussed. Because most animal studies investigate the role of communication in social recognition, the article will focus on communication-based social recognition systems. Several evolutionarily important behavioral contexts of communication-based social recognition are described, with an emphasis on acoustically mediated social recognition systems, and three experimental approaches to the study of social recognition in animals are briefly discussed. Finally, a general model of communication-based social recognition is outlined, making explicit how different perspectives on social recognition may be integrated. Readers of this article, especially those not accustomed to thinking about

the behavior of nonhuman animals, should keep the following two points in mind:

1. We should expect social recognition systems to differ among species, and these differences should reflect adaptations to different species-typical social environments within constraints imposed by an animal's perceptual and cognitive systems.
2. What humans experience as individual recognition likely represents one end of a continuum of complexity in the evolved perceptual and cognitive abilities that underlie social recognition.

Components and Mechanisms of Social Recognition

Here, 'social recognition' will refer to the ability of animals to recognize different **social categories** of individuals within their own species. The nature of these social categories is always an empirical question. They may be very broad—for example, related versus unrelated individuals, or familiar versus unfamiliar individuals—or each social category may correspond to a particular individual, so that multiple, familiar individuals are recognized as distinct social categories, as is the case for humans.

Social recognition systems have five necessary components:

1. Animals must provide information about their membership in a social category using so-called 'signature signals' or other recognition cues that differ between the social categories that pose the recognition problem;
2. Animals must perceive differences in the signature signals and recognition cues that identify particular social categories;
3. Animals must compare a perceived signal or cue to an internal neural representation that may be either innate or learned;
4. Animals must decide whether a perceived signal or cue matches their internal neural representation; and
5. Animals must possess a behavioral repertoire diverse enough to allow different behavioral responses to different social categories.

These components are explained in further detail later in this article, in the context of communication-based social recognition systems. Readers are referred to Beecher (1990; 1991), Sherman *et al.* (1997), and Bradbury and Vehrencamp (1998) for well-developed and thoughtful treatments of the components of recognition systems.

Animal behaviorists have identified several potential mechanisms that can mediate social recognition. The two mechanisms that have been the subject of most empirical and theoretical studies are 'phenotype matching' and 'familiarity.' An animal's phenotype refers to its observable appearance, characteristics, and behaviors, and it is influenced by the genes it inherits from its parents and by its environment. Phenotype matching occurs when animals match another animal's phenotype to an innate or learned representation of either their own phenotype ('self-referent phenotype matching') or that of a familiar individual. Because the relatedness of two individuals is proportional to the number of copies of genes that they share, and the degree of similarity in their phenotypes is influenced by the number of shared genes, phenotype matching can be one way that animals behaviorally discriminate between relatives and non-relatives, or among animals related by different degrees. In some cases, related individuals, such as siblings, may also live in a common environment that can influence their phenotypes in similar ways, for example, by giving rise to similar odors. Such cues can also mediate social recognition based on phenotype matching, and this represents one form of social recognition that is not based on communication signals.

Social recognition may also be based on mechanisms that involve an acquired familiarity with the phenotypic characteristics that distinguish among social categories. In other words, instead of matching an individual's phenotype to their own or that of another individual, animals learn about and remember the phenotypes of the individuals comprising social categories through prior observations of, or interactions with, those individuals. In this case, recognition is mediated by comparing sensory input with a previously learned representation of the phenotype that identifies the social category posing the recognition problem. Much of the work on the role of familiarity in social recognition has focused on the ability of animals to learn to recognize social categories based on differences in communication signals, and this will be the topic of the remainder of this article. Before describing communication-based social recognition systems in more detail, however, it is worthwhile to first consider a number of perspectives on social recognition in nonhuman animals.

Perspectives on Social Recognition in Animals

Among animal behaviorists, there are different perspectives on the question of social recognition in animals that stem as much from the diversity of social

recognition systems as from the rich diversity of approaches used to study animal behavior. One of these perspectives is based in ethology, the biological study of behavior that developed in the first half of the 20th century and attempts to answer questions about the causal mechanisms, development, evolution, and function of animal behaviors. It is from an ethological perspective that social recognition is most often treated as a communication problem. Researchers working from this perspective often define social recognition operationally, in terms of the behavioral discriminations that animals make among social categories and the features of communication signals or other recognition cues that make discrimination possible. Thus, an ethological perspective tends to emphasize the sensory input that makes recognition possible and the behavioral interactions that result from recognition.

The field of behavioral ecology developed as an outgrowth of ethology in the 1970s and focuses on the adaptive value of social behaviors, the ecological and social factors that influence these behaviors, and the mechanisms that allow these behaviors to evolve. Behavioral ecological perspectives on social recognition are more often concerned with recognition as an evolutionary adaptation for directing appropriate social behaviors toward other members of an animal's social group and the implications of recognition for survival and reproduction. Behavioral ecologists also address questions related to the genetic mechanisms that underlie the evolution of social recognition and the ecological and social factors that favor the evolution of social recognition systems.

Following the cognitive revolution that occurred in psychology in the 1950s and 1960s, many of the principles of cognitive psychology, which emphasize internal mental processes, began making important contributions to the study of behaviors in a diversity of animal species in the 1980s and 1990s. This culminated in approaches to animal behavior variously termed 'animal cognition,' 'cognitive ecology,' and 'cognitive ethology.' From a cognitive perspective, social recognition is often treated as a question about social knowledge and social categorization and is defined representationally, in terms of the complexity, specificity, and dimensionality of the internal representations of familiar individuals that result from previous experience. Thus, the cognitive perspective tends to emphasize not sensory input and behavioral output, nor the evolution of social recognition, but instead the internal processes and representations that are involved in social recognition and the roles that such representations play in social interactions.

All of these perspectives are valuable because they address different, but related, questions about social

recognition that complement one another. Efforts that integrate these different perspectives will likely continue to shed new light on both the mechanisms and evolution of social recognition systems in animals. As described below, the study of communication-based social recognition systems provides rich opportunities for integrating these perspectives.

Communication-Based Social Recognition Systems

A simple conceptualization of animal communication would consist of an animal acting as a 'sender' to produce a 'signal' that is perceived by another animal acting as a 'receiver.' Communication-based social recognition can be defined operationally as occurring when receivers direct appropriate behaviors toward one or more particular social categories of senders in response to signals, while withholding these behaviors from other social categories of senders, based on an acquired familiarity with distinctive properties of the signals produced by the sender or senders of the social categories to which the behaviors are directed. Several important points about this definition should be made explicit. First, recognition is an inherently internal product of the receiver's nervous system that must be inferred by researchers from the receiver's discriminative behavioral responses to signals produced by senders of different social categories. Second, recognition is based on familiarity with communication signals; that is, learning plays a critical role in allowing receivers to form memories that encode the distinctive properties of signals that distinguish social categories of senders. Finally, the above definition does not require that recognition based on communication signals involve the formation of mnemonic representations that are more complex than representations of signals themselves. However, the possibility that social recognition involves an integrated, multifaceted neural representation of the sender as an external referent is certainly not excluded by focusing on communication-based social recognition.

Defined in this manner, communication-based social recognition has been demonstrated in fish, amphibians (frogs and salamanders), reptiles, birds, and mammals. Moreover, social recognition is mediated by communication signals in a diversity of sensory modalities, including vision, audition, chemoreception, and electroreception, and it occurs in a number of evolutionarily important behavioral contexts. Four behavioral contexts in which communication-based social recognition has been widely studied are kin recognition, territorial neighbor

recognition, mate recognition, and so-called 'true individual recognition.'

Behavioral Contexts of Communication-based Social Recognition

Kin Recognition Some animals learn to behaviorally discriminate among related and unrelated individuals, or among individuals related by different degrees, based on differences in communication signals. This form of social recognition, termed 'kin recognition,' is commonly associated either with choosing an optimally related mate, for example to avoid the deleterious effects of inbreeding, or with directing certain behaviors toward relatives that function to increase their survival and reproduction. The study of kin recognition was greatly advanced by the formulation of kin selection theory by behavioral ecologists. Kin selection theory can explain the evolution of some of the apparently altruistic behaviors stemming from kin recognition as adaptations that allow individuals to propagate copies of their own genes into the next generation by improving the survival and reproduction of genetically related individuals.

Kin recognition based on chemical signals called pheromones is well known from rodents and other mammals. Parent-offspring recognition is a form of kin recognition that has evolved numerous times in animals that provide parental care for their offspring, especially in species that have social systems in which the offspring from different sets of parents intermingle while still under the care of their parents. Parent-offspring recognition based on acoustic signals has been studied in colonially breeding species, such as some swallows, seabirds (e.g., penguins), pinnipeds (e.g., seals), and bats. In these colonial species, the young are often left in a communal crèche, sometimes consisting of thousands of densely packed individuals, while the parents leave the area to forage. Parents and offspring are able to reunite in these very crowded social conditions by recognizing individually distinctive vocalizations.

Territorial Neighbor Recognition In species in which individuals defend territories, territory holders commonly exhibit behaviors that indicate that they recognize their nearby territorial neighbors, a form of social recognition termed 'territorial neighbor recognition.' Most commonly, territory holders are shown to exhibit low levels of aggression toward their nearby, established neighbors and high levels of aggression toward unfamiliar 'strangers' that may attempt to take over the territory or to establish a new nearby territory. Displays of lower levels of aggression toward familiar neighbors are thought to evolve in

species that defend long-term multipurpose or breeding territories, as opposed to feeding territories. This form of territorial neighbor recognition is usually presumed to be an evolutionary adaptation that allows territory holders to avoid the costs of repeated aggressive interactions with neighbors that already possess their own territory and therefore represent less of a threat to territory ownership than strangers that may attempt a territory takeover.

Songbirds represent the most thoroughly studied taxon when it comes to neighbor recognition. Territorial male songbirds discriminate among neighbors and strangers, and even among multiple neighbors, based on a combination of individual differences in songs and spatial cues related to the location of a neighbor's territory. Some songbirds even appear to retain long-term memories of the songs of their neighbors from previous breeding seasons. Similar acoustically mediated recognition systems have also been described in territorial seabirds, fish, and frogs, although long-term memories for neighbors' signals have not been investigated in these taxa. Neighbor recognition has also been investigated in territorial lizards, which can recognize their neighbors based on visual and chemical cues. Some electric fish may also recognize neighbors based on individual differences in self-generated electrical signals known as electric organ discharges.

Mate Recognition Another form of social recognition, termed 'mate recognition,' refers to behavioral discrimination by an individual between its mate or breeding partner and other members of the same species. Mate recognition can play a role in maintaining the pair bond and in synchronizing shared parental duties, such as the care of eggs or young. An ability to recognize one's mate is particularly important in socially monogamous species that form long-term pair bonds. Mate recognition based on acoustic signals has been most studied in animals that live in large colonies, such as colonial seabirds, in which parents coordinate their parental care duties, and in which spatial cues may provide little assistance in locating a mate. Because of other uses of the term 'mate recognition' in the literature, it is important to distinguish this form of social recognition from 'species recognition'; 'mate recognition' is often used to describe the recognition of an individual of the opposite sex as a member of the same species and therefore as a potential mating partner.

'True Individual Recognition' Finally, a number of studies of so-called 'true individual recognition' demonstrate that some animals recognize multiple, familiar, and often unrelated individuals as distinct and

unique social categories. This form of social recognition, which bears its somewhat anthropocentric name in part because it approaches more closely our own human experience, appears to function in animal species with highly developed social structures, in which individuals often live in organized social groups. For example, in bottlenose dolphins, in which individuals form long-lasting associations, individual dolphins can discriminate among multiple familiar individuals based on individual differences in so-called 'signature whistles.' Some birds, such as the song sparrows described later in this article, may also be capable of such true individual recognition based on individual differences in vocalizations.

A number of studies of social cognition in nonhuman primates have established that some primates not only recognize multiple familiar individuals as distinct social categories – both visually and acoustically – but they also possess social knowledge about these individuals, such as the social alliances they form, their relatedness to other individuals, and their rank order in dominance hierarchies. This is the case, for example, with group-living baboons, which are discussed in more detail later. Thus, it seems clear that, like humans, some other animals, such as highly social, group-living primates, are able to form integrated, multifaceted representations of multiple familiar individuals that are more complex than a mere representation of communication signals or other simple cues associated with these individuals.

Methods Used to Investigate Communication-Based Social Recognition

Because social recognition is an internal process that involves comparing sensory input to an internal neural representation, and because nonhuman animals cannot simply tell us about their recognition experiences, the study of social recognition in animals requires observations and experiments that inform us about an animal's recognition abilities based on its behavioral interactions with other individuals or its behavioral responses to communication signals from different social categories of senders. Three experimental designs that are commonly used to investigate communication-based social recognition are 'discrimination experiments,' 'habituation-discrimination experiments,' and 'conditioning experiments.'

Discrimination Experiments In a discrimination experiment, typically two different signals are presented to test the hypothesis that the intended receiver will behaviorally discriminate among the signals, at least one of which is presumed to be familiar to the subject. The alternatives might be familiar versus

unfamiliar signals, the signals of two different familiar individuals, or the unmodified signal of a familiar individual versus an experimentally modified version of the same signal. Experiments usually consist of either presentations of different alternatives in separate test periods separated by some intervening time interval, or simultaneous presentations in a two-alternative choice test. Some experiments use actual conspecific individuals as stimuli instead of experimentally presented communication signals.

Habituation-Discrimination Experiments The habituation-discrimination paradigm involves repeatedly presenting a response-eliciting stimulus during an initial ‘habituation phase’ until the response habituates. The stimulus is often a communication signal from a particular social category, although real individuals are sometimes used. During a subsequent ‘discrimination phase,’ subjects in the control group experience additional presentations of the habituating signal, and subjects in experimental treatment groups experience novel signals that are in some way different from the habituating signal, such as a signal from a different social category. The prediction is that if subjects perceive the novel stimulus as the signal of a new or different social category, then the habituated responses of the treatment groups should be greater than those of the control group during the discrimination phase.

Conditioning Experiments In conditioning experiments, subjects are trained, using classical or operant conditioning techniques, to respond differently to signals from different social categories of senders. In contrast to discrimination experiments and habituation-discrimination experiments, which take advantage of an animal’s natural behavioral repertoire and can therefore be conducted in the field, conditioning experiments are conducted under controlled laboratory settings that involve the experimenter determining what constitutes a correct behavioral response. In classical conditioning experiments, the behavioral response often involves some sort of reflex to a stimulus (e.g., Pavlov’s salivating dogs). The responses in operant conditioning experiments often involve behaviors such as pecking a lighted response key or pressing a lever in response to a stimulus to obtain a food reward and to avoid punishment. Once animals are trained to distinguish among social categories with a certain level of correct responses, recognition abilities are then tested in probe trials in which test signals belonging either to the same social categories or to different ones are presented to test the subject’s ability to distinguish among social categories.

A Model of Communication-Based Social Recognition

Given the importance of communication in the social recognition systems of animals, including humans, it is worth illustrating a general model of how communication signals can mediate social recognition. One requirement for communication-based social recognition is that communication signals be distinctive among the social categories of senders that pose the social recognition problem. These so-called ‘signature signals’ can arise when the signals produced by senders of different social categories differ in the presence/absence of certain signal attributes, or as illustrated in [Figure 1](#), when the among-category variation in signals exceeds the variation that occurs within social categories.

The two-dimensional and three-dimensional plots in [Figure 1](#) illustrate two important points. First, signals usually vary in multiple dimensions that can potentially provide independent information about a sender’s membership in a particular social category. Second, the signals of different social categories may be well separated along some signal dimensions, while there may be extensive overlap along other signal dimensions. For example, the signals of social categories 4 and 5 in [Figure 1](#) overlap considerably along signal property 2 but are well separated along signal properties 1 and 3. It may be the case that at least some social categories overlap on all signal properties. We should, therefore, expect receivers to evolve to use as recognition cues those signal properties that most reliably distinguish among senders from different social categories.

The comparative work of Beecher and colleagues on vocally mediated parent-offspring recognition in swallows has highlighted the fact that evolution can also act directly on the signals produced by senders, making them more distinctive among social categories in species in which social recognition is evolutionarily advantageous. The calls of chicks in colonial-breeding cliff swallows and banks swallows, in which young are left in communal crèches, and in which parents rely on calls to reunite with their chicks, are more individually distinct than the calls of chicks in the solitary-breeding barn swallows and rough-winged swallows, in which the requirements for parent-offspring recognition are less demanding.

The Basic Model

[Figure 2](#) depicts a multistage hierarchical model of communication-based social recognition that highlights the internal processes of the receiver’s nervous system that mediate recognition. While the stages in the model may be expected to vary somewhat

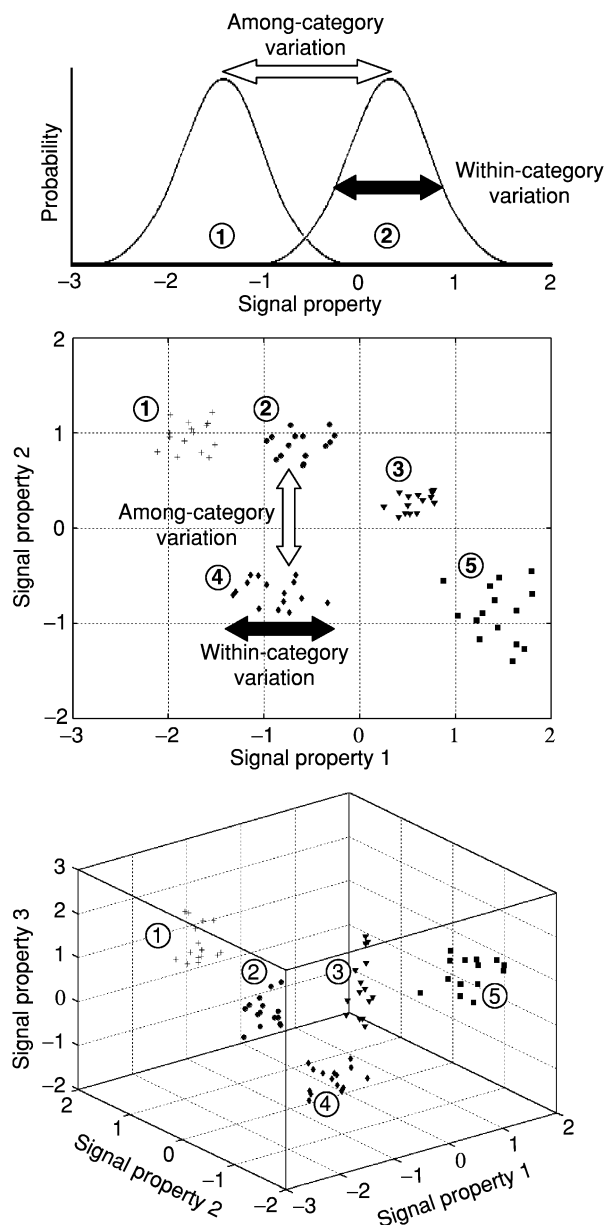


Figure 1 Schematic illustrations of distinctiveness in communication signals among social categories of senders. *Top*: Two probability density functions illustrating the likelihood that two social categories (1 and 2) have the specified values of a single signal property. *Middle*: Scatter plot illustrating the values of 15 signals from each of five social categories (individuals in this case) in a two-dimensional 'signal space.' Each axis represents values for a different signal property. For example, for an acoustic signal, the two signal properties might represent spectral frequency and signal duration. *Bottom*: Scatter plot illustrating the separation among social categories in a three-dimensional signal space bounded by values of three signal properties. Axis values in all three plots represent deviations of signal properties from a standardized population mean value of zero. (Top and middle figures adapted from Insley *et al.*, 2003.)

according to sensory modality, for the most part, similar or parallel processes should be expected across sensory modalities.

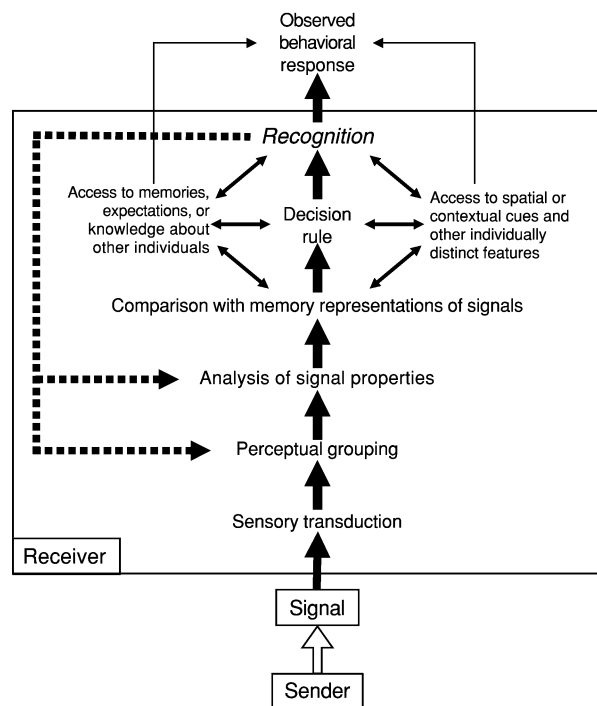


Figure 2 Schematic model of communication-based social recognition. The model depicts the processes involved in recognition that take place in the receiver's nervous system. The open arrow (*bottom*) depicts the requirement that senders produce signals that are distinctive among the social categories of senders posing the recognition problem (see Figure 1). Thick black arrows depict bottom-up processes leading from sensory transduction of a signal to the behavioral output of the receiver. Dashed arrows depict potential top-down influences of recognition on earlier perceptual processes. Thin black arrows depict possible associations between the mnemonic representation of the signal and other sources of information encoded in memory that can influence the decision rule and recognition, as well as the observed behavioral output. Note that the hierarchical arrangement of stages in the model does not necessarily imply that processing between stages is organized sequentially. (Adapted from McAdams, 1993.)

The perceptual processes involved in communication-based social recognition begin in the receiver's sensory system, with the transduction of communication signals into neural activity. The sensory system may then be required to perform some kind of perceptual grouping, by which the neural representation of the to-be-recognized signal is perceptually segregated from those of other signals, stimuli, or noise in the environment and integrated into a coherent perceptual object based on the signal's physical and temporal properties. Once a perceptual object of a perceived signal has been formed, the sensory system must analyze this representation to determine the perceived signal's salient properties. The properties of a receiver's perceptual representation of the signal must then be compared to those of a mnemonic representation of the signal that was formed as a result of previous

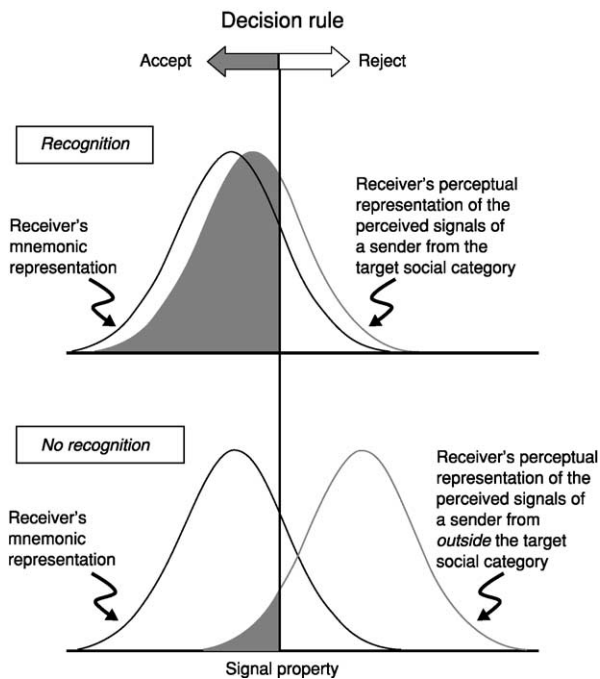


Figure 3 Matching between perceptual and mnemonic representations of signals. Receivers must use some form of a decision rule to determine whether or not their perceptual representation of a signal adequately matches the representation stored in their memory. The shaded area represents the probability that the perceived signals of a sender from the to-be-recognized target social category (*top*), or a sender from outside the target category (*bottom*), will be accepted (i.e., recognized) as coming from a sender of the target social category, given the location of the receiver's decision rule (vertical bar). The variance in the receiver's mnemonic and perceptual representations of a sender's signals can arise from sources such as within-individual variation or habitat-induced variation in the sender's signals and internal noise resulting from spontaneous neural activity and the statistical nature of stimulus-driven neural activity in the receiver's nervous system.

recognition learning. At this stage, receivers must use some decision rule, or matching algorithm, to determine whether their perceptual representation of the signal adequately matches their representation in memory, followed by a judgment about the sender's category membership.

The matching process between a receiver's perceptual and mnemonic representations of a sender's signal is sometimes modeled as two probability density functions of the values of some signal property that serves as a recognition cue (Figure 3). The probability distributions on the left in Figure 3 represent the receiver's mnemonic representation, which encodes a range of values for a particular signal property that can be attributed to senders from a particular social category with a specified probability; the distributions to the right represent the receiver's perceptual representations, which encode a range of values for the same signal property after perceiving a signal,

again with a specified probability. If there is an adequate match between the perceptual and mnemonic representations, as illustrated in the upper panel of Figure 3, then recognition can be said to occur and the receiver should accept the sender as belonging to a particular target social category (e.g., mate, parent, offspring, or neighbor). The lower panel illustrates a situation in which there is an inadequate match, resulting in the rejection of the sender as belonging to the particular target social category. Evolution should equip receivers with a decision rule that maximizes the number of correct behavioral responses while minimizing the number of recognition errors. Thus the location of the decision rule should depend on the relative benefits of correct responses, the costs of errors, and the probabilities of correct and incorrect responses given the degree of overlap among the signal properties of individuals posing the recognition problem.

Finally, for observers and experimenters to acquire evidence that recognition has occurred, it is necessary that receivers respond differently to signals from different social categories of senders. It is also important to bear in mind, however, that the internal process of recognition may, in fact, occur in the absence of any overt behavioral discrimination if the most evolutionarily appropriate behavior is to respond similarly to different social categories of senders. The fact that recognition can occur in the absence of a behavioral discrimination is a perennial problem in the study of animal recognition systems, especially in the interpretation of negative results.

The Extended Model: Integrating Ethological and Cognitive Perspectives

As stated earlier, we should expect animal recognition systems to differ among species, and these differences should reflect species differences in ecology, phylogenetic history, and the complexity of perceptual, social, and communication systems. A consideration of how species may be expected to differ provides a way to integrate the ethological and cognitive approaches to studying social recognition.

Dimensions of Communication-Based Social Recognition The mnemonic representations of communication signals that are formed through recognition learning and that mediate social recognition (Figures 2 and 3) can be expected to differ among animal species along three dimensions: specificity, complexity, and temporal stability (Figure 4).

'Specificity' refers to the breadth of the social categories that represent the social recognition problem and can range from dichotomous social categories (e.g., related versus unrelated, familiar

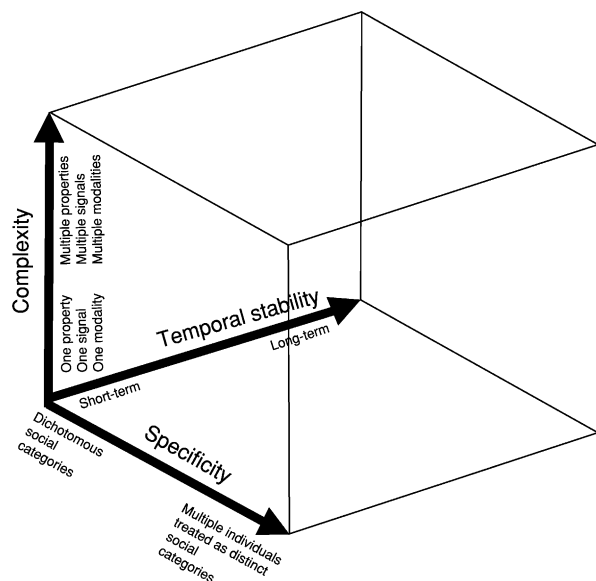


Figure 4 Three dimensions of communication-based social recognition. Species should be expected to differ in the specificity, complexity, and temporal stability of their mnemonic representations of recognized communication signals, as well as in the extent that these representations are integrated with other sources of information.

versus unfamiliar, or mate versus non-mate) to the situation where multiple familiar individuals are treated as distinct and separate social categories, such as in so-called ‘true individual recognition.’

‘Complexity’ can refer to at least three different characteristics of a recognition system. First, because multiple properties of communication signals (e.g., spectral and temporal properties of acoustic signals) can exhibit variation that potentially can be used for recognition (Figure 1), complexity can refer to the number of different signal properties encoded in memory within a particular sensory modality. Second, in species that communicate using a repertoire of signals in a particular sensory modality, complexity can refer to the number of signal types that are recognized from a particular social category. Finally, because social recognition in some animals is mediated by multiple sensory modalities, such as vision and audition, complexity can also refer to the number of different sensory modalities involved in recognition.

‘Temporal stability’ refers to the time over which encoded representations of signals persist in memory. In species in which individuals interact only briefly, relatively short-lived memories may be sufficient to solve any particular recognition problem, whereas in species in which individuals interact over longer periods, or with longer intervals between interactions, long-term memories may be required for social recognition.

Integration of Signals with Other Information Questions related to the extent that mnemonic representations of communication signals are integrated with other sources of information or social knowledge go to the heart of combining ethological and cognitive perspectives on social recognition. Other sources of information may not only facilitate recognition of communication signals but may also have more direct influences on an animal’s behavioral response (Figure 2). This information may include memories of previous social interactions, expectations about future social interactions, and previous knowledge about other individuals gained through observations and previous social interactions. The way that representations of acoustic signals can be integrated with other forms of social knowledge is perhaps best illustrated with two examples from the literature.

As mentioned above, an integration of representations of communication signals with social knowledge about recognized individuals is known from primates with complex social structures. For example, Cheney and Seyfarth (1999) used ingenious field playback tests to demonstrate that some species of monkeys, such as baboons, possess information about the family relationships of other individuals. In one experiment, pairs of unrelated female baboons were presented with acoustic playbacks that simulated a fight occurring either between two of their familiar relatives or between two familiar individuals that were not related to either subject. When the acoustically simulated fight, which consisted of previously recorded threat grunts and screams, was presented, females looked toward the speaker longer during the playbacks and looked toward each other longer following playbacks when the simulated fight was between their relatives, as opposed to between two non-kin. Females were also more likely to interact in a friendly manner following a fight between two non-kin compared to a fight between two of their relatives. These results can be interpreted as indicating three important aspects about vocally mediated social recognition in baboons. First, subjects recognized the fighting individuals by their threat grunts and screams, two acoustically different signals. Second, subjects recognized the relatedness between one of the simulated fighters and themselves. Third, subjects recognized the relatedness between the other fighter and the other paired subject. Thus, representations of familiar acoustic signals were integrated with other social knowledge about the senders that included information about relatedness to self and relatedness to others.

The extent to which such integration between representations of signals and social knowledge plays a role in the social recognition systems of

non-primates has unfortunately received much less attention. However, in a study of song sparrows, a songbird in which males recognize their territorial neighbors, the results of playback tests by Beecher *et al.* (1996) suggested that territorial males in this species may also possess social knowledge about their territorial neighbors. In song sparrows, neighboring territorial holders tend to share a number of song types in their song repertoires. When the songs of a familiar neighbor were played back from the neighbor's territory, subjects responded by singing a song type that they shared with that neighbor, but that was different from the song type sung by the simulated neighbor. In contrast, when a stranger's song was presented from a neighbor's territory, subjects responded with a song type from their repertoire that they did not share with that particular neighbor. These results suggest that male song sparrows recognize an individual neighbor as a distinct social category (i.e., 'true individual recognition'), that they possess knowledge about the song types that they do and do not share with their recognized territorial neighbors, and that this social knowledge plays a role in social interactions over territory boundaries.

In addition to social knowledge about other individuals, receivers may also possess information about the significance of current spatial or contextual cues related to the context in which the signal was perceived (Figure 2). Spatial location is often regarded as an important cue in some forms of recognition. For example, what could appear on the surface to be parent-offspring recognition may, in fact, represent behaviors guided by a simple rule followed by a parent, such as 'find the nest and feed the young in the nest.' Therefore, studies of social recognition often strive to demonstrate the location-independence of behaviors thought to be guided by social recognition. In some recognition systems, however, spatial or contextual cues may also function as what psychologists refer to as 'occasion setting stimuli,' in which the recognition of a signal in one context elicits one behavioral response, while recognition of the same signal in a different context elicits a different response. One example of this may be the location-specificity of reduced levels of aggression between territorial neighbors. In songbirds, hearing a neighbor's songs from the direction of the neighbor's territory elicits low levels of aggression, while hearing the same song played back from a different or 'incorrect' location elicits an intense aggressive response. It is usually presumed that a familiar neighbor singing from an unfamiliar location represents a threat to the status quo of established territorial boundaries. Thus, information about context can directly influence a receiver's behavioral response to a recognized signal.

Looking Forward

One challenge for future research is to understand the nature of the neural representations that underlie communication-based social recognition in terms of their specificity, complexity, and temporal stability; the processes that lead to their formation; and the extent to which neural representations of communication signals are associated or integrated with other encoded information and social knowledge about the sender. A second challenge for future comparative research is to discover the ecological and phylogenetic bases of similarities and differences among species in the learned representations involved in social recognition and their underlying neural mechanisms. More effort should be made by animal behaviorists to integrate, both within and across species, an understanding of the internal processes mediating social recognition, such as those illustrated in Figure 2. It will be important in these endeavors to keep in mind that the representations underlying recognition in different animal species likely fall along continua of specificity, complexity, and temporal stability and are likely to differ in the extent to which they are integrated into multifaceted representations of recognized individuals. Therefore, exploration of social recognition in animals will require a genuine willingness to examine recognition systems in terms delimited by the animals' social, perceptual, and communication systems.

See also: Alarm Calls; Animal Communication: Deception and Honest Signaling; Animal Communication Networks; Animal Communication: Overview; Animal Communication: Parent-Offspring; Animal Communication: Vocal Learning; Birdsong; Cognitive Basis for Language Evolution in Non-human Primates; Communication in Marine Mammals; Frog and Toad Communication; Non-human Primate Communication.

Bibliography

- Aubin T & Jouventin P (2002). 'How to vocally identify kin in a crowd: The penguin model.' *Advances in the Study of Behaviour* 31, 243–277.
- Beecher M D (1989). 'Signalling systems for individual recognition: an information theory approach.' *Animal Behaviour* 38, 248–261.
- Beecher M D (1990). 'The evolution of parent-offspring recognition.' In Dewsbury D A (ed.) *Contemporary issues in comparative psychology*. Sunderland, MA: Sinauer Associates. 360–380.
- Beecher M D (1991). 'Successes and failures of parent-offspring recognition in animals.' In Hepper P G (ed.). 94–124.

- Beecher M D, Stoddard P K, Campbell S E & Horning C L (1996). 'Repertoire matching between neighbouring song sparrows.' *Animal Behaviour* 51, 917–923.
- Beer C G (1970). 'Individual recognition of voice in the social behavior of birds.' *Advances in the Study of Behaviour* 3, 27–74.
- Bradbury J W & Vehrencamp S L (1998). *Principles of animal communication*. Sunderland, MA: Sinauer Associates.
- Cheney D L & Seyfarth R M (1990). *How monkeys see the world: inside the mind of another species*. Chicago: Chicago University Press.
- Cheney D L & Seyfarth R M (1999). 'Recognition of other individuals' social relationships by female baboons.' *Animal Behaviour* 58, 67–75.
- Colgan P (1983). *Comparative social recognition*. New York: Wiley.
- Falls J B (1982). 'Individual recognition by sounds in birds.' In Kroodsma D E & Miller E H (eds.) *Acoustic communication in birds*. New York: Academic Press. 237–278.
- Gheusi G, Bluthé R-M, Goodall G & Dantzer R (1994). 'Social and individual recognition in rodents: Methodological aspects and neurobiological bases.' *Behavioural Processes* 33, 59–88.
- Gheusi G, Goodall G & Dantzer R (1997). 'Individually distinctive odours represent individual conspecifics in rats.' *Animal Behaviour* 53, 935–944.
- Hepper P G (1991). *Kin recognition*. Cambridge: Cambridge University Press.
- Innsley S J, Phillips A V & Charrier I (2003). 'A review of social recognition in pinnipeds.' *Aquatic Mammals* 29(2), 181–201.
- Johnston R E & Bullock T A (2001). 'Individual recognition by use of odours in golden hamsters: the nature of individual representations.' *Animal Behaviour* 61, 545–557.
- Lambrechts M M & Dhondt A A (1995). 'Individual voice discrimination in birds.' In Power D M (ed.) *Current ornithology*. New York: Plenum Press. 115–139.
- Mateo J M (2003). 'Kin recognition in ground squirrels and other rodents.' *Journal of Mammalogy* 84, 1163–1181.
- McAdams S (1993). 'Recognition of auditory sound sources and events.' In McAdams S & Bigand E (eds.) *Thinking in sound: the cognitive psychology of human audition*. Oxford: Oxford University Press. 146–198.
- Nakagawa S & Waas J R (2004). "'Oh sibling, where are thou?" – a review of avian sibling recognition with respect to the mammalian literature.' *Biological Reviews* 79, 101–119.
- Pfennig D W (2002). 'Kin recognition.' In Pagel M (ed.) *Encyclopedia of evolution*. Oxford: Oxford University Press. 592–595.
- Sayigh L S, Tyack P L, Wells R S, Solow A R, Scott M D & Irvine A B (1999). 'Individual recognition in wild bottlenose dolphins: a field test using playback experiments.' *Animal Behaviour* 57, 41–50.
- Seyfarth R M & Cheney D L (2000). 'Social awareness in monkeys.' *American Zoologist* 40, 902–909.
- Sherman P W, Reeve H K & Pfennig D W (1997). 'Recognition systems.' In Krebs J R & Davies N B (eds.) *Behavioural ecology: an evolutionary approach*, 4th edn. Malden, MA: Blackwell Publishing. 69–96.
- Shettleworth S J (1998). *Cognition, evolution, and behavior*. Oxford: Oxford University Press.
- Stoddard P K (1996). 'Vocal recognition of neighbors by territorial passerines.' In Kroodsma D E & Miller E H (eds.) *Ecology and evolution of acoustic communication in birds*. Ithaca, NY: Cornell University Press. 356–374.
- Tang-Martinez Z (2001). 'The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation.' *Behavioural Processes* 53, 21–40.
- Temeles E J (1994). 'The role of neighbours in territorial systems: when are they 'dear enemies'?' *Animal Behaviour* 47, 339–350.
- Zayan R (1994). 'Mental representations in the recognition of conspecific individuals.' *Behavioural Processes* 33, 233–246.

Indo-Aryan Languages

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Indo-Aryan languages (sometimes also called 'Indic' languages) are spoken in India, Pakistan, Bangladesh, Nepal, Sri Lanka, Bhutan and Maldives – the group of seven countries also known as the South Asian Association of Regional Cooperation (SAARC) countries. More than two-thirds of the total population of South Asia speaks Indo-Aryan languages. Owing to 20th-century migrations, considerable numbers of Indo-Aryan speakers have settled in non-SAARC countries, especially in Europe and

North America. Indo-Aryan constitutes the largest language group in the Indo-European language family in terms of numerical weight of speakers (said to be approximately one-fifth of the total world population, the total number of speakers exceeding 700 000 000) as well as in terms of the total number of languages in the family (more than 70, of which 24 or more enjoy official status and have literary history). Some of the major languages in the family, both in terms of number of native speakers and literary history, are Hindi, Urdu, Bengali (known to its native speakers as Bangla), Assamese, Punjabi, Gujarati, Marathi, and Oriya. Sanskrit, in terms of historical significance and role in the development of modern