The evolution of vocal learning

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Vocal learning, in which animals modify their vocalizations to imitate those of others, has evolved independently in scattered lineages of birds and mammals. Comparative evidence supports two hypotheses for the selective advantages leading to the origin of vocal learning. The sexual selection hypothesis proposes that vocal learning evolves to allow expansion of vocal repertoires in response to mating preferences for more complex vocalizations. The information-sharing hypothesis also proposes that vocal learning evolves to allow expansion of vocal repertoires, but in this case in response to kin selection favoring sharing of information among relatives.

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Introduction

Although vocal learning has evolved multiple times in vertebrates, relatively few lineages possess this ability [1,2]. Vocal learning is especially rare among mammals, and among primates is well developed only in humans [3]. The rarity of vocal learning may be explained in part by the complexity of the neurological underpinnings that this ability seems to require [2]. Given the complexity of vocal learning as an adaptation, and its centrality to the life histories of some species, it is not surprising that attention has been given to explaining its evolution. Because the evolution of vocal learning in any one lineage, including our own, is typically a one-off affair, progress in testing ideas on the evolution of vocal learning requires a comparative approach. This approach is challenging because the lineages that have evolved vocal learning are few and diverse, hampering the application of formal comparative methods, which require a much larger number of taxa for statistical comparison. Nonetheless, progress is only possible by synthesizing patterns across multiple lineages, as we attempt here in a qualitative fashion.

When we speak of vocal learning, we are referring specifically to vocal production learning, in which signalers alter the form of their vocalizations by imitating the vocalizations of others [4]. Additional types of vocal learning occur, such as usage learning, in which signalers learn the context in which to produce specific vocalizations, and comprehension learning, in which receivers learn to modify their response to vocalizations produced by others [4]. These additional forms of vocal learning have a wider taxonomic occurrence [1] and perhaps can be accomplished without the considerable neural apparatus that undergirds vocal production learning [2], and consequently their evolution seems less puzzling.

Because vocal production learning requires complex neural adaptations that are presumably costly, this type of learning is not expected to evolve except in response to some compensating fitness advantage. Some of the hypothesized advantages of vocal learning are experienced by an individual only when most or all of the other signalers in its population are vocal learners and receiver response has evolved to adjust to this circumstance. Advantages such as these are not relevant to the evolutionary origin of vocal learning because they only would accrue when the trait has already evolved, although they may be important to its evolutionary maintenance. Our focus here is principally on the origins of vocal production learning, and thus on the benefits that accrue to the first individuals that begin to modify their vocalizations based on the sounds they hear from others.

Advantages of song learning in songbirds

Many of the proposals on the selective advantages of vocal learning have emerged from the study of song learning in songbirds. The songs of songbirds typically have dual functions in mate attraction and territory defense [5]. Song development in songbirds appears to be universally influenced by imitation learning, but as there are over 4000 species of songbirds (suborder Passeri), there is tremendous scope for variation in patterns of learning [6]. One typical pattern is for young males to memorize songs or parts of songs in the first few months of life [7] in the neighborhood where they will later establish their own territories [8]. The memorized sounds later guide song development when the young males begin to sing as they approach their first breeding season [9].

In an early and still influential paper, Nottebohm [10] suggested that one of the two main advantages of vocal

learning in songbirds is the production of vocal dialects, which he argued would be advantageous in promoting genetic adaptation to local environmental conditions. Nottebohm assumed that males learn the local dialect where they are born, and that females learn preferences for their own local dialects and then choose mates that sing those dialects. Song learning would thus promote assortative mating between males and females that have been selected for adaptation to local conditions (Figure 1; Hypothesis 1). Various aspects of this scenario have since been challenged on empirical grounds [11,12]: whether males actually learn songs where they are born rather than after they disperse, whether females actually prefer to mate with males singing their own natal dialects, and whether dialect populations actually show genetic differences indicative of local adaptation. Beyond these empirical problems, the vocal dialect hypothesis also has some logical difficulties. First, a hypothesis to explain the evolution of vocal learning must provide a selective advantage to the male that learns, not an advantage to the female that chooses to mate with him or to the population to which he belongs. The vocal dialect hypothesis can be stated in terms of an individual level advantage to the learner, though often it is stated otherwise. Second, and more critically, the vocal dialect hypothesis provides a selective advantage to song learning only if songs already vary geographically and females already prefer local variants. Although it seems logically possible for geographic variation in song to occur without song learning, in practice this

does not happen [12], at least not at a relevant geographic scale. If geographic variation in song does not occur unless song learning is already established, then the vocal dialect hypothesis can explain the maintenance of vocal learning but not its origin.

The second main advantage of vocal learning proposed by Nottebohm is in meeting female preferences for complex sounds [10] (Figure 1; Hypothesis 2). Nottebohm assumed that learned vocalizations can achieve greater complexity than innate vocalizations, an assumption that still seems reasonable. He proposed that females generally prefer to mate with males having more elaborate songs. Nottebohm could adduce little evidence for this assumption at the time, but since then laboratory experiments and field studies both have shown that female songbirds prefer more complex song in many species [13,14] though not all [15].

In some songbirds, female preferences for complex song may currently be adaptive because of associations between song complexity and male quality [16•]. The 'developmental stress hypothesis' suggests that brain structures underlying song learning develop during a period in which other aspects of the phenotype are developing, and in which the young bird is particularly susceptible to developmental stress. Those individuals that escape stress, or whose genotypes are resistant to stress, develop more complex and more accurately imitated songs as well as more robust phenotypes overall

Figure 1
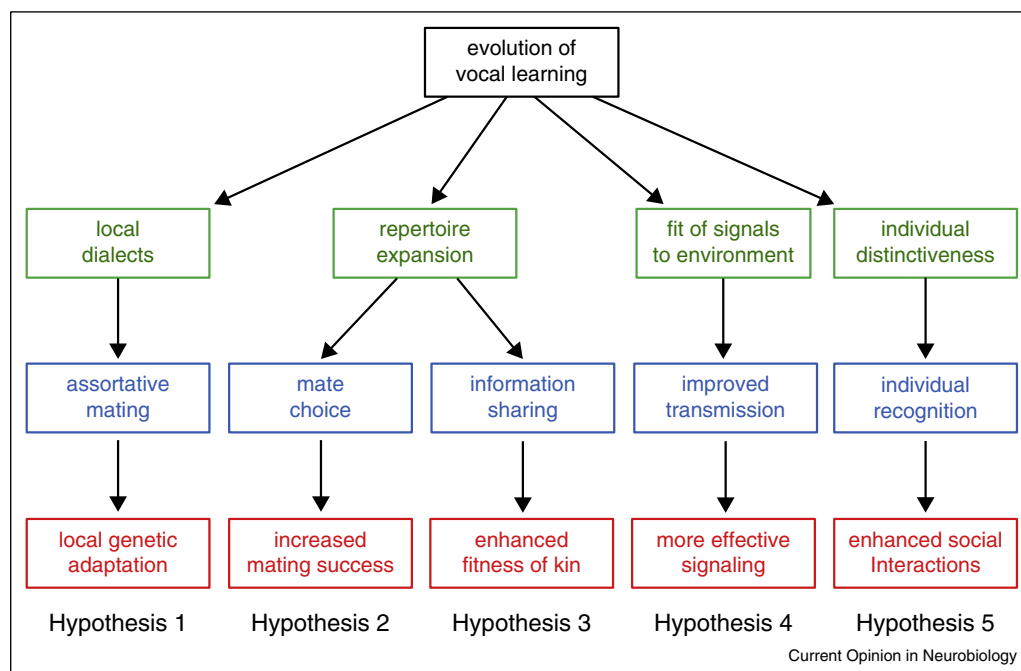
Five hypotheses on the selective benefits leading to the evolution of vocal learning. For each hypothesis, vocal learning has a proximate effect (in green) that translates by some mechanism (in blue) to a selective benefit (in red). The hypotheses are the (1) vocal dialect hypothesis, (2) sexual selection hypothesis, (3) information sharing hypothesis, (4) environmental adaptation hypothesis, and (5) individual recognition hypothesis.

[17,18,19[••]]. The developmental stress hypothesis predicts associations between male quality and vocal complexity specifically for learned songs. Unlearned vocalizations are expected to be less effective as indicators of male quality because their development is simpler at both the behavioral and neural levels, and consequently is less susceptible to environmental disruption. Thus the hypothesis provides a benefit for female preferences for well-learned songs once song learning is established, but does not help explain the initial evolution of song learning [17]. Female preferences for complex song might, however, have existed before the evolution of song learning, as a form of sensory bias. Sensory bias for complex sounds can arise because behavioral responses habituate to repeated exposure to the same stimulus and recover when the stimulus changes, yielding a higher overall response to a varied stimulus [20]. Biased responses on the part of females thus might produce non-adaptive preferences for complexity that could potentially explain the origin of song learning. A classic test for sensory bias is to determine whether females possess the hypothesized preference in species lacking the preferred trait [21,22]; thus progress could be made on testing the sexual selection hypothesis by measuring preferences for complex song in additional species in which males sing only simple songs [20].

Another hypothesis for the origin of bird song learning invokes environmental adaptation for sound transmission (Figure 1; Hypothesis 4). Starting in the 1970s, Morton [23] and others [24,25] showed that the acoustic properties of bird songs affect how well they propagate through the environment, and that different habitats select for different acoustic properties. Hansen [26] argued that if young birds are more likely to learn songs that they can hear well, then learning would increase the degree to which songs are adapted to the existing habitat. In other words, a young bird learns what has transmitted well to him, and so his songs will transmit well to others [27[••]]. Because the advantage of vocal learning under this 'environmental adaptation hypothesis' accrues to the learner and operates regardless of whether other individuals also learn, the hypothesis can explain the origin of vocal learning as well as its maintenance. Recent work has provided further evidence for acoustic adaptation of songs to habitats [28,29], and in addition evidence that such adaptation is stronger in birds that learn than in those that do not [30]. The major weakness of this hypothesis is that differences in songs between habitats tend to be small [31,32], suggesting that the advantages of acoustic adaptation may be marginal.

Advantages of vocal learning in humans

The literature on human language evolution has focused more on possible selective advantages of language as a whole than on the advantages of component faculties such as vocal learning. When component faculties have been considered, abilities other than vocal learning have drawn more attention, such as the capacity to use and understand recursion [33] or the ability to use syntax to determine meaning [34]. Nevertheless, we can glean some additional ideas on the selective advantages of vocal learning by considering human evolution.

Jackendoff [34] has suggested that one of the earliest steps in the evolution of human language was the acquisition of the ability to use 'an unlimitedly large class of symbols.' He points to the disparity in lexicon size between non-human animals, typically with a few dozen call types, and modern humans, with tens of thousands of words. Jackendoff argues that hominids must have had to adapt to learning the increased number of symbols, a point that is reinforced if one notes the poor vocal learning abilities of non-human primates. Further, Jackendoff assumes that 'any increase in explicit expressive power of the communicative system is adaptive,' without specifying why this would be so. In our view, the most reasonable hypothesis on this last point is that increased communication ability in the hominid line was favored largely by kin selection for information sharing among relatives [35,36]. Combining the assumption that vocal learning is needed for vocabulary expansion with the idea that vocabulary expansion is favored by kin selection for information sharing gives a sufficient explanation for the origin of vocal learning in the human lineage. We will term this explanation the 'information-sharing' hypothesis (Figure 1; Hypothesis 3).

The information-sharing hypothesis shares with the sexual selection hypothesis the assumption that vocal learning allows an expansion of vocabulary size, but substitutes kin selection for sexual selection as the selective benefit explaining why vocabulary expansion is favored. Sexual selection itself has been advocated as an explanation for the evolution of human language. Darwin [37] suggested that early progenitors of man used their voices primarily in singing during courtship, incorporating in their song imitations of natural sounds. More recent authors have adopted this suggestion of a musical protolanguage [36,38], and Fitch has argued that sexual selection would have been responsible for the elaboration of such a protolanguage [36]. If so, sexual selection for more elaborate vocalizations would explain the origin of vocal learning in hominids just as has been proposed for birds.

Advantages of vocal learning in parrots and dolphins

Parrots and dolphins may seem an odd pairing, but both are vocal learners, and they use their learned vocalizations in similar ways. Some cetaceans, such as humpback whales (*Megaptera novaeangliae*), have elaborate, learned vocalizations that appear to function in the same way as do bird songs, in attracting mates and repelling rivals [39]. Bottlenose dolphins (*Tursiops truncatus*) do not employ vocal learning in acquiring elaborate songs, but rather in

developing 'signature whistles,' relatively simple vocalizations that are unique to specific individuals [40,41]. Dolphins give their own signature whistles when separated from close associates, suggesting that these vocalizations function in promoting social cohesion [42]. Dolphins occasionally give the signature whistle of another individual, especially when matching a whistle that they have just heard, which implies that whistles can be used to address and perhaps even label other individuals [43,44]. Similarly, many parrots do not possess elaborate songs, but instead use vocal learning in developing short, individually distinctive contact calls [45••,46]. Like dolphin signature whistles, the contact calls of parrots seem to function in promoting social cohesion; they are used, for example, to attract other individuals to foraging groups [47] and in identifying mates [48]. Some parrots rapidly modify their contact calls to match those of individuals they are interacting with [49], again suggesting that these calls are used to address specific individuals. Certain songbirds also possess simple learned calls that function in maintaining social cohesion within mated pairs or flocks [50,51].

The existence of recognition systems based on simple, learned vocalizations suggests the hypothesis that vocal learning enhances individual recognition and thereby promotes social cohesion (Figure 1; Hypothesis 5). This hypothesis can be stated in terms of individual advantage to the signaler, that is a caller might benefit in certain social contexts from making itself more recognizable to others. In addition, the hypothesis is capable of explaining the origins of vocal learning: if learning increases how recognizable an individual is, that advantage would likely accrue to a learner even if no other individuals in its population are vocal learners. Nottebohm [10] doubted whether vocal learning is necessary for individual recognition, however, pointing to evidence that individual recognition of calls occurs in various seabird species that are presumed not to be vocal learners [52]. Nottebohm further doubted that vocal learning does anything to enhance vocal recognition, as logically the increases in vocal repertoire size allowed by vocal learning should make recognition harder, not easier. Additional examples of individual recognition of unlearned vocalizations have come to light since Nottebohm's criticism [53,54•], making the case for an 'individual recognition' advantage even more dubious. Explicit tests of the effects of vocal production learning on individual recognition would help to clarify further the position of this individual recognition hypothesis.

A stronger argument can be made that vocal learning should enhance group (rather than individual) recognition, especially if animals disperse between groups so that they sometimes need to converge on a new group's signature [51]. This hypothesis is similar to the vocal dialect hypothesis, and runs into the same logical problem — that group specific signatures are unlikely to occur unless vocal learning has already evolved. Thus group recognition is a possible explanation for the maintenance of song learning, but not for its origin.

Conclusions

The five major hypotheses on the evolution of vocal learning we have outlined (Figure 1 and Table 1) should be considered with respect not only to the taxa already mentioned but to at least two additional groups for which there is good evidence of vocal learning: hummingbirds, which learn elaborate vocalizations analogous to song [55,56•], and bats, which learn signature calls used for individual and group recognition [57,58•].

Table 1

Five hypotheses on origin of vocal production learning

Hypothesis	Possible application	Comments
Vocal dialect hypothesis — vocal learning evolves to promote geographic variation in vocal signals, which in turn allows assortative mating by site of origin and hence promotes local adaptation	Taxa with learned mating signals that vary geographically such as songbirds and some parrots	Cannot explain the origin of vocal learning because small scale geographic variation does not occur until vocal learning is already in place
Sexual selection hypothesis — vocal learning enables increases in the complexity of the vocal repertoire that are favored by female preferences for vocal complexity	Taxa with learned mating signals such as songbirds, some whales, and perhaps even humans	Gives an immediate advantage of vocal learning to males if females have a pre-existing bias favoring greater vocal complexity
Information sharing hypothesis — vocal learning enables expansion of the vocal repertoire in a system in which kin selection favors greater information sharing	Taxa in which learned vocal signals provide environmental information to others — that is, only humans	Gives an immediate advantage of vocal learning to the learner but has a narrow taxonomic application
Environmental adaptation hypothesis — vocal learning promotes acoustic adaptation of vocal signals to the local habitat	Taxa such as songbirds that have long range vocal signals and that are philopatric to habitats	Gives an immediate advantage of vocal learning to the learner but the benefits are likely to be marginal
Individual recognition hypothesis — vocal learning allows vocal signals to become more individually recognizable and thereby promotes social cohesion	Taxa with vocal signals used in individual recognition such as dolphins, parrots, and bats	Individual recognition of vocal signals occurs in animals without vocal learning so learning is not necessary and is perhaps not even conducive to recognition

The individual recognition hypothesis has the broadest potential application of the five hypotheses, in that so many of the taxa showing vocal learning use this ability in developing signature calls or whistles. Nevertheless, we do not think that this hypothesis is a viable explanation for either the origin or the maintenance of vocal learning because of the strong likelihood that vocal learning is not actually advantageous for individual recognition. The vocal dialect hypothesis can also be rejected on logical grounds, because any advantage of advertising geographic identity is only realized after vocal learning is widespread enough to establish geographic variation in vocal signals.

The environmental adaptation hypothesis is most appropriate for those vocalizations that are transmitted over some distance, which would include most mate attraction signals and some individual recognition signals. Also necessary for this hypothesis is that a species occupies multiple habitats with different sound transmission properties, and that each individual occupies one such habitat rather than travelling through all of them, as might happen in whales. With this second restriction, the hypothesis may be limited to songbirds and hummingbirds. The hypothesis offers a benefit of learning that we suggest is marginal, but which could have operated in conjunction with some more significant benefit, as none of the proposed advantages are mutually exclusive.

We suggest that the most plausible explanations for the origin of vocal learning are the sexual selection and information-sharing hypotheses. These two hypotheses are related in that both assume that the important effect of vocal learning is to enable increases in the number and complexity of vocalizations. Under the sexual selection hypothesis, expansion of a vocal repertoire is favored because of female preferences in mating, so this hypothesis is supported by the many cases in which learned vocalizations function in courtship. Under the information-sharing hypothesis, expansion of the vocal repertoire is favored because of kin selection for sharing information with relatives, which fits only with the human case. Neither of these hypotheses provides an obvious explanation for the occurrence of vocal learning in taxa with recognition systems, but in at least some of these groups vocalizations are also used in mate attraction. Thus it is possible that the mechanisms of vocal learning evolved due to sexual selection for repertoire expansion in these groups also, and were later co-opted for recognition.

Conflict of interest statement

Nothing declared.

Acknowledgements

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