Current Biology
Magazine

CellPress

Quick guide

Duet singing in plain-tailed wrens

Melissa Coleman[1] and Eric Fortune[2]

What are plain-tailed wrens? Plain-tailed wrens (Figure 1) are songbirds that live on the slopes of the Andes mountains at altitudes between 2200 and 3200 meters above sea level near the equator. These territorial wrens are 'bamboo specialists' — they are found exclusively in stands of dense chusquea bamboo, which can make them difficult to see. It is not difficult to find the wrens, however, as they sing duet songs at amplitudes over 80 dB that can be heard at distances of over 200 meters. These duets are remarkable in their speed and precision: they sound as if a single bird is singing.

Females and males alternate singing short syllables that are about 300 milliseconds or less in duration with about 20 millisecond intervals between syllables. If a male sings syllables labeled a and c, and the female sings syllables B, D, and E, the duet might be aBcDE (Figure 2). This pattern, known as a motif, can be repeated over a hundred times during a duet song that can last over two minutes. But, like a jazz musician, these birds frequently vary their performance by changing syllables and shifting the order of syllables. Interestingly, these birds can also sing in choruses in which additional females and males will all sing the same syllables at the same time.

Why do birds duet? Why some species of birds sing duets is not fully understood. If you play a recording of a plain-tailed wren duet near or within a territory of a pair of wrens, they will respond by approaching the speaker and singing. This behavior is believed to be a form of territorial defense; however, this sort of territorial defense by singing is also found in hundreds of other species of songbirds that do not sing duets. One hypothesis is that duetting might be more effective for territorial defense because two birds are singing rather than a single bird. Duets may also be used to reduce the possibility of extra-pair copulations — a hypothesis known as mate guarding. By singing together to produce duet songs, both birds can better keep track of their mates within the dense bamboo forest. Another possibility is that the songs are used to attract and keep mates. Similar to other cooperative forms of mating displays, both females and males may choose mates based on their singing performances. These are not mutually exclusive hypotheses, and it is likely that duets have multiple roles in the social lives of these birds.

How do plain-tailed wrens learn to sing duets? Although how plain-tailed wrens learn to perform duets has not yet been studied, song learning in other species of songbirds has been investigated intensively. Songbirds must hear appropriate songs while they are juveniles. These songs provide a form of memory or template that the bird will, in turn, try to match with its own vocal performance. The matching process requires that the bird hear its own vocalizations. We have no reason to believe that this does not also occur in plain-tailed wrens.

Nevertheless, duetting in plain-tailed wrens is more complex. First, females and males each sing syllables that are not produced by the other sex. This begs the question: how do the birds learn the appropriate sex-specific syllables? One idea is that the birds have an innate filter for syllables of their sex. This notion is supported by the fact that we have never observed a bird singing syllables from the repertoires of both sexes. Alternatively, perhaps juveniles learn all syllables from both sexes and later in life only produce their own syllables. This idea is supported by the observation that an area of the songbird brain used in song production has neurons that are activated by playback of syllables from both sexes.

Second, the birds appear to learn the coordination of duet singing with specific partners. Partners with little experience singing together produce less precisely coordinated and shorter duets than pairs of wrens that have more experience singing together in the wild. This suggests that there are two categories of learning for duet production: first, learning the sex specific syllables that the bird sings; and second, learning how to coordinate duetting with a partner.

Figure 1. An adult plain-tailed wren at Siempre Verde, Imbabura Province, Ecuador.

Why study duet singing in plain-tailed wrens? We study duet singing as a way to understand how individual animals coordinate their behavior to cooperate with other individuals. Cooperation is important for many species and especially for humans: the greatest human achievements have all depended on cooperation between people. One of the challenges of studying the mechanisms of cooperation is identifying the routes and categories of information that is shared between individuals. Consider two people dancing — each person simultaneously uses visual, tactile, and acoustic cues to coordinate their learned patterns of movements. The cues can be subtle and vary over time during the dance.

Plain-tailed wrens, in contrast, can coordinate their duets using acoustic cues alone, and females and males rarely sing at the same time. Rather, they rapidly alternate singing syllables back and forth, so that at any moment information is only flowing from the female to the male, or *vice versa*. When a female sings, she and her male partner hear her song syllable. In the next moment, they switch roles and the male produces his syllable that is also heard by both birds. When a bird hears its own syllable, it receives autogenous or 'self-generated' feedback about what it just sang. Autogenous feedback is necessary for song learning and maintenance in all species of songbirds. When a wren hears its partner's syllable, it receives heterogenous or 'other-generated' feedback that is used to coordinate the duet. Heterogenous feedback is used to control the timing and acoustic features of the next syllable produced by a female or male plain-tailed wren. Each syllable, therefore, has a different role for the

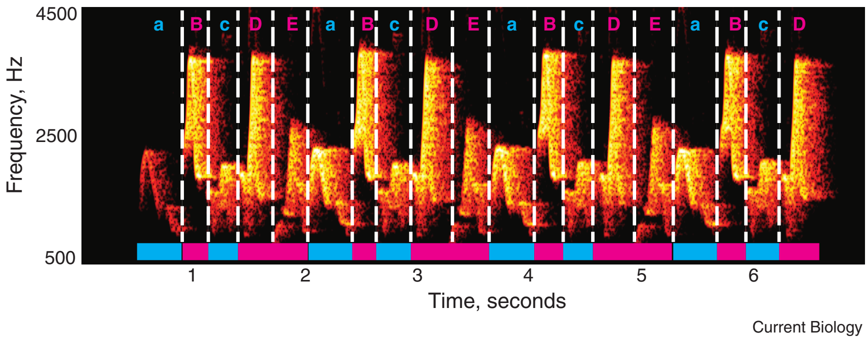

Figure 2. A sound spectrogram of a duet produce by a male and female pair of plain-tailed wrens.
Male syllables are indicated by blue bars below and blue letters above, whereas female syllables are indicated by magenta. Syllable intervals are marked with dashed vertical lines. This duet is composed of 3 complete motifs of aBcDE and a partially complete motif, aBcD.

female and for the male. A male syllable, for example, is an autogenous signal for the male and a heterogenous signal for the female.

The goal of our work is to reveal computational strategies used in the brains of individuals to control cooperation. This segregation of autogenous and heterogenous feedback into discrete, alternating epochs in plain-tailed wrens allows us to disentangle how sensory information is used in the brain of each bird to control cooperative behavior. We can play recordings of female and male syllables to awake or anesthetized wrens to probe the effects of autogenous or heterogenous signals on neurons that control singing.

Where would you look in a brain to find neurons that control cooperation? The brain areas that are used for learning and production of song in songbirds were identified in the 1970s — they include a group of telencephalic nuclei (brain areas) that are not found in other species of birds. These areas, known together as the 'song system', have different roles in song learning, perception, and production. One of these areas, known as HVC, has neurons that have both motor and sensory properties. That is, these neurons are active during singing, but are also activated by playback of the bird's own autogenous song. In this way, HVC is a site of sensory and motor integration specifically related to modulation of motor activity by autogenous feedback.

The song system was identified in species in which only males sing, and therefore only produce autogenous feedback. In contrast, plain-tailed wrens, and perhaps many other species of duetting birds, use both autogenous and heterogenous information to control singing. As both female and male wrens produce autogenous feedback when they sing, we expect to observe activity in HVC related to autogenous syllables in both sexes. However, because the birds also rely on heterogenous information for the control of song production, we expect that there must also be activity related to heterogenous information. To understand how brain circuits control cooperative behavior, it is necessary to identify how autogenous and heterogenous information is encoded by neurons in the brain and how these codes affect motor neuron circuits that control duet singing.

How are duets controlled by the brain? Determining the roles of neurons in the control of behavior usually involves placing electrodes into the brain to measure the numbers and patterns of action potentials that are generated either while the animal produces the behavior or in response to sensory stimuli. For example, to determine the roles of heterogenous and autogenous signals in HVC, one can play duets, male syllables, female syllables, and other songs to the wrens while recording action potentials in HVC. Indeed, this was the first neurophysiological experiment that we conducted with these birds.

Our experiments revealed that HVC neurons in both males and females respond best to the duet song, which is composed of both autogenous and heterogenous syllables. In other words, these neurons respond best to the complete duet that neither bird can sing by itself: that is, the cooperative output of the pair of birds. This suggests that each of the wrens not only 'know' their own parts, but also have a form of memory, or template, for the combined cooperative behavior.

What are the implications of this finding? This result suggests that cooperation may require that each participant not only knows its own part of the cooperative performance, but also the structure or dynamics of the combined output. Consider two people who have never seen humans dancing. Let's teach each person their respective steps to the Cha-Cha, but in isolation. After each person learns their own part well, we bring both of them into a room. Given that neither person has ever seen a dance, they wouldn't even know that the steps were meant to be performed with a partner, let alone how their steps might be coordinated. In the absence of insight into the structure of the cooperation, it seems unlikely to us that our participants would successfully dance a Cha-Cha. But if we give them a template for this cooperative performance — perhaps asking a pair of dancers to demonstrate a Cha-Cha just one time — our participants would be able to coordinate their individual performances.

What else can we learn from studying the plain-tailed wrens? Cooperative behaviors are complex and involve more than simply coordinating the timing of motor programs between individuals. Cooperation can also include adapting to unpredictable conditions. In wrens, for example, the birds sometimes start duets when they are separated by more than 5 meters. Due to the speed of sound, long distances cause significant delays as the sound travels between the birds. The wrens adapt to these delays by altering the timing of their singing. How are these delays computed in their brains to produce the correct timing of their syllables?

Cooperating animals also routinely generate variations in their performances. As in a jazz performance, where musicians are free to improvise provided that their improvisations fit within the structure of the tune, variations in animal cooperative performances also follow complex rules. Wrens produce variations in their duets but maintain the overall duet structure. How is the structure of the duet encoded in the song system, and how are variations generated from within this structure?

Over time, we hope not only to learn more about the specific mechanisms that plain-tailed wrens and other animals use to coordinate their behavior, but also to describe cooperative processes in mathematical terms. One application of these sorts of mathematical descriptions is to implement them in artificial systems, such as co-robots — robots that work with people. To safely cooperate with people, co-robots need to use algorithms that are well-tuned to the rules and mechanics of cooperation with people. These algorithms must be sufficiently predictable so that a person can work with the robot, but also sufficiently flexible to accomodate the natural range of variations that people make when they are cooperating.

Where can I find out more?

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[1]W.M. Keck Science Dept. of Claremont McKenna, Pitzer, and Scripps Colleges, 925 N. Mills Avenue, Claremont, CA 91711, USA. [2]Federated Department of Biological Sciences, New Jersey Institute of Technology and Rutgers University, 323 Dr Martin Luther King Jr. Boulevard, Newark, NJ 07102, USA. E-mail: mcoleman@kecksci.claremont.edu (M.C.); eric.fortune@njit.edu (E.F.)