

Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals

Peter L. Tyack, (Biology Department, Woods Hole Oceanographic Inst, Woods Hole MA 02543 USA), ptyack@whoi.edu

Abstract

The classic evidence for vocal production learning involves imitation of novel, often anthropogenic sounds. Among mammals, this has been reported for African elephants, harbor seals, and dolphins. A broader taxonomic distribution has been reported for vocal convergence, where the acoustic properties of calls from different individuals converge when they are housed together in captivity or form social bonds in the wild. This kind of vocal convergence has been demonstrated for animals as diverse as songbirds, parakeets, bats, elephants, cetaceans, and primates. For most of these species, call convergence is thought to reflect a group-distinctive identifier, with shared calls reflecting and strengthening social bonds. Pooling data on vocal imitation and vocal convergence suggests a wider taxonomic distribution of vocal production learning among mammals than generally appreciated. The wide taxonomic distribution of this evidence for vocal production learning suggests that perhaps more of the neural underpinnings for vocal production learning are in place in mammals than is usually imagined. One ubiquitous function for vocal production learning that is starting to receive attention involves modifying signals to improve communication in a noisy channel.

Key words: vocal learning

Introduction

The ability to modify the acoustic structure of a vocalization based on auditory input is called vocal production learning. Janik and Slater (1997, 2000) distinguish the ability to produce sounds that are similar or different from an acoustic model from contextual learning, in which an existing signal is used in a different context as a result of experience with how other individuals use the signal. A key distinction involves whether animals simply learn new contexts for the use of existing signals or whether they actually modify the acoustic properties of the sounds they produce to be more or less similar to sounds they hear. The best evidence for production learning has involved imitation of novel sounds, but evidence for this is limited, especially for mammals. Attempts to use geographic variation in signals has been a problematic source of evidence for production learning, especially if such studies do not include detailed study of effects of the social and acoustic environment. Here I argue that growing evidence for vocal convergence as animals form groups suggests that vocal production learning may have broader taxonomic distribution than suggested by vocal imitation. But proving that convergence is true production learning requires careful quantitative analysis of acoustic features of calls before and after exposure.

The best data on production learning in non-human animals comes from the songbirds (Catchpole and Slater 1995; Kroodsma and Miller 1996). Evidence for production learning in birds is strongest for males learning bird song. Once a male hatches, he listens to songs and forms memory traces of the songs that are closest to an inherited sensory template. Sometimes after a seasonal delay, he will produce a variety of sounds, slowly narrowing his song production to match those he has heard. Some songbirds have a song repertoire limited to this early period, others continue to learn new songs as adults. One of the classic methods to study the role of auditory input on vocal production is to raise animals in isolation. For many songbird species, if a male is raised in isolation or is deafened, his vocal production differs dramatically from birds with normal auditory input. This suggests that songbirds must compare auditory input to their vocal production in order to learn how to match their memory.

Evidence for vocal production learning in mammals is much more limited than for birds. Janik and Slater (1997) conclude that evidence for imitation of new sounds is limited to humans and marine mammals. The dearth of evidence for production learning among non-human primates is something of a surprise, given the highly developed imitative skills of humans, and given the profound impacts that deprivation from hearing speech has on vocal development in humans. For example, Hammerschmidt et al. (2000) reared rhesus macaques in two conditions: with their mothers or separated from their mothers at birth and housed with other infants. They report high variation within each individual in acoustic structure of calls during the 5 month period of study. There were some age-related changes in structure of all call types studied, but isolation from adults did not appear to affect these changes; variation in weight explained variation in all but one call parameter for macaque coo calls. Rearing in isolation from conspecific adults could interfere with so many general developmental processes, that some have studied the

effects of deafening to study how lack of auditory input alone may affect vocal production. Winter et al. (1973) reported no differences in acoustic parameters for calls of one deafened squirrel monkey that had been reared in isolation compared to normal monkeys. Talmadge-Riggs et al. (1972) found no differences in calls of normal vs deafened adult squirrel monkeys, suggesting that auditory feedback is not required for normal vocalization in this species. Hammerschmidt et al. (2001) extended the earlier study of Winter et al. (1973) by rearing squirrel monkeys in three conditions: normal, raised with a mother who could not call, and congenitally deaf. For all 12 call types studied, they found age-related changes in one or more acoustic parameters. There was a high level of variability in calls throughout the 20 month study, and the calls of both animals deprived of hearing adult calls fell within the range of calls produced by normally raised monkeys. This suggests that auditory input had little effect on call production, and that age-related variation in calls seemed to be primarily caused by physical growth.

Vocal Imitation

Perhaps the most direct evidence for production learning involves animals that can imitate unusual signals, such as when parrots imitate human speech. This kind of evidence for imitation is well documented for several avian taxa. However, attempts to train non-human primates to imitate speech have provided primarily negative evidence (Hayes & Hayes, 1952). Among other mammals, there is a case of a harbor seal (*Phoca vitulina*; Ralls et al., 1985) and an Indian elephant (*Elephas maximus indicus*; Holden 2006) imitating speech. African elephants have also been reported to imitate the sounds of a truck (Poole et al. 2006). Bottlenose dolphins, *Tursiops truncatus*, have also proven skilled at imitating synthetic computer-generated frequency modulation patterns (Richards et al. 1984). In general, when animals can be shown to produce precise imitations of sounds that are not part of the normal species repertoire, that provides solid evidence that auditory input is influencing vocal output. Such evidence is limited to very few species.

Janik and Slater (2000) point out the difficulty in demonstrating vocal production learning unless the subject produces a novel vocalization. When a bird, elephant, or a seal imitates human speech precisely, the evidence is quite strong. When an animal makes slight modifications to an existing sound, the case may be less clear. However, if we only accept as evidence for vocal production learning, cases where animals can be raised in artificial settings and tested for their ability to imitate arbitrary anthropogenic signals, we may err on the side of not understanding all of the taxa that may be capable of production learning.

Production of calls that differ from auditory model

Most work on production learning has focused on evidence that animals learn to produce vocalizations that match an auditory model, but several problems might select for learning to produce a sound that diverges from a model. For example, if vocal learning were used to facilitate the development of individually distinctive vocal signatures,

animals might learn to produce signals that differed from those it heard (Tyack 1997). However, Fripp et al. (2004) suggest that dolphins develop signature whistles that are distinctive with respect to their common associates by imitating the whistles of a member of the population with whom they associate rarely. Another reason to produce a sound that differs from auditory input involves shifting the frequency of a call outside of a noise band. Slabbekoorn and Peet (2003) have shown that great tits (*Parus major*) increase the frequency of their songs when in urban noise, which emphasizes low frequencies. Lesage et al. (1999) report a similar increase in the frequency of calls of beluga whales in the presence of low-frequency vessel noise. Janik and Slater (1997, 2000) would consider this kind of shift in frequency a valid form of production learning, one that is more complex than changes in level or duration of calls. This kind of frequency shift has been described before in the context of Doppler compensation (Schnitzler 1973; Trappe & Schnitzler 1982) or jamming avoidance (e.g. Ulanovsky et al. 2004) in bats, but this well known phenomenon has not typically been considered in discussions of vocal production learning. This may stem from the tendency of those interested in vocal production learning to focus on development of communication signals rather than shorter term accommodation of calls, especially those used for functions other than communication. However, the problem of communicating in noise is ubiquitous and should not be ignored in discussions of vocal production learning.

Use of vocal production learning to compensate for varying noise

Some of the solutions to the problem of communication in varying noise, which is faced by all animals with sensitive hearing, may also involve vocal learning mechanisms. There has been growing awareness that animals may have evolved mechanisms to compensate for varying ambient noise. Potential mechanisms for increasing the detectability of signals include waiting to call until noise decreases, increasing the rate of calling, increasing signal intensity, increasing the signal duration, and shifting signal frequency outside of noise band. Even though the first two of these mechanisms indicate that auditory input modifies vocal behavior, they do not involve production learning by the definition of Janik and Slater (1997, 2000) because they do not involve novel vocalizations, but the last one, involving a shift in frequency out of the band of an auditory model, certainly does. Whether increasing the level or the duration of a signal in response to increased level or duration of noise represents vocal production learning is debatable. Janik and Slater (1997, 2000) suggest that there may be several different levels of complexity in production learning. They suggest that changes in the amplitude or duration of a signal may stem from relatively simple changes in the state of muscles of the respiratory system. By contrast, they suggest that changing frequency parameters of a signal may require more complex changes of the sound production apparatus, including acoustic filters. The ability of animals to shift the frequency of a call out of a noise band mentioned in the last section clearly qualifies as a complex form of vocal production learning as defined by Janik and Slater (1997, 2000). By this standard, the second and third changes represent vocal production learning, but of a simpler sort than shifting frequency. Responding to noise by increasing the intensity of signaling is well known in humans as the Lombard effect. It has been demonstrated in nightingales (*Luscinia megarhynchos*) in response to traffic noise by Brumm (2004) and in beluga whales

(*Delphinapterus leucas*) in response to shipping noise by Scheifele et al. (2005). Foote et al. (2004) have shown that killer whales (*Orcinus orca*) increase the length of their calls in the presence of increased vessel noise. These mechanisms that modify vocal behavior to compensate for varying noise may be an important function of vocal production learning, and of simpler versions of modifying vocal output based on auditory input, such as increasing calling rate when noise is elevated or waiting to call until noise has declined. These mechanisms for timing calls with respect to interfering noise are well developed in anurans (Zelick & Narins, 1983) as well as birds (Brumm, 2006) and mammals (Egnor et al., 2007). I believe that the role of noise compensation mechanisms in the evolution of vocal learning may have been underestimated.

Geographical and Temporal Variation in Calls

One indirect method to look for evidence of production learning involves studying temporal and geographical variation of calls. For example, the songs of the humpback whale, *Megaptera novaeangliae*, differ across different ocean regions (Winn et al., 1981), and within a population all of the singing males track continuous changes in the song (Payne et al., 1983; Payne & Payne, 1985). At any one time the songs of one whale will be more similar to those of others nearby than its own song several months later (Guinee et al., 1983). Most biologists have concluded that this process of continuous change requires production learning, but Cerchio et al. (2001) speculate that humpbacks might inherit a set of rules governing song change. In my view, the clincher for production learning in humpback whales is the observation of Noad et al. (2000) of what they call a “cultural revolution” among humpbacks. When a few humpbacks singing the song from the west coast of Australia swam to the east coast, the east coast song was rapidly and completely replaced by the West coast song. This means that nearly all of the humpbacks in the east coast population must have abruptly ceased the slow process of change ongoing in the east coast song and adopted an entirely different song. The combination of geographical and temporal change in humpback song is very difficult to explain by any mechanism other than vocal production learning.

The history of using geographical variation in calls as evidence for production learning illustrates pitfalls. For example, early papers on geographical variation in pant hoots of chimpanzees (*Pan troglodytes*) suggested that this variation was evidence for production learning in this species (Mitani et al. 1992; Mitani and Brandt 1994; Clark Arcadi 1996). Mitani et al. (1999) reassessed the interpretation of geographical variation in chimpanzee calls. They concluded “The preceding observations suggest that genetically based rather than cultural [sensu McGrew, 1992] differences are likely to underlie any vocal variations that exist between Mahale and Kibale chimpanzees.” [p. 147] and that “Ecological factors related to differences in habitat acoustics, the sound environment of the local biota, or body size are likely to contribute to the observed macrogeographic variations in chimpanzee calling behavior.” [p. 149]

Elephant seals (*Mirounga angustirostris*) provide another cautionary tale regarding the use of dialects as evidence for vocal learning. Le Boeuf and Peterson (1969) described well defined local dialects in the pulse rates and other acoustic parameters of threat

vocalizations of male elephant seals from various islands off the California coast. They drew analogies to dialects in songbirds and humans, suggesting that young elephant seals copied the vocalizations they heard on their own island. However, once these authors were able to record more longitudinal data, the story became more complex. Le Boeuf and Petrinovich (1974) found that the pulse rates of individual seals did not vary across years, but that the mean pulse rate at a newly colonized island slowly changed from year to year, moving closer to the rates found on large established colonies. They found that most of the breeding males at the new colony were recruited from established ones, and they hypothesized that the original founders of the new colony happened by chance to have pulse rates at the low end of the normal distribution from the established colonies. As more males came from the established colonies to the new one, the pulse rates recorded at the new colony were less affected by the initial sampling bias, and the initial differences were reduced.

In both the chimpanzee and elephant seal cases, initial enthusiasm to interpret geographical variation in calls as evidence for production learning became tempered by new data and a growing appreciation of alternative hypotheses. I argue that the effort to use dialects as evidence for vocal production learning has been problematic. Very different phenomena have been called dialects, with geographic scales from ocean basins or continents to boundaries with scales of meters. Differences in call structure may tempt early observers to draw analogies with dialects in humans or birds, but many mechanisms other than production learning may lead to such differences. As Janik and Slater (1997, 2000) point out, these differences may stem from contextual learning. Animals may also differ in their usage of communication signals based upon differences in social setting and behavioral context, differences that may not be obvious at the early stage of defining dialects. There has also been increasing appreciation that subtle differences in habitat can select for differences in call structure. Animal vocalizations may be selected so that the signals can better be detected given the ambient noise and sound transmission characteristics of the habitat (Slabbekoorn & Smith, 2002). Even for sympatric animals, small differences in location of calling or receiving may change the desired qualities of a signal (Parris, 2002).

Vocal dialects have been described among killer whales (Ford 1991) and sperm whales (Whitehead et al. 1998), but dialects in these highly mobile animals, do not only occur across broad geographical regions, but also are defined by sympatric social groupings. Differences in killer whale calls closely follow matriline, and there is a correlation between coda repertoire and mitochondrial haplotype in sperm whales. The correlation between call variation and genetic variation in these cases makes it difficult to rule out genetic influences on call variation.

I would argue that the only way to address these problems is to take a more fine-grained look at the auditory environment of individual animals and the process by which they modify their vocal behavior. Sanvito et al. (2007) show how more detailed longitudinal data on vocal development in elephant seals provides much stronger data on production learning than does study of dialects. Sanvito et al. (2007) recorded 29 male elephant seals throughout vocal development. The observed changes in vocalizations observed are well

explained by vocal learning, with young peripheral males imitating vocalizations produced by established successful males. In this case, the initial interpretation of dialects as evidence for vocal learning (LeBoeuf & Peterson, 1969) did not stand up to further analysis (LeBoeuf & Petrinovich, 1974), but it would have been incorrect to interpret this problem as evidence against vocal production learning in elephant seals.

Vocal Convergence

Evidence for production learning that derives from convergence of acoustic features of calls among adults has a broader taxonomic spread than either evidence of vocal imitation or effects of auditory deprivation in early vocal development. This may surprise some readers as a dominant model for vocal development has emphasized critical periods early in development for forming auditory memories, followed by vocal practice, with narrower, more stable vocal repertoires among adults. However, many studies have shown that when animals are caged together or form natural groups, their calls become more similar than neighbors in different cages or groups. One of the earliest of these studies involved the black-capped chickadee (*Parus atricapillus*). Mammen and Nowicki (1981) recorded the calls of chickadees from four wild winter flocks. Each group was captured and put in an aviary. Birds from three of the aviaries were rearranged to form new flocks, and the calls of members of each new flock converged in acoustic features within a month. Similar convergence among vocalizations of birds caged together come from budgerigars (Farabaugh et al. 1994, Hile et al. 2000) and Australian magpies (Brown et al. 1991).

Poole et al. (2006) analyzed calls of many African elephants, including a male that was housed with female Asian elephants. The calls recorded from this male were more similar to the chirp vocalization of the Asian elephant females than any of the normal calls recorded from African elephants. This seems to represent a case of inter-specific vocal convergence.

In spite of the lack of evidence for vocal imitation and for effects of auditory input on vocal production during development in most non-human primates, there is evidence of call convergence among adults of the following species: pygmy marmosets (*Cebuella pygmaea*; Elowson & Snowdon, 1994; Snowdon & Elowson, 1999), cotton-top tamarins (*Saguinus oedipus*; Weiss et al., 2001; Egnor & Hauser 2004) and chimpanzees (*Pan troglodytes*; Mitani & Gros-Louis, 1998; Marshall et al., 1999; Crockford et al., 2004). Elowson and Snowdon (1994) tracked changes in trill vocalizations of two groups of pygmy marmosets that were recorded before and after they were put into acoustic contact in separate cages in the same room. Acoustic measures of frequency and bandwidth shifted “as if the animals were tracking one another’s acoustic production.” (p. 1273) Snowdon and Elowson (1999) followed up this study by tracking the trill calls of pygmy marmosets as they paired with a new mate. Three of the four pairs showed convergence in acoustic features of trills during the first 6 weeks following pairing. Two of these pairs could be recorded three years later, and the degree of change in trills was higher in the 6 weeks after pairing than in the following 3 years. Weiss et al. (2001) reported that male and female cotton-top tamarins had more similar calls within a cage compared to between

cages. Marshall et al. (1999) compared pant hoot calls of male chimpanzees from two captive colonies and from a wild site. The acoustic features of pant hoots from each colony and site converged with distinct differences in pant hoots from each group. Marshall et al. (1999) argue that these data show that male chimpanzees modify their pant hoots to converge on a version that is shared within a group.

This process of vocal convergence has been monitored among wild chimpanzees as they form social bonds. Mitani and Gros-Louis (1998) studied pant hoot choruses in wild chimpanzees. They showed that individual chimpanzees modified features of their pant hoot to match those of the individual with whom they were chorusing. Crockford et al. (2004) measured pant hoots and genetic distance of wild chimpanzees of two neighboring communities and a more distant community. They found no support for genetic differences explaining variation in acoustic structure of the calls. Pant hoots from chimpanzees of each of two neighboring communities were more distinctive than those from the distant community, leading Crockford et al. (2004) to conclude not only for vocal convergence within a group but also vocal divergence between neighboring groups.

The process of vocal convergence has been followed as wild bottlenose dolphins (*Tursiops* sp.) form social bonds. In several field sites, it has been observed that as male *Tursiops* mature, they form alliances with one or two other males. Allied males are sighted together 80 % of the time, and the alliances typically last for many years, often until one partner dies (Connor et al., 1992; Wells, 2003). Smolker and Pepper (1999) studied the whistle vocalizations of three male bottlenose dolphins as they formed an alliance. Over the course of three years, the whistles of all three dolphins, which initially were quite different, converged and became more similar. Watwood et al. (2004) were not able to study the convergence process, but they were able to confirm that pairs of males within an alliance had whistles that were more similar than comparisons to males from a different alliance.

Boughman (1997) describes similar group-distinctive calls in foraging groups of greater spear-nosed bats (*Phyllostomus hastatus*). During their second year, female greater spear-nosed bats join a social group of unrelated females that is defended by a single male. Females in these social groups will sometimes forage together. When they leave on a foraging trip and when at the foraging sites, they make screech calls that recruit group members more than other bats. Boughman (1997) shows that the screech calls of bats within a group are group-distinctive, and Wilkinson and Boughman (1998) argue that the bats use these calls to maintain contact with long-term associates traveling to and within feeding areas. Playback of screech calls outside of the roosting cave and at foraging sites show that bats respond to screeches by calling and approaching the speaker. After having found these results in wild bats, Boughman (1998) studied vocal convergence during experimental transfers of captive bats from one group to another. She used two groups of wild-caught adult bats and their offspring, each group of which was maintained in a separate room. Before transfer, the offspring formed a separate roost from the adults in each room, and their calls had begun to differ slightly. She recorded screech calls of some of the younger bats, then transferred them from one room to another at the age at which bats will typically join a social group. Before the transfer, calls of the transfer bats

differed from those of the group that they joined. Within a month after the transfer, calls had converged, and after five months, they were almost indistinguishable. This demonstrates that call convergence in these bats occurs through production learning, with both residents and transfers modifying their calls to come up with a new shared group-distinctive call.

One of the striking things about convergence of calls among adults as they form a group is that evidence for this capability appears to be so much more widespread than evidence that auditory input influences early vocal development. The ease of manipulating the social environment of captive animals and testing for convergence suggest that this is a useful method for comparative studies of vocal production learning. Janik and Slater (2000) highlight the importance of discriminating between vocal production learning, in which an animal modifies the acoustic structure of its vocalization to create a signal that is more or less similar to the model, versus contextual usage learning, in which an animal learns to produce an existing signal in a new context as a result of learning about usage of the signal by other individuals. The production of chirps typical of Asian elephants by an African elephant that was housed with Asian elephants seems to be a clear case of vocal production learning, because the chirp sound does not seem to be part of the normal repertoire of African elephants. But more subtle convergence of acoustic features within a call type is harder to define as vocal production learning by their definition. As long as studies show that an animal changes a call to use a previously unused area of acoustic feature space after hearing calls in that area, I would argue that this provides evidence for a more subtle form of vocal production learning than that shown by evidence of imitation of highly unusual sounds. Methods to quantify this usage of acoustic feature space may need to be fine tuned, but I would argue that understanding the function and taxonomic breadth of vocal production learning requires the inclusion of this phenomenon as well as imitation of completely novel sounds.

Possible functions of convergence

Most studies of vocal convergence suggest a role for providing group recognition and maintaining cohesion of groups. Mundinger (1970) in the first description of vocal convergence in bird calls suggests "Taken as a whole the data provide support for the hypothesis that avian vocal imitation is sometimes employed for recognizing and maintaining contact with other members of the species." (p 482) The coo call of Japanese macaques is thought to function to maintain contact (Sugiura 1998). Tanaka et al. (2006) compared coo calls from two groups of Japanese macaques, and found differences between the two groups that develop 6-7 months after birth. Sugiura (1998) conducted a playback experiment that took advantage of a macaque's tendency to respond with a coo when it hears one emitted by a member of their group. Sugiura (1998) found that macaques modified their contact call to match acoustic features of the played back contact call. Miller et al. (2004) show that killer whales engage in exchanges of the same signal, and Miller (2002) shows by comparing the amount of energy in high vs low frequencies in such a known signal, a killer whale not only should be able to tell where another whale is, but also whether it is swimming towards or away. There is likely more of this kind of complexity in how animals use calls for coordination of movement and for

maintaining cohesion than has been demonstrated to date, especially for animals that move in three dimensions and are often out of sight of one another.

Mammen and Nowicki (1981) demonstrated that some acoustic features of chickadee calls are individual-specific while others converge as birds form temporary flocks. They point out that the contexts when the chickadee call is used suggest a role for individual recognition and flock cohesion; the chickadee call is used as a contact call during group travel or as birds separate while foraging, when one bird separates from the flock, while the flock mobs a predator, and during inter-flock encounters at group territory boundaries. Mammen and Nowicki (1981) discount the idea that flock calls would help chickadees maintain contact. Chickadee flocks are small and calls are so individually distinctive that they argue that convergence is not necessary for this contact function. They do suggest that convergence might speed up recognition of flock members, which might be useful in inter-flock competition or in the presence of a predator. The whistles of allied male bottlenose dolphins show a pattern of initial individual distinctiveness and convergence similar to that described by Mammen and Nowicki (1981) for chickadee calls. Smolker and Pepper (1999) follow Mammen and Nowicki's (1981) argument that it is unlikely members of an alliance require converged whistles in order to recognize one another. Rather they suggest that alliance signatures are directed towards other males to signal a greater threat, or towards sexually receptive females, who might either be more likely to select the alliance for mating or to be less likely to try to leave the alliance.

Among early papers on vocal imitation in mammals, Andrew (1962) suggests "it may have been advantageous for an individual to be able to distinguish his own group from others at a distance. In this way disastrous attempts to join the wrong group could be avoided;" (p 586) Brown and Farabaugh (1997) support this idea for Australian magpies (*Gymnorhina tibicen*) "Presumably, group-specific chorus song may aid magpie's recognition of groupmates vs intruders during the melee of a territorial battle, as well as aiding in synchronizing their aggressive activities." (p 119)

Several studies on vocal convergence suggest that group-distinctive vocalizations may be used as a password for access to shared resources. Feekes (1977, 1982) found that male yellow-rumped caciques (*Cacicus ceta*) share a group-specific songs within a breeding colony, and she suggests that "colony-specific song may be a 'password' distinguishing strangers and familiar inhabitants." [p. 147] She specifically suggests that colony-specific songs may allow "strange males to be immediately recognized and expelled." [p. 147] Wilkinson and Boughman (1998) argue that greater spear-nosed bats use a group-distinctive screech call as a badge to exclude non-members from access to food resources. They found that greater spear-nosed bats tended to call more and forage in larger groups when feeding on concentrated rather than dispersed resources. Tracking of movements showed that females from the same group foraged more close together compared to a female from a different group. However, females from more than one group were found at a feeding site. Wilkinson and Boughman (1998) argue that females can defend rich feeding sites and that a group should be more effective for this defense than an individual. They suggest that when a bat at a feeding site hears an approaching bat, the guarding bat could call to announce discovery of the approacher, and the

approacher might be required to produce the same call as a password. Such a system would require that screeches be difficult to imitate spontaneously for them to be honest indicators of group membership. They suggest that the pattern where it takes months for bats to learn to converge suggests sufficient difficulty for rapid copying.

A different view of vocal convergence emphasizes the role of imitation as an affiliative signal to ease the integration of new members into a group (Mammen & Nowicki, 1981). There is a rich literature showing that when a human wants to establish a social relationship with another, s/he will modify many aspects of his or her communication to match the partner (Giles, 1984). A speaker will be particularly likely to accommodate and match the speech of a more powerful or influential partner. Communication accommodation emphasizes a process that unlike the password discussed above, can easily and quickly take place as parties begin to interact.

Many animal studies have pointed out the similarities between the predictions of communication accommodation theory for humans and observations in animals as diverse as non-human primates (Snowdon & Elowson, 1999; Mitani & Gros-Louis, 1998), dolphins (Tyack, 2003), parrots (Vehrencamp et al., 2003), and several other avian species (Brown & Farabaugh, 1997). Vehrencamp et al. (2003) conducted playback experiments with orange-fronted conures (*Aratinga canicularis*) and suggest that conures increased the similarity of the calls they used to respond to playback calls as an affiliative signal during the initial exchange. Mitani and Gros-Louis (1998) conducted a study to test three hypotheses about call convergence in chimpanzees. Chimpanzees use pant hoots to recruit allies and to maintain cohesion (Mitani & Nishida, 1993). Mitani and Brandt (1994) showed that males who are associating and producing a chorus of pant hoots tend to produce acoustically similar calls. One possibility was that the chorusing context might trigger a particular type of call. Another was that low-ranking chimpanzees might mimic high-ranking ones, producing calls that converge on those of high-ranking chimpanzees. The third hypothesis was that chimpanzees actively modify their calls to match those of the chimpanzees with which they are chorusing. This hypothesis predicts that when chimpanzee A is chorusing with chimpanzee B, he would produce calls more similar to B than when he is chorusing with another chimpanzee. Mitani and Gros-Louis (1998) did not find a significant difference in pant hoots produced by chimpanzees when they were alone compared to when they were chorusing. They also found that low-ranking males did not often chorus with high-ranking males, and low-ranking males were did not produce calls more similar to the alpha male than to each other. Both pairs of male chimpanzees with sufficient calls to compare similarity when they chorused with each other vs with other chimpanzees produced calls that were significantly more similar when chorusing together vs chorusing with other males. Mitani and Gros-Louis (1998) suggest for chimpanzees and the many cases listed above that vocal accommodation functions to strengthen social bonds between individuals.

There are several aspects of speech accommodation that are quite similar to vocal convergence. Some of the literature on speech accommodation focuses on short dyadic interactions, but is equally appropriate for longer term development of shared communication patterns as a group forms. In both speech accommodation and vocal

convergence, as interactants form social relationships, features of their vocal communication may converge. If the theory of communication accommodation were broadened to animal vocal convergence, it would predict that animals would converge as an affiliative gesture, to facilitate social integration and cohesion. This is quite similar to the predictions of a group cohesion function for vocal convergence in animal calls. This view seems entrenched enough in our culture for the movie "Close encounters" to be able to assume the audience would understand that imitating sounds of an extraterrestrial should be viewed as a friendly act.

An alternative interpretation stems from studies of how songbirds can use song matching to escalate aggressive interactions. One of the first effects of aggressive song matching noted was that some song birds may match a song played back in their own territory, and that the probability of matching a rival song correlates with the probability or intensity of attack (Krebs et al. 1981). This result suggests that matching an opponent's song can heighten the warning or escalate the threat. As adult male songbirds establish their breeding territories, they familiarize themselves with the calls of their neighbors. Playback of a neighbor's song from the neighbor's territory elicits weaker responses than either playback of a stranger's song from the same place, or of the neighbor's song from outside its territory (Falls & Brooks 1975). This shows that by listening to song and by locating where it is coming from, a male songbird can determine whether a stranger is present in a neighboring territory. This observation suggests that a newcomer might benefit by being able to copy the songs of local males. Wilson and Vehrencamp (2001) tested this idea by playing back to a male song sparrow (*Melospiza melodia*) either a neighbor's song (neighbor), the same song produced by a stranger (mimic), or a novel song produced by the stranger (stranger). They found that male sparrows tended to respond as strongly to the mimic song as the stranger song, suggesting that they were able to discriminate whether the same song type was sung by a neighbor or by a stranger. When a bird hears a neighbor singing from its normal territory, it may reply not by matching the same song, which might escalate the interaction, but rather by selecting another song that the two share within their song repertoires (Beecher et al. 1996). If the bird instead hears the song of a stranger, it is more likely to match the song and escalate the interaction.

The idea of vocal accommodation theory that vocal matching always is affiliative stand in sharp contrast to the idea that song matching in birds signals to escalate a threat, and that deceptive mimicry elicits retaliation. The one theme that strikes me as common between these two situations, however, is that the signaler can match the call of another in order to communicate that the response is meant to target the specific earlier caller. This interpretation was highlighted by Thorpe and North (1965) for imitation of calls. This may stem from sensory systems that are more likely to detect or weight signals similar to those just sent out. Miller et al. (2004) and Sugiura (1998) suggest that by rapidly responding to a call with a match, a respondent can direct the response directly to a specific caller. One of the intriguing questions about this kind of matching is whether such a signal can functionally refer to the associated signaler. If a signal takes on a predictable association with an individual as in the case of dolphin signature whistles, or a group as in the case of vocally converged group signals, it may form the basis for a

learned and arbitrary signal that becomes associated with a social referent. The question of how rich such reference is for non-human animals has barely been addressed.

Evidence for vocal convergence as animals form groups suggests that if group-distinctive calls are important, this might be an important function for vocal learning. Few animal groups split precisely along reliable patterns of genetic variation, so it is difficult to imagine a mechanism by which animals could inherit group-distinctive calls. Vehrencamp et al. (2003) argue that “While a system of recognition based on memorization of individual- or family-specific call variants does not depend on vocal learning by senders, a system of group recognition based on the convergence of call structure among strongly associated group members does require vocal learning (Bradbury and Vehrencamp 1998). Thus understanding the mechanism used to organize fission-fusion societies may have broad relevance to the evolution of vocal learning in general.” (P.38).

Little is known about the genetic underpinnings of the neural mechanisms required for vocal learning in birds and mammals. Without such information, it is difficult to predict how many times vocal learning may have originated in evolution, and how difficult and unlikely such origins may be. Pooling the data on vocal imitation and vocal convergence suggests a wider taxonomic distribution of vocal production learning among mammals than generally appreciated. Imitation of anthropogenic sounds has been reported for African elephants, harbor seals, and dolphins. Vocal convergence has been reported for bats, humpback whales, several species of toothed whales, African elephants and several species of non-human primates. The wide taxonomic distribution of this evidence for vocal production learning suggests that perhaps more of the neural underpinnings for vocal production learning are in place in mammals than is usually imagined.

This observation raises the question of whether selection is constantly acting on the timing and extent of modifiability of vocal repertoires. Many species may inhabit social and ecological niches where modifiable repertoires are not advantageous, and modifiability may not be obvious in these taxa. For example, many songbirds with vocal production learning inherit templates that restrict the kinds of sounds they copy. It may require particularly predictable social and acoustic environments for the young to be freed to have a broader innate template for what sounds to learn. Species requiring mechanisms to manage grouping in fission-fusion societies may develop specific forms of modifiability that are likely to enable the development of group-distinctive calls. Development of group-distinctive calls may require specific parameters for vocal learning, depending upon the patterns of association typical of a population. Too little influence of auditory input on vocal output and there might not be enough change to allow convergence. Too much of a tendency to copy what you hear could lead to a cultural revolution instead of distinctive calls within small groups. For example, the humpback whales of the eastern Australian coast studied by Noad et al. (2000) shared a vocal tradition of a song that was shared among the population. When the song of western Australia arrived on the east coast, it swept through the eastern population with such popularity, that it completely replaced the east coast song, removing the distinctiveness not just between groups but between whole populations. Rather than

having a single group-distinctive signal, killer and sperm whales have complex patterns of group-distinctive repertoires of calls. The development of individual repertoires that include several examples of a call type rather than a single group-distinctive call might result from differing rates of copying and copy error. Some features of sperm whale codas, such as the wide spread of coda repertoires shared across groups might be explained by such a phenomenon. Sexual selection at any time could take the rudiments of vocal learning and select for obvious and exaggerated displays.

Andrew as early as 1962 pointed out

it may well be that song learning has evolved purely as a simple means of insuring the transmission of complex species-specific song, and that the existence of dialects is a functionless by-product. That this method of transmission appears to allow enough variability to permit individuals to be recognized by slight differences in the form of their song (10) is probably also important.

The matter is complicated by the fact that it is not yet possible to establish the course of evolution of song learning in any line of passerine evolution. It is even possible that extensive learning is primitive within the group, and that this faculty has been lost in some lines (11). However, it is clear that mimicking can be evolved in the absence of any very high level of intelligence when there is a need for the acquisition during development of complex species-specific, group-specific, or individual-specific patterns of vocalization. [p 586]

Andrew (1962) suggests that perhaps vocal learning may have been more widespread taxonomically at an earlier stage of evolution, and has been lost in some lines. Another way to look at this is to recognize that the pattern of presence or absence of vocal learning depends heavily upon the criteria for presence and absence, and for what assumptions to make about taxa for which relevant data are not available. The phylogeny of vocal learning would look very different depending upon the evidence required to demonstrate its existence. Spontaneous imitation of novel sounds, often speech sounds produced by animals raised with humans, has a relatively narrow distribution. But vocal convergence seems to be much more widespread. It may also be that the genetic underpinnings for neural mechanisms linking vocal output to auditory input are even more widespread for ubiquitous problems such as adapting signaling to compensate for noise. Such relatively simple mechanisms have not normally been included in discussions of vocal production learning. But as long as they provide neural pathways to link auditory input with vocal motor output, they might form the substrate for evolution to work on in taxa that encounter niches with added uses for vocal learning. It is sobering that after more than 40 years of work in this area, the questions raised by Andrew (1962) are still so open. While behavioral research helps to understand current functions of vocal learning, I think that research on the genetic underpinnings of the neural mechanisms will be required to understand the evolutionary origins of vocal learning.

The point brought up by Andrew (1962) with respect to geographical dialects in birdsong suggests a parallel null hypothesis that perhaps some patterns of communication signaling in mammals are functionless byproducts of vocal learning. For a given pattern of production learning in vocal development throughout the lifetime, different patterns of sociality could lead to different patterns of communication signals. For example, inshore dolphins that rely upon strong individual social bonds living within highly fluid social

groupings, might be expected to develop individually distinctive calls that converge on calls of close associates. Coastal killer whales that live in highly stable groups from which neither sex emigrates might use the same pattern of vocal development to develop a group-distinctive repertoire of calls. Sperm whales which are highly mobile pelagic animals usually sighted in groups formed of two more stable units might be expected to form a more geographically dispersed set of groups sharing call repertoires. We know that these species have very different social organization; we do yet know whether or how vocal learning mechanisms may have been selected to produce the communication systems that have been observed.

In the case of bird song, the question of whether dialects might stem from random copying processes gave rise to a series of models to predict dialect patterns based upon the number of neighbors and error rates for copying (e.g. Goodfellow & Slater 1986; Lachlan & Slater, 2003). These models meant to understand geographical dialects were organized in terms of spatial distribution. For animals as mobile as marine mammals, I think it would be important to model social structure as well as space. This kind of modeling to test whether specific matching patterns and error rates couple with association patterns lead to individual- and group-specific repertoires may help test ideas for functions of vocal production learning in mammals and specify critical measurements such as patterns of association, vocal development, lifetime patterns of vocal matching, and rates of copying errors.

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