tion for the threshold temperature that will initiate thermoregulatory behaviors, a range of thresholds can evolve. This phenomenon is manifest as genetic variance in the propensity to perform thermoregulatory tasks such as fanning and in the more precise regulation of brood nest temperature by genetically diverse colonies compared with genetically uniform colonies, especially when stressed.

Our study has shown how random genetically determined differences in task threshold can enhance the stability of a self-organized biological system. We suggest that most aspects of colonial life would also be enhanced by variance in task threshold among the worker population.

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Steroid-Dependent Auditory Plasticity Leads to Adaptive Coupling of Sender and Receiver

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For seasonally breeding vertebrates, reproductive cycling is often coupled with changes in vocalizations that function in courtship and territoriality. Less is known about changes in auditory sensitivity to those vocalizations. Here, we show that nonreproductive female midshipman fish treated with either testosterone or 17β-estradiol exhibit an increase in the degree of temporal encoding of the frequency content of male vocalizations by the inner ear that mimics the reproductive female's auditory phenotype. This sensory plasticity provides an adaptable mechanism that enhances coupling between sender and receiver in vocal communication.

Among seasonally breeding vertebrates (*1*), one might expect hearing sensitivity to change concurrently with vocal parameters (*2,3*) to maximize detection and localization of conspecifics. Studies of evoked potentials in birds and humans are consistent with this assumption (e.g., *4, 5*), but there are reports of disparities between the peak frequency sensitivity of the auditory periphery of females and the dominant frequency of male vocalizations (e.g., *6, 7*). These results have been used to support the hypothesis that male vocalizations exploit such differences between vocal parameters and female peripheral frequency sensitivity (*7, 8*). Here, we report that, for the adult female auditory system of a seasonally breeding fish, steroid hormones can induce an improvement in the precision of temporal encoding by the primary auditory filter within the inner ear to the dominant frequency components of male advertisement calls. Thus, steroid hormones, like other neuromodulators (*9*), can mediate context-dependent auditory plasticity that, in this case, improves frequency encoding and thereby enhances frequency coupling between sender and receiver in a vocal communication system.

Acoustic communication is essential to the reproductive success of the nocturnally breeding teleost fish, the plainfin midshipman (*Porichthys notatus*) (*10*). Males and females migrate seasonally from deep ocean sites into the shallow intertidal zone along the Pacific coast of North America. Males build nests under rocky shelters and produce long duration (>1 min) advertisement calls or "hums" at night to attract reproductive females that use the hum to detect and locate nesting males (*10, 11*).

The main organ of hearing in midshipman is the inner ear's sacculus, which is innervated by the eighth cranial nerve (*10*). Neurophysiological studies of midshipman and teleosts in general show that, although saccular afferents do encode frequency into the rate of action potential firing (spikes per second), frequency is most accurately encoded by the temporal firing pattern (i.e., phase locking) of the spikes in response to the time-varying fine structure of an acoustic waveform (*12–14*). Measures of phase locking show much less variability than do spike rate profiles, can explain the variability in spike rate measures, and remain stable over a wide range of stimulus levels and durations (*14*). Thus, phase locking by saccular afferents provides a robust periodicity code of the frequency com-

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ponents of vocalizations, is the primary mechanism for sending frequency information to the brain, and can explain the frequency discrimination behaviors of teleost fish (*13, 14*). Phase locking is also a more accurate gauge of frequency encoding below 1 kHz for vertebrates in general (*15, 16*).

Like many vocal communication signals among vertebrates (*3*), the midshipman male's advertisement hum is multiharmonic, with a fundamental frequency (F_0) close to 100 Hz (*10*). The seasonal onset of male advertisement calling in midshipman during the breeding season coincides with a dramatic enhancement in the degree of phase locking by the female's sacculus to the upper harmonics of the male's hum, including the second ($F_1 \sim 200$ Hz) and third ($F_2 \sim 300$ Hz) harmonics that often contain either as much as or more energy than F_0 (*10*). Enhancing the sensitivity of the sacculus to the hum's upper harmonics should improve detection of male vocalizations, in part because higher harmonics propagate farther in shallow water environments such as those where midshipman nest as a result of the inverse relationship between water depth and the cutoff frequency of sound transmission (*17, 18*). The encoding of hum F_0 by saccular afferents is also enhanced by harmonics (*19*).

Similar to other seasonally breeding vertebrates (*1*), the yearly onset of midshipman reproductive behavior is associated with increases in circulating levels of steroid hormones. Approximately 1 month before the beginning of spawning, midshipman females show peaks in circulating plasma levels of both testosterone (T) and 17β-estradiol (E_2) (*20*). Here, we tested the hypothesis that T and E_2 can induce the reproductive phenotype of the sacculus in a nonreproductive individual. We collected nonreproductive females from their offshore habitats when their steroid levels were naturally low (*20*) and randomly treated ovariectomized individuals with either T, E_2, or no steroid, using either silastic or silicone elastomer implants (*21*). These females survived for 23 to 37 days before neurophysiological analysis (*12*). Extracellular recordings of single-afferent discharges, taken from randomly sampled eighth-nerve fibers that innervate the hair-cell epithelium of the sacculus, were used to construct isointensity profiles that show the degree of temporal encoding over a frequency range for individual afferents. Responses to pure-tone stimuli from 60 to 400 Hz at an intensity like that near calling males (130 dB re 1 μPa) (*17*) were recorded for 161 afferents in 36 adult nonreproductive females (9 T, 16 E_2, and 11 controls with implants that contained no steroid). Stimuli consisted of 500-ms tones with 50-ms rise and fall times presented for eight repetitions at a rate of one every 1.5 s. As in our previous studies of wild-caught females (*12*), responses were measured by calculating the vector strength of synchronization (VS), a measure of phase locking; VS varies from 0 for a random distribution to 1 for perfect synchronization (*22*). A Rayleigh Z test (*23*) determined whether synchronization to pure tones was significantly different from random ($P < 0.05$).

Response profiles of individual saccular afferents revealed an increase in phase-locking precision at higher frequencies among steroid-treated, nonreproductive females relative to nonreproductive female controls (*21*). Median and quartile values for the entire population of saccular afferents (Fig. 1A) reflected individual response profiles and showed that for nonreproductive females, VS gradually declined from 0.85 to 0.28 between 60 and 400 Hz. In comparison, median VS values for T- and E_2-treated nonreproductive females remained relatively high up to 300 Hz, followed by a gradual decline toward 400 Hz, although VS values still remained higher relative to nonreproductive females (Fig. 1A). There was a significant difference in the isointensity profiles of VS median values for the entire population sampled between control and steroid-treated, nonreproductive females [Wilcoxon paired-sample test (*23*), P values < 0.001]. VS increments were minimal close to F_0, but increased by 50 to 100% over the F_1 and F_2 range (Fig. 1B). T- and E_2-treated fish did not differ from each other ($P = 0.35$), which is consistent with the concurrent elevation of both steroids during the period of gonadal recrudescence that occurs just before the onset of the midshipman's breeding season (*20*).

Although best frequency (BF), the frequency that evoked the highest VS, was not reflective of the broad upward shift in VS values observed across the frequency range beyond F_0, it varied from 60 to 140 Hz for controls and from 60 to 320 Hz for steroid-treated females. Median BF was significantly higher in T-treated (100 Hz) and E_2-treated (80 Hz) fish than in controls (70 Hz) (Kruskal-Wallis one-way ANOVA, Dunn's method for pairwise multiple comparisons, $P < 0.05$). Females given control implants had T and E_2 levels that were low ($\bar{x}$ T = 0.76 ± 0.56 ng/ml, $n = 10$; $\bar{x}$ E_2 = 0.21 ± 0.10 ng/ml, $n = 8$), like those of nonreproductive females (*20*). In contrast, females given T and E_2 implants had elevated levels of T ($\bar{x}$ = 37.9 ± 24.2 ng/ml; $n = 9$) and E_2 ($\bar{x}$ = 5.3 ± 2.4 ng/ml; $n = 16$), respectively. These T levels were about 4.75 times as high as the maximum reported for wild-caught females in the spring prenesting period, when these levels naturally peak. However, there was no difference in the isointensity profiles between T-implanted females with either high (>60.0 ngT/ml; $n = 3$ animals, 19 afferents) or low (<7.5 ngT/ml; $n = 3$ animals, 18 afferents) T levels (Wilcoxon

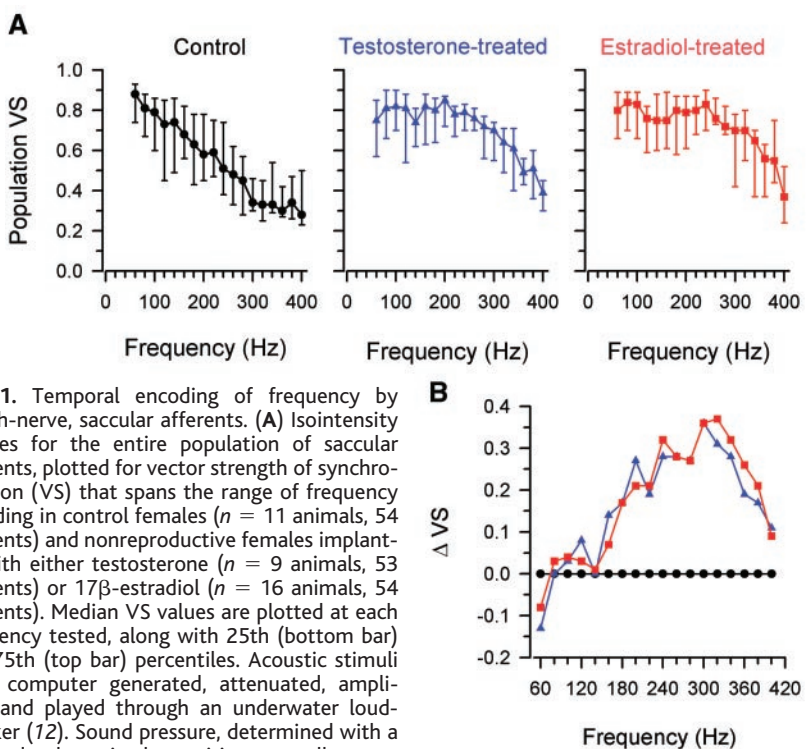

Fig. 1. Temporal encoding of frequency by eighth-nerve, saccular afferents. (**A**) Isointensity profiles for the entire population of saccular afferents, plotted for vector strength of synchronization (VS) that spans the range of frequency encoding in control females ($n = 11$ animals, 54 afferents) and nonreproductive females implanted with either testosterone ($n = 9$ animals, 53 afferents) or 17β-estradiol ($n = 16$ animals, 54 afferents). Median VS values are plotted at each frequency tested, along with 25th (bottom bar) and 75th (top bar) percentiles. Acoustic stimuli were computer generated, attenuated, amplified, and played through an underwater loudspeaker (*12*). Sound pressure, determined with a minihydrophone in the position normally occupied by the fish's head, was equalized across test frequencies with computer software. Experiments were conducted in a soundproof room. (**B**) Profiles of the differences in the population VS values between control nonreproductive females (black circles) and either testosterone-treated (blue triangles) or 17β-estradiol–treated (red squares) nonreproductive females at each frequency tested (derived from Fig. 1A).

paired-sampled test, $P = 0.15$). Both the females with low T levels and the E_2-implanted females had, respectively, T and E_2 levels similar to the levels in prenesting spring females (*20*). Consistent with naturalistic decrements in VS measures for reproductive females held in captivity beyond the breeding season (*12*), the increases in phase-locking precision appeared to be gradual over a period of about 1 month; the isointensity profiles from nonreproductive females with T implants for 9 to 14 days ($n = 3$ animals, 13 afferents) did not differ from those of controls ($P = 0.55$).

The observed changes in saccular response profiles were related to the temporal encoding of the stimulus waveform's fine structure rather than to changes in auditory thresholds. Auditory threshold at BF was determined for a subset of 16 afferents from 13 fish (5 T-implanted, 6 E_2-implanted, and 2 controls) and found to be similar between nonreproductive controls ($\bar{x} = 105 \pm 8$ SD dB re 1 μPa; $n = 7$ afferents) and steroid-treated, nonreproductive females ($\bar{x} = 101 \pm 7$ SD dB re 1 μPa; $n = 9$) (t test, $P = 0.28$).

Given that we are recording from primary afferents, the changes described above suggest the possibility that the effects on frequency encoding could potentially stem from direct steroid action on the inner ear's sensory epithelium. Existing evidence in both humans and rodents shows estrogen receptors in the cochlea; however, the functional importance of their presence remains unknown (*24, 25*). In support of a comparison to the mammalian phenotype, we identified estrogen receptor alpha in the midshipman's sacculus (Fig. 2), following methods similar to those we used to clone a partial cDNA for the midshipman aromatase gene (*21*, *26*).

Because T- and E_2-treated fish showed identical changes in phase-locking precision, the observed changes in frequency encoding may be almost entirely due to E_2, which circulates at levels two to three times as high as does T in reproductive female midshipman (*20*). An essentially E_2-dependent effect would also be consistent with other studies, showing that many of the influences of T on the vertebrate nervous system are due to its conversion to E_2 by the enzyme aromatase, which is especially abundant in teleost brain, including that of midshipman (*1, 26*). Further support for estrogen effects on hearing come from studies of human and rodent females with Turner's syndrome, a genetic aberration that results in the loss of ovarian E_2 production; these individuals exhibit a progressive loss in high-frequency hearing at the level of the eighth nerve and cochlea (*27*).

The expanded sensitivity to the male advertisement call's second and third harmonics (peaks in the frequency spectrum at 200 and 300 Hz) was nearly identical between steroid-treated nonreproductive and wild-caught reproductive females (Fig. 3). Males may also show steroid-dependent, seasonal plasticity in frequency encoding that could similarly enhance conspecific detection. [The frequency-encoding profiles of nonreproductive males resemble those of nonreproductive females (*14*)]. The steroid-induced changes in temporal encoding observed here may depend on changes in the filtering properties of the hair-cell membrane and/or the hair cell–afferent synapse (*15, 28–31*). Similar mechanisms of auditory plasticity may also be operative in other vertebrate groups where multiunit or evoked potential studies have suggested either seasonal or steroid-related changes in audition (*4, 5, 32, 33*). This includes proposals that cyclical changes in the auditory frequency sensitivity of human females at differing stages of the menstrual cycle may be dependent, at least in part, on the influences of steroid hormones (*4, 34*).

We show that the degree of temporal encoding of frequency is not a fixed trait, but rather that it can have a steroid-dependent plasticity that supports adaptive coupling of female frequency encoding to the male's advertisement call. The mismatch between the low-frequency tuning of the female frog's auditory system and the higher peak in the male's frequency spectrum that has been used to support the sensory exploitation hypothesis (*7*) may yet be due, in part, to the testing of females with a nonreproductive-like auditory phenotype. The adaptive auditory plasticity shown here may contribute to an individual's sensitivity to contextually relevant signals, including those used for social communication, in a variable environment.

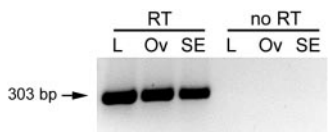

Fig. 2. Estrogen receptor in inner ear's saccular epithelium. Identification of estrogen receptor alpha (ERα) expression in the saccular epithelium (SE) of the inner ear by reverse transcription polymerase chain reaction (RT-PCR), using midshipman-specific primers from an ERα clone (*21*). A predicted 303–base pair (bp) product is seen in positive control tissues, liver (L), and ovary (Ov), as well as in the SE of four ovariectomized females implanted with 17β-estradiol, as was done for the neurophysiological experiments (*21*). No amplification occurred in negative control lanes without reverse transcription (no RT) of L, Ov, and SE.

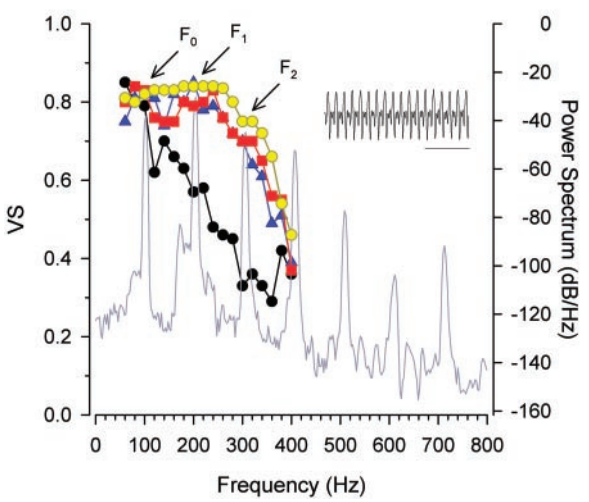

Fig. 3. Match between vocal characteristics and the degree of frequency encoding of eighth-nerve, saccular afferents. Shown here is a combined plot of the phase-locking precision of saccular afferents as a function of the vector strength of synchronization (VS, left *y* axis) and the power (amplitude) spectrum of a hum advertisement call from a nesting male midshipman fish (right *y* axis, in relative dB values); inset shows the temporal waveform of this call recorded at 16°C at the nest site (scale bar, 50 ms). Frequency is plotted along the *x* axis for both sets of measures. Shown here are median VS values of afferents emphasizing the overlap in frequency sensitivity between testosterone-treated (blue triangles) and 17β-estradiol–treated (red squares) nonreproductive females (from Fig. 1A) and wild-caught reproductive females (yellow circles) (from *12*). Whereas all of these females show robust encoding of the fundamental frequency (F_0) and the second and third harmonics (F_1, F_2) of the male advertisement call, the saccular afferents of nonreproductive females (black circles) (from Fig. 1A) show comparable encoding only for frequencies close to F_0.

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Cognitive Imitation in Rhesus Macaques

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Experiments on imitation typically evaluate a student's ability to copy some feature of an expert's motor behavior. Here, we describe a type of observational learning in which a student copies a cognitive rule rather than a specific motor action. Two rhesus macaques were trained to respond, in a prescribed order, to different sets of photographs that were displayed on a touch-sensitive monitor. Because the position of the photographs varied randomly from trial to trial, sequences could not be learned by motor imitation. Both monkeys learned new sequences more rapidly after observing an expert execute those sequences than when they had to learn new sequences entirely by trial and error.

Can a monkey do what a monkey sees? For more than a century, scientists have tried, with little success, to formulate objective answers to this deceptively simple question. Measures of what a student sees while observing an expert perform a task have been poorly defined, as have the criteria for determining which actions count as imitative and which can be explained by the principles of conditioning. These problems reflect definitions of imitation that have relied exclusively on motor tasks. For example, in 1898, Thorndike defined imitation as "learning to do an act from seeing it done" (*1*). A half-century later, Thorpe proposed a more behavioral definition: "copying a novel or otherwise improbable act" (*2*). Although Thorndike's and Thorpe's definitions of imitation have since been qualified and elaborated (*3*–*5*), neither has been superseded. As a consequence, most research on imitation has focused exclusively on what a subject does at the expense of determining what the subject knows.

Here we describe an example of cognitive imitation, a type of observational learning in which a naïve student copies an expert's use of a rule—for example, learning someone's password at an ATM by looking over the user's shoulder. Because the observer already knows how to enter numbers on the keypad, no motor learning is necessary. The distinction between cognitive and motor imitation is based on the same logic that is used to differentiate cognitive and motor learning in asocial settings (*6*). In the former, the subject must learn to represent external events in their absence—for example, remembering someone's password. In the latter, an external event is available as a cue for the response in question—for example, an expert's motor behavior.

To investigate cognitive imitation, we trained monkeys to execute simultaneous chains, a task in which the subject is required to learn a cognitive rule rather than specific motor actions. The task requires subjects to respond, in a prescribed order, to photographs that are displayed simultaneously on a touch-sensitive monitor (Fig. 1A) (*7*, *8*). Random variation of the positions of the photographs from trial to trial ensures that the subject cannot use a particular motor sequence to execute the task (Fig. 1B) (*9*). Eliminating that possibility was critical; many previously reported instances of imitation in nonhuman primates have been criticized because they may be interpreted as instances of individual learning triggered by the mere presence of a conspecific [social facilitation (*10*, *11*)] or by their interaction with a particular object and/or behavior in a particular location [stimulus/local enhancement (*2*–*4*)] (*12*).

Simultaneous chains are typically learned by trial and error from feedback that follows each response, correct or incorrect. Correct responses are followed by brief (0.5 s) visual and auditory feedback; errors are followed by a variable (5 to 10 s) time-out, during which the screen is dark. Subjects received a food reward only after they responded correctly to all four items on the monitor (A → B → C → D) (*9*). A trial ends either when the subject responds incorrectly to an item or when the subject responds correctly to all of the items on the screen. On a four-item list, the probability of a subject guessing the correct sequence on the first trial and thereby earning a food reward is $1/4! = 0.04$.

In the current study, two monkeys were each provided with the opportunity to learn new lists by cognitive imitation rather than by trial and error. On those lists, one monkey was designated as the "expert," the other as the "student." The expert had previously learned to execute the target list at a high level of proficiency. The student had no prior experience with the target list but was allowed to observe the expert execute that list before testing (*13*). Learning a list in this manner is much more difficult than learning someone's password at an ATM by looking over the user's shoulder, because on an ATM the spatial positions of the number buttons never change.

Our subjects were two male rhesus macaques, Horatio and Oberon. Both subjects had acquired considerable expertise at learning lists by trial and error in previous experiments (*8*). In the present study, subjects learned to execute 70 different four-item lists of arbitrarily selected photographs in two adjacent sound-attenuated chambers. The interior walls of each chamber contained a window made of tempered glass. When an opaque partition was placed between the

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