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## PUTTING DISTANCE BACK INTO BIRD SONG WITH MIRROR NEURONS

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BIRD SONG IS one of the most fascinating and complex examples of animal communication, and the quest to understand its evolution and function has fueled the careers of many behavioral ecologists, psychologists, and neurophysiologists. The research questions cover the gamut of how brains are wired, how individuals learn songs, the mechanics and energetics of sound production, why some sounds are more effective at intimidating rivals than others, how females judge mate quality by sound alone, and, more recently, how environmental pollutants and noise disrupt sound production and avian communication systems. But have we lost sight of an essential aspect of bird song—that it is a signal adapted to communicate over distance? “Distance” may refer to the meters separating most territorial songbirds, or to the centimeters between colonial Purple Martins (*Progne subis*) or Brown-headed Cowbirds (*Molothrus ater*) displaying to one another. How do birds perceive their distance from rivals? Here, I explain the “ranging hypothesis”—which states that listeners determine their distance from singers by assessing the amount of degradation in the perceived signal by comparing it with an undegraded version stored in memory (Morton 1982, 1986)—and consider how new neurological studies provide support for this hypothesis.

It is widely accepted that a listener benefits immensely from being able to detect the distance between itself and a signaler, and that birds range the songs that they hear (Richards 1981, Wiley and Godard 1996). So why do we need to “put distance back into bird song”? The controversial aspects of the ranging hypothesis are twofold: (1) that birds can range songs effectively only if the songs they hear are contained within the listener’s memory, and (2) that many aspects of bird song (e.g., song learning, song dialects, repertoire size, and matched countersinging) may have evolved as a result of the need to memorize songs to be able to range. For instance, I have previously argued that song learning evolved not only to develop songs to sing but also, perhaps surprisingly, to allow for more effective listening (Morton 1996).

### SONG RANGING IS IMPORTANT TO BIRDS

The context for singing is usually either repulsion of conspecifics in order to monopolize resources important to fitness (food, nest sites, and mates) or attraction of the opposite sex to increase mating success. The distance separating participants can have a large effect on the costs and benefits that ensue, depending on the behavioral responses of both parties. Many studies have shown that listeners gauge the intensity of their response according to the perceived threat of an intruder, whether the threat is related to the status or quality of the rival or to its distance from the listener. For instance, if a rival sings from outside a bird’s territory boundary, the time and energy invested in physical or vocal territory defense may be largely wasted because of the existence of other competing activities, such as foraging or defending against more serious challenges and attracting mates. Decisions to attack, sing, or ignore imply drastically different time and energy expenditures and consequences that are not trivial to individual fitness. The question that remains is how *can* birds judge distance of singers with precision?

Spherical divergence in sound energy, which causes a song’s overall amplitude to drop over distance, is not a reliable cue for ranging (Morton 1982, McGregor 1994, Naguib and Wiley 2001). By simply turning its head, a singer changes a song’s apparent amplitude, because songs are directional (Patricelli et al. 2007) and singers may vary amplitude from one song to another (Anderson et al. 2008) or vary them with changes in environmental background noise (Brumm and Todt 2002). Temperature and wind gradients produce “shadow zones” that affect song amplitude in a frequency-specific manner (Wiley and Richards 1982), which is why we can hear people whispering across a cold lake but must shout to be heard over a sunny field. Experienced birders think that they can range bird song fairly well, but birds require sophisticated precision in ranging because this affects social interactions that have profound effects on fitness.

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Birds have a remarkable ability to resolve sound in the time domain; they are time analyzers as well as frequency analyzers. Their ability to resolve fine temporal structures of 1–2 ms greatly exceeds human abilities (Dooling et al. 2002) and, moreover, birds can perceive echoes off habitat features such as tree trunks (Blumenrath and Dooling 2006). Echoes reveal the inevitable physics as sound propagates through habitat and bounces off objects; this is useful for ranging because degradation increases with the distance that sound travels. Any song recorded from a distance of a few meters or more from the source has measurable degradation, defined as the many changes in a signal at a given distance compared with the signal's structure at its origin. Degradation arises from spherical spreading (–6 dB per doubling of distance traveled), atmospheric absorption, diffraction by temperature and wind gradients, scattering, reverberations, amplitude fluctuations, habitat, turbulence (Morton 1975, Naguib and Wiley 2001), height (because of the absorptive and reflective effects that the ground has on sound; Mathevon et al. 2005), and differences in the rate at which song components attenuate (e.g., notes within a song syllable; Gish and Morton 1981).

Many studies have shown that sound degradation influences how birds respond to the songs they hear (reviewed in Morton 1986, McGregor 1994, Naguib and Wiley 2001). In territorial defense, degraded songs are treated with low-energy responses, as though the singer is not threatening, whereas undegraded songs receive energetic responses, corresponding to the distance from itself that the listener judges an intruder to be (Morton 1986). Listeners often sing in response to degraded song but fly toward the playback location and even attack the speaker in response to undegraded songs (Richards 1981). In playback studies specifically designed to compare birds' ability to range songs, degraded songs are treated differently than less degraded songs (e.g., Richards 1981, Morton 1982, McGregor and Krebs 1984, Shy and Morton 1986, Morton and Derrickson 1996).

#### DOES SONG RANGING REQUIRE MEMORIZED SONGS?

The ranging hypothesis not only addresses birds' ability to perceive echoes and degradation to judge distance; it also proposes that if a bird has already memorized a song type, it can compare the incoming sound to the undegraded model in its brain and accurately measure distance from singer (Morton 1982, 1986). The dichotomy of "in memory" versus "not in memory" is biologically based and supported by the neurological mechanism of song learning and responses to auditory inputs (see below).

The challenge in testing this hypothesis is to measure the accuracy of ranging in relation to whether the songs heard by the bird are in its memory or not. A clear experimental design to test for ranging ability is to present a stimulus (a recorded song) at a known distance from the focal bird, control for other circumstances that may influence acoustic properties (e.g., amplitude of the playback, habitat, weather, and social interference from conspecifics), and then assess how the focal bird perceives distance by watching what it does (e.g., the intensity of aggressive response) in response to circumstances that have different fitness consequences (e.g., playback inside vs. outside the territory). The assumption is that if the focal bird cannot ascertain the distance to the playback, it must investigate the whereabouts of the challenger; or, if it can range the challenger and perceives the distance to be large, the territorial response will be weak. Alternatively, if the focal bird can range the playback accurately and the threat is high, the bird should respond quickly, accurately, and with aggression.

To design the playback itself, a typical approach has been to first create recordings of naturally degraded songs by broadcasting undegraded songs and re-recording them at specified distances through natural habitat, and then to conduct playback experiments while controlling for the amplitude of the playback (e.g., Richards 1981, McGregor and Krebs 1984). One can also use natural degradation and play back undegraded song from different distances to the focal bird (Shy and Morton 1986, Morton et al. 2006). Artificially degraded playback songs can be produced by re-recording songs in a reverberant room (e.g., Morton et al. 1986, Wiley and Godard 1996), although I have argued that such playbacks differ in important ways from natural degradation and, therefore, may interfere with a bird's ability to range in the first place (Morton et al. 2006).

If this is not tricky enough, one must also control whether the song chosen for playback is likely in, or not in, a focal bird's memory. I say "likely" because a field researcher can be certain that a song is in memory if the bird sings it, but it is difficult to know whether songs are not "in memory" because some species learn songs during development but do not perform them as adults. For instance, each male Kentucky Warbler (*Geothlypis formosa*) has a single song that differs from those of most neighbors (Tsipoura and Morton 1988) and appears to be able to range their own song type just as well as a neighbor's song (Wiley and Godard 1996), but it is not known to what extent a bird also has neighbor songs, though unsung, in memory. One way to solve this problem is to treat foreign songs as "not in memory," assuming that song types from populations sufficiently far away have virtually no chance of being in a focal bird's memory. If a playback experiment (controlling carefully for all of the above) broadcasts equally degraded songs that are in memory, versus not in memory, then the ranging hypothesis predicts that the focal bird will better range the "in memory" song and, therefore, that its aggressive response will reflect the actual threat posed by the intruder.

Shy and Morton (1986) played undegraded songs in four treatments: familiar (in memory) versus unfamiliar (not in memory) and at two distances with different social consequences (in territory vs. outside territory). The ranging hypothesis predicts that birds can better determine distance—and, therefore, threat—if the song is in memory. The amount of degradation heard by the focal bird was natural, and the focal bird was first located so that its distance from the playback speaker was known. "In memory" songs were those that the focal bird had performed, whereas "not in memory" songs were from another population (>500 km away) that did not share song types with the study population but were otherwise similar (Borror 1956). When songs were "in memory," the focal bird responded more aggressively to songs inside versus outside the territory, indicating that ranging was occurring. However, when they heard "out of memory" songs, focal birds did not respond more aggressively to songs coming from inside their territory (even though the amplitude was louder) and expended much energy searching for the intruder even though the playback was not a threat (i.e., off territory).

Morton et al. (2006) used a similar experimental design (familiar vs. unfamiliar song, close vs. far playback distance) to test the ranging hypothesis in Blue-headed Vireos (*Vireo solitarius*). The interesting twist is that playbacks were performed while males were on their nests incubating, which provided for a more powerful experimental design because (1) the distance to playback was controlled; (2) males do not normally leave the nest until their mate arrives to replace them, so premature departure during a playback signals a very strong response; and (3) the male's ranging ability could be assessed

in a novel way, after the playback was over, by monitoring his ability to locate the now-silent playback site when his mate relieved him from incubating. Males were more likely to leave the nest during playback and, when they did so, approached the speaker more closely in response to playback of local songs (which were assumed to be in memory) than foreign songs (assumed not to be in memory).

Studies such as these would seem to provide strong support for the ranging hypothesis, yet other playback studies report that song familiarity did not affect ranging ability (Wiley and Godard 1996) and lead to the conclusion that birds can use general aspects of degradation alone, without comparison to an undegraded memorized version, to accurately range distance (Naguib and Wiley 2001). It is agreed that birds can judge degradation only by comparing the incoming song with an undegraded model, but some argue that personal experience with a particular song might allow a receiver to at least approximate a signaler's distance. That birds can range "not in memory" songs to some extent should not be surprising, and the crux of the matter is how well, exactly, can birds range the songs of competitors and what are the fitness consequences of sloppy ranging.

The ranging hypothesis is based on the premise that birds have the ability to compare an incoming song with a perfect internal representation of the song in its own memory, thereby allowing the bird to better measure degradation in the heard song (Morton 1986). It is not good enough for a bird to be merely familiar with a song, for instance if a neighbor has sung it countless times. Instead, I have long argued that there is a neurological process by which songs that were stored in memory during development are required for excellent distance perception. Determining whether this occurs in birds may be difficult to test conclusively in behavioral field experiments, but the answer may be written, evolutionarily speaking, into the wiring of bird brains.

#### MIRROR NEURONS AND THE RANGING HYPOTHESIS

A physical mechanism linking song production and hearing was proposed more than 25 years ago by Williams and Nottebohm (1985), who argued that a bird may somehow use motor inputs to neural tissue to activate memory of what its own memorized song sounds like when produced. In White-crowned Sparrows (*Zonotrichia leucophrys*), auditory response properties of units in a telencephalic nucleus were shown to exhibit considerable selectivity for the individual's own song (Margoliash 1983, Margoliash and Konishi 1985). In the same species, Volman (1993) later discovered dynamic changes in response properties of higher-vocal-center (HVC) neurons during the plastic phase of song learning. These neurons became more responsive to the bird's own vocalizations than to those songs used to tutor it, perhaps because of auditory feedback from the bird's vocalizations as it practiced singing. An increase in the stability, number, and size of dendritic spines, the major sites of excitatory synaptic transmission, may underlie this process (Roberts et al. 2010).

Recent advances in the neurobiology of bird song (for an excellent summary and for a review of the song-system pathways in the avian brain, see Mooney 2009) began with the discovery of mirror neurons in frontal regions of the Southern Pig-tailed Macaque (*Macaca nemestrina*) cortex. These neurons discharge when the monkey performs an action, but also when it sees another individual performing the same action (Kohler et al. 2002, Rizzolatti and Craighero 2004). The songbird forebrain contains similar neurons, which fire when the bird sings a particular song as well as when it hears that song (Tchernichovski and Wallman

2008). Such one-to-one auditory-vocal correspondence, whereby what you hear depends on what you know how to sing, would seem to be a necessary neural mechanism for ranging with precision.

Prather et al. (2008) implanted a miniature motorized microdrive to sample projection neurons in the RA (hearing) and area X of the HVC ( $HVC_x$ ; song production) and played back vocalizations to freely active, awake, and vocalizing Swamp Sparrows (*Melospiza georgiana*) and domesticated Bengalese Finches (*Lonchura striata*). Their goal was to identify individual neurons displaying a precise auditory-vocal correspondence that would allow auditory neural activity to be evaluated against the bird's vocal activity. Individual  $HVC_x$  neurons responded when the birds sang a specific song or, critically, when they heard the same song in a playback. Neurons were finely tuned: only one song type in the bird's repertoire evoked auditory activity in a given neuron. The researchers played back a variety of songs, including the bird's own song and other Swamp Sparrow songs and discovered that there was no activity from  $HVC_x$  neurons if songs were not in the memory of the bird.

An incoming song could also activate the receiver's auditory-vocal neurons if it was very similar to one in the bird's memory. A consequence of the precise temporal resolution of these neurons is that individual notes in Swamp Sparrow song syllables are perceived categorically (Prather et al. 2008). Prather et al. (2008:308) conclude that "the selective auditory responsiveness of  $HVC_x$  cells extends to similar vocal sequences produced by other birds, making auditory-vocal  $HVC_x$  neurons well suited to a role in communication."

This exciting discovery provides a neurophysiological basis to field experiments on ranging that used natural degradation protocols: A bird must have the perceived song in its own memory to accurately determine distance and respond appropriately to the level of threat (e.g., McGregor et al. 1983, Shy and Morton 1986). If the song is not in its memory, a bird cannot differentiate well between a song played from within its territory and a song played off its territory. Although it remains to be shown experimentally, the presumed mechanism underlying this behavior is that song degradation reduces firing of the corresponding mirror neurons.

Nearly all efforts to explain song learning and its neurological basis focus on song output. Critical periods for song development, subsong, crystallization, tutors, and the song pathways in the brain are studied from the standpoint that birds learn songs to sing them. This is to be expected because the production of songs and the learning of them seem to go hand in hand. Of course birds learn songs in order to sing them, but the ranging hypothesis suggests another function for song learning: better distance estimation when songs are heard (Morton 1996).

Birds sing more songs during their song-learning period (i.e., memorize the songs) than they eventually perform as adults (Marler and Peters 1982, McGregor and Avery 1986). Captive-raised Swamp Sparrows sang 4 to 5 times more syllable types during the subsong-learning period than were used in performed song after crystallization. One young bird sang 19 syllable types in subsong but performed only 3 types as an adult. Marler and Peters (1982) termed this "developmental overproduction and selective attrition." I propose that the role played by these "unsung songs" is to make birds better listeners (i.e., better at ranging). These songs are not lost or winnowed but are stored in the brain for future use, though not to make song (see also Nottebohm et al. 1990). This hypothesis predicts that unsung songs are still present in the memories of songbirds after adult repertoires are crystallized.

Indeed, Swamp Sparrows retain neurons trained to respond to songs that are not found in adult repertoires. Prather et al. (2010) recorded neuronal responsiveness in HVC in laboratory-raised anesthetized Swamp Sparrow to assess responses to different types of auditory exposure during their song-learning period. They played songs in the bird's adult repertoire, songs used to tutor them, and songs the individuals had never heard. Prather et al. (2010:10586) explained their results in this way:

Effective tutor songs were not simply those that were acoustically similar to songs in the adult repertoire. Moreover, the strength of tutor song responses was unrelated to the number of times that the bird sang copies of those songs in juvenile or adult life. Notably, several neurons responded most strongly to a tutor song performed only rarely and transiently during juvenile life, or even to a tutor song for which the bird was not known to have memorized. Thus, HVC neurons representing songs in the adult repertoire also appear to retain a lasting record of certain tutor songs, including those imitated only transiently.

Individual HVC neurons almost always responded to songs in the subject's adult vocal repertoire, but the more interesting result was that neurons also fired when birds heard songs that were learned but not performed as an adult. In other words, those neurons "mirror" (fire) only when those songs are produced by other individuals.

In species with repertoires, and in unstable neighborhoods (i.e., migratory species) where territory owners must deal with "new kids on the block" that are ignorant of existing and past territorial boundaries, one would expect stronger selection for ranging mechanisms. If each song type is an arrow, it is better to have more arrows in the quiver to match and threaten newcomers. This applies not only to the songs produced (which is what the observer can measure) but also to unsung songs that have a biological function, as shown with mirror neurons, and which I argue is the mechanism that allows listeners to range a wider variety of opponents. White-throated Sparrows show a genetically based song-learning capacity, with migratory populations learning more songs in subsong than sedentary forms (Nelson et al. 1996a), even though all perform only a single song in adulthood. Migratory populations contain individuals that sing a variety of song types, which may explain why it is selectively advantageous to learn more subsongs that can later be used for ranging.

Mirror neurons also give us insights into how singers can intimidate rivals by "allowing" themselves to be ranged. Matched countersinging occurs when a defender sings the same song type just produced by a challenger; if the challenger changes song type, the defender follows suit. We now know that this behavior by the defender triggers mirror neurons in the rival that are individually tuned to each specific song in succession (Prather et al. 2008). By deliberately "matching" the song of a singing intruder, the defender assures that the intruder knows precisely where the territory owner is. Site dominance gives owners the upper hand in territorial disputes, which is why defenders likely benefit from being ranged (Morton et al. 2000).

In some species or populations, individuals within a population all share the same song types, whereas each geographically separated population has distinct songs (e.g., dialect species). Here, singers' distances from each other are easily ranged by all contestants because they sing the same dialect and, neurologically speaking, they all learned the same songs and therefore have mirror neurons that fire when hearing any song produced by neighbors. In dialect

species, such as western populations of White-crowned Sparrows, all birds sing the same song over many generations within their dialect boundary (e.g., Derryberry 2009). Young sparrows memorize several song types in their hatching year, then select from memory the song that best matches the dialect where they attempt to breed the next year (Nelson and Marler 1994, Nelson et al. 1996b). This social situation predicts that selection would *not* favor retention of unsung songs because birds would not encounter "foreign" songs to range once they breed and become geographically bound within a single dialect. Accordingly, such species apparently only retain neurons that respond to adult song with intra-dialect selectivity, forgetting their unsung songs (Margoliash 1986).

The evidence from research by Prather et al. (2010) strongly suggests that song learning has evolved for both the production of songs and for their perception. I contend that the likely function of mirror neurons is to improve perception of distance to the singers. Mirror neurons show that the dichotomy in the ranging hypothesis between "in memory" and "not in memory," the source of much debate, has an underlying mechanism that affects song perception. From the listener's standpoint, learning songs that are not sung makes perfect sense: more songs stored in memory mean better ranging, especially for species with large repertoire sizes. The ranging hypothesis provides an adaptive explanation for why individuals benefit from retaining songs in their memory that they do not sing.

It is hoped that future use of song playback will acknowledge that "all songs are not alike" when it comes to predicting the outcomes of responses to them.

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