

Title	Song pattern discrimination by the zebra finch
Sub Title	
Author	前川, 正夫(Maekawa, Masao) 宇野, 広幸(Uno, Hiroyuki)
Publisher	慶應義塾大学大学院社会学研究科
Publication year	1997
Jtitle	慶應義塾大学大学院社会学研究科紀要 : 社会学心理学教育学 (Studies in sociology, psychology and education). No.45 (1997.) ,p.31- 40
JaLC DOI	
Abstract	
Notes	シンポジウム : Pattern recognition in humans and animals
Genre	Departmental Bulletin Paper
URL	https://koara.lib.keio.ac.jp/xoonips/modules/xoonips/detail.php?koara_id=AN0006957X-00000045-0031

慶應義塾大学学術情報リポジトリ(KOARA)に掲載されているコンテンツの著作権は、それぞれの著作者、学会または出版社/発行者に帰属し、その権利は著作権法によって保護されています。引用にあたっては、著作権法を遵守してご利用ください。

The copyrights of content available on the KeiO Associated Repository of Academic resources (KOARA) belong to the respective authors, academic societies, or publishers/issuers, and these rights are protected by the Japanese Copyright Act. When quoting the content, please follow the Japanese copyright act.

SONG PATTERN DISCRIMINATION BY THE ZEBRA FINCH

*Masao Maekawa and Hiroyuki Uno**

Two different techniques, training by GO/NOGO operant conditioning and recording neuronal responses, were used to investigate the mechanisms underlying the song note discrimination of the zebra finch.

We recorded auditory responses to a song note and its modified notes in the lateral portion of the magnocellular nucleus of the anterior neostriatum (IMAN) of normal adult male and female zebra finches and of adult zebra finches reared in auditory isolation during the sensitive period. Neurons that selectively responded to a single harmonic suppression pattern of the song note were found exclusively in the normal male birds, while neurons that responded to multiple harmonic suppression patterns were found in the brains of all three bird groups. These results suggest that emergence of neurons that respond selectively to a single harmonic suppression pattern, is dependent on normal song learning and the emergence of neurons that respond to multiple harmonic suppression patterns is independent of normal song learning.

Adult male zebra finches were successfully trained to discriminate between two sounds which differed in their harmonic suppression patterns. Tests revealed that the birds' response to the sound stimuli was based on the presence or absence of the second harmonic, the harmonic that cued responding during training. We also found that birds who produce many song notes showing harmonic suppression tend to require fewer trials before reaching criterion in training on the GO/NOGO operant conditioning task. These results suggest that birds use the presence or absence of the harmonic as a discriminative cue and that discriminative abilities are strongly related to the song learning.

Key Words: auditory learning, harmonic suppression, operant conditioning, bird

Introduction

Young male zebra finch learn their songs by hearing songs of adult conspecific birds during a sensitive period extending from 20 to 65 days after hatching (Immelmann, 1969; Eales, 1985). Song learning consists of two phases, sensory and sensori-motor learning. Birds hear and memorize adult songs as a song model during sensory learning and then match their own songs to the memorized song model during sensori-motor learning (Immelmann, 1969; Konishi, 1965; Marler, 1970; Slater *et al.*, 1988). Song production is controlled by discrete brain nuclei (See Fig. 1) (Nottebohm *et al.*, 1976; Yu & Margoliash, 1996). The vocal motor command flows from the high vocal center (HVC) to the robust nucleus of the archistriatum (RA). RA, in turn, innervates the tracheosyringeal portion of the hypoglossal nucleus (nXIIIts) which consist of the motor neurons controlling vocal muscles

of the avian vocal organ, the syrinx. Area X, the dorso-lateral nucleus of the medial thalamus (DLM) and the lateral part of the magnocellular nucleus of the anterior neostriatum (IMAN) form an indirect pathway connecting HVC and RA (See Fig. 1) (Okuhata & Saito, 1987; Bottjer *et al.*, 1989). Electric lesions of the bilateral IMAN disrupt normal song learning of the young bird (Bottjer *et al.*, 1984; Scharff & Nottebohm, 1991). IMAN is thought to be involved in the song learning. Field L is an auditory area in the bird's telencephalon and is homologous to the mammalian primary auditory cortex (Karten, 1968). The HVC receives direct and indirect input from Field L (Kelley & Nottebohm, 1979; Fortune and Margoliash 1992).

Neurons in these song control nuclei respond to sound stimulation, especially to the bird's own song (Doupe & Konishi, 1991; Katz & Gurney, 1981; Lewicki & Arthur, 1996; Margoliash & Fortune, 1992; Sutter & Margoli-

* Department of Physiology, Dokkyo University School of Medicine, Mibu, Tochigi 321-02, Japan.

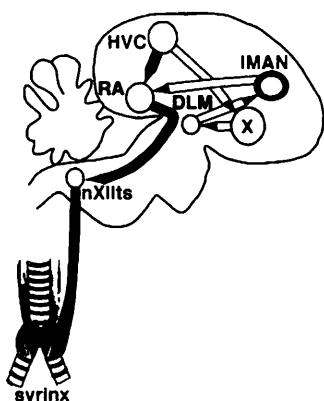


Fig. 1. Schematic drawing of the song control nuclei. Filled arrows indicate the main information flow in the descending motor pathway from the HVC to the syrinx via the RA and nXIIIts. Open arrows indicate the main information flow in the circuit connecting indirectly the HVC and the RA, formed by the area X, DLM and IMAN. Neuronal responses were recorded in the IMAN which is encompassed by a thick line.

ash, 1994; Vicario & Yohay, 1993; Volman, 1996; Williams, 1989). The auditory inputs may reflect the involvement of vocal control nuclei in auditory perception (Brenowitz, 1991). However, neurons in the vocal nuclei of young finches before song learning, do not show selective responses (Doupe, 1997; Volman, 1993). This suggests that the selective responses in the vocal nuclei emerges during song learning.

In the adult IMAN, neurons respond selectively to the birds' own songs and selectivity is much higher in the IMAN than in area X and HVC (Doupe & Konishi, 1991; Maekawa & Uno, 1996). The selective responses of the adult IMAN depend on the specific time sequence of the song notes in the zebra finch song (Doupe, 1997). When the sequence of the song notes was changed artificially, neuronal responses diminished. However, the frequency structure responsible for the selective responses of the IMAN neurons is not yet clear.

A candidate for this frequency structure is the harmonic suppression pattern of the zebra finch song. Zebra finch songs include formant like structures which consist of several harmon-

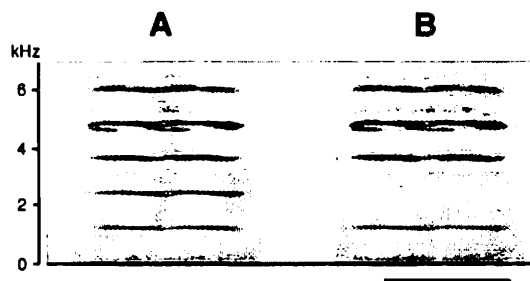


Fig. 2. Sonograms of the GO stimulus sound (A) and NOGO stimulus sound (B) used in the training session. The GO sound included the complete five harmonics, while the second harmonic of the NOGO sound was suppressed by 40 dB. Ordinate: frequency (kHz), abscissa: time. Bar: 50 msec.

ics (Williams *et al.*, 1989). In their song, one or more harmonics are frequently suppressed and the form of the harmonic suppression pattern (HSP) differs among birds. We will use the abbreviation "HSP" for the word "harmonic suppression pattern." Birds are able to discriminate among HSPs (Cynx *et al.*, 1990). Thus, the HSPs might be used for individual discrimination.

We hypothesize that neurons in the IMAN would respond selectively to the HSPs and the response patterns might underlie the discriminative behavior of the birds, and that the selectivity to HSPs emerges during song learning. To test this hypothesis, we conducted two experiments. As a first step, to discover the strategy birds use as cues for discriminating among different sounds, we trained birds to discriminate between two sounds differing in HSP. In the next experiment, neuronal responses to the different HSPs were recorded within the IMAN of the normal male zebra finches and within the IMAN of the auditory isolated and female birds.

Material and methods

Operant conditioning

Six normal adult male zebra finches (*Taeniopygia guttata*) were used in operant conditioning and test trials and also for song-recording. The birds were naive, caged individually and reared on a 16:8 hours light:dark cycle. Ten additional birds were used for operant conditioning and song recording. The body weight of experi-

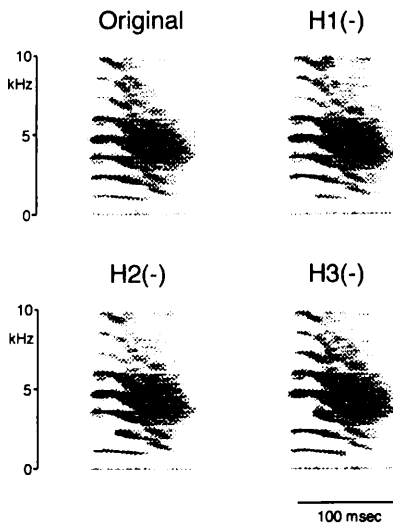


Fig. 3. Sonograms of the sounds used in the recording of neuronal responses. The original note (Original) was one of the notes in the song of a zebra finch, which is similar to the distance call. One of three harmonic (from fundamental to the third harmonic) was suppressed by 40 dB. H1(-): fundamental was suppressed, H2(-): second harmonic was suppressed, H3(-): the third harmonic was suppressed. Bar: 100 msec.

mental birds during the experiment was at about 90% of free-feeding weight.

Sounds used in the training and test session were made by artificially modifying a song note recorded from a bird not used in the experiment. This note was very similar to the distance call of the zebra finch (See Fig. 3). The note consisted of two elements. The first third (CF) consisted of several harmonics with a fundamental frequency of approximately 1.2 kHz and it was 28.5 msec long. The second two-thirds (FM) included several narrow-band frequency downward modulations. This note was used also in the neurophysiological experiment. The sound formed by sequentially combining two CF components resulting in a 57 msec long note were used in the experiment (See Fig. 2). Matching of the frequency axis of the two sounds was checked by viewing their sound spectrogram. Frequency components above 7 kHz were filtered out maintaining five harmonics from fundamental to the fifth harmonic. The note, includ-

ing all five harmonics, was used as the GO stimulus sound (See Fig. 2A). To make different HSPs, one to four harmonics were suppressed by using digital filter. These stimuli were used in the training and test session. The note in which the second harmonic was suppressed (abbreviated as H2(-)) was used as the NOGO stimulus in the training sessions (See Fig. 2B).

The training and test sessions were carried out in a small wire cage placed within a sound attenuated box. The response panel consisted of two sensitive microswitches (observation key and response key) with light emitting diodes (LEDs) on one wall of the wire cage. The bird could trip the microswitch by pecking a LED. Sound stimuli were generated by a digital-analog converter and then fed into a 10 kHz lowpass filter. Filtered sounds were delivered from a loud speaker placed beneath the roof of the box. The peak sound pressure levels were set to 83 dB SPL.

The birds were deprived of food several hours prior to each training and test session. During training sessions, the birds were trained to discriminate between two harmonically different sounds, the GO sound and the NOGO sound. To initiate a trial, the birds were trained to peck the observation key when it was illuminated with green light. The sound stimuli were then delivered twice with a 400 msec interval from the loud speaker. Sounds were delivered in a random order. Immediately after the sound presentation, the red light of the response key was turned on for 2 sec. If the birds pecked the response key within 2 sec after the GO sound they were rewarded with 3 sec access to food. However, if the bird pecked the response key within 2 sec after the NOGO sound the house light turned off for 16 sec. Nothing else happened. Daily training sessions consisted of 100 trials. Training continued until the correct responses for three consecutive sessions exceeded 90 percent, the learning criterion.

After the birds reached this criterion test sessions were carried out in order to determine which cues the birds used for discriminating between the different harmonic structures. The probe stimuli were chosen to examine the effect of the presence or absence of second harmonic and the effect of number of harmonics on the

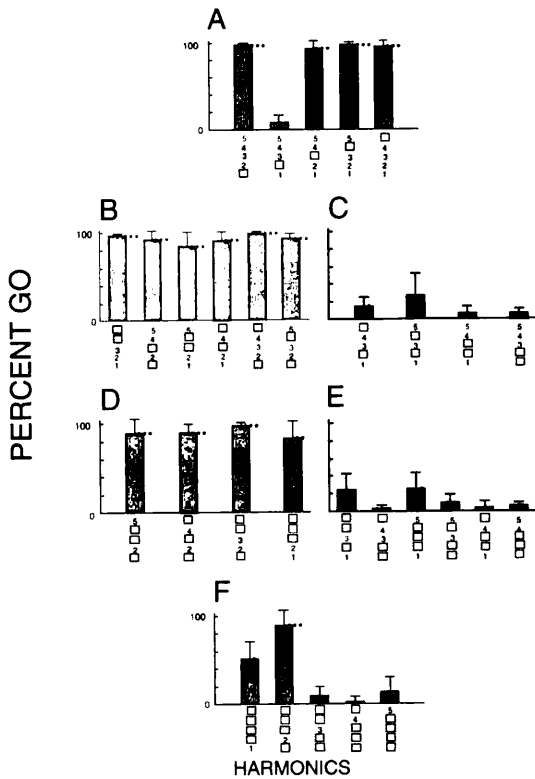


Fig. 4. Mean percentages and standard error of the mean of GO responses to harmonic suppression patterns during the test session. Birds showed GO responses to the sound which included the complete second harmonic, but not to the sound in which the second harmonic was suppressed. Numbers below the each histogram indicate harmonics that were present in the stimulus sound, and open squares indicate harmonics that were absent. A: Only one harmonic was suppressed. B: Two harmonics were suppressed and sounds included the second harmonic. C: Two harmonics including the second harmonic were suppressed. D: Three harmonics were suppressed and sounds included the second harmonic. E: Three harmonics including the second harmonic were suppressed. F: Four of five harmonics were suppressed. ***, $P < 0.0001$, **, $P < 0.001$, *, $P < 0.05$ (VS. responses to the sound lacking second harmonic.)

sound discrimination task. We prepared 31 different sounds including one harmonic to five harmonics (See Fig. 4). Within each group of sounds with the same number of harmonics, each sound differed in the combination of the harmonics. Reinforcement was reduced to a random 80 percent for correct responses. Probabilities that the trial was a probe trial were set between 10 to 17 percent. For each probe stimulus, 24 trials were conducted for each bird. Data obtained from sessions in which the mean correct response in the presence of the GO/NOGO stimuli was less than 90 percent were discarded from the data analysis. Student's t-test was used to determine whether the differences of the percent of go-responses to each probe stimuli were significant.

We recorded songs (directed songs) which male zebra finches sing to their female birds using a digital to analog tape recorder. Two hours recording per a day were done for five days. We observed the power spectrogram of the recorded song to calculate the number of harmonic suppressions. If the sound pressure levels of the corresponding harmonic were 6 dB less intense than those of the adjacent neighbors we regarded that harmonic as suppressed. Recording neuronal responses.

Twenty eight normal adult male zebra finches (*Taeniopygia guttata*), 10 auditory isolated male zebra finches and 26 female zebra finches were used for this experiment. Adult male birds that were used in the experiment of operant conditioning were not used in this experiment. Most of the birds were purchased from an aviary shop.

The birds were administered neuroleptanalgesia (intraperitoneal injection of droperidole, 4 mg/kg and pentazocine, 1 mg/kg) (Evans 1979) and their heads were fixed in a stereotaxic instrument as previously described (Okuhata and Saito 1989). Tungsten electrodes insulated with cashew extract were used to record multi-unit extracellular potentials, with an indifferent electrode placed under the skin of the neck. The auditory responses were recorded in a sound attenuated room. Neuronal activity was amplified and filtered from 100 Hz to 10 kHz and digitized at 50 kHz with 16 bit resolution (Mac ADIOS II board, GW instrument).

The recorded multi-unit spikes were divided into several groups depending on spike peak amplitude using software window discrimination on the Super Scope II software (GW instrument). Peristimulus time histograms (PSTHs) binned in 10 ms intervals, were produced on line from 400 ms recordings of responses to 25 repeated stimuli delivered at 0.1 Hz using Super Scope II software and stored in a Macintosh computer. The mean spontaneous rate was calculated from a 100 ms prestimulus baseline recording and subtracted from each PSTH. If the number of spikes of the PSTH during sound stimulation was more than 10 spikes, neurons were classified as responding to the sound stimulation.

The recording sites were marked with electrolytic lesions (20 μ A anodal current for 8 sec) at the end of the experimental session. The animals were then perfused through their carotid artery with a saline solution followed by 4% paraformaldehyde in phosphate buffer (pH 7.4). The brain was dissected out and serial sagittal (50 μ m) sections were cut and stained using cresyl violet and luxol fast blue.

Sound stimulation was delivered from a loud speaker 1.3 m from the bird's head. Sound pressure levels were monitored using a Blüel Kjær condenser microphone and fixed at 70 dB at the peak value near the eardrum of the bird. Sounds were presented at 0.1 Hz and repeated 25 times.

Sound stimuli included a single note recorded from a zebra finch song (original note) and its modified song notes (See Fig. 3). The original note was similar to the distance call, which is acquired during song learning (Zann, 1985) and commonly used among zebra finches. For the modified notes, the harmonic structure of the CF component was artificially changed. One of three harmonics (from the fundamental to the third harmonic) was suppressed by 40 dB. The original note, three different modified notes, a tone burst and a noise burst were presented through the loud speaker.

Auditory isolation

In order to disrupt normal song learning young birds, purchased from an aviary shop or bred in the laboratory, were reared individually by hand in sound attenuated (by 30 dB at 1 kHz)

boxes prior to song learning, that is from about 20 days after hatching. They could not hear songs of adult male zebra finches.

Results

Behavioral experiment

(1) Strategy for Discrimination

The birds discriminated between the two sounds differing in the HSP reaching the learning criterion after 2200 to 5900 trials. The test sessions revealed that the birds used the presence or absence of the second harmonic as the discriminative cue (See Fig. 4). When only one of harmonics was suppressed, the birds made significantly more ($P < 0.0001$) go-responses to the note that included the normal second harmonic than to the note with second harmonic suppressed (NOGO sound) (See Fig. 4A). When two or three harmonics were suppressed, they also made significantly more (H12: $P < 0.001$; others: $P < 0.0001$) go-responses to the note which included the normal H2 than to the note with H2 suppressed (See Fig. 4B-E). When sounds included only one harmonic, they made significantly more ($P < 0.0001$) go-responses to H2 itself than to other harmonics, although they tended to respond ($P < 0.05$) to the first harmonic, but not go to third, fourth and fifth harmonics (See Fig. 4F). They tended to make few responses to the sound composed of few harmonic including the first harmonic (H134, H 15: $P < 0.05$).

(2) Discrimination and Song Repertoire

We recorded songs of the birds who reached the learning criterion and calculated the number of notes in which any one of harmonic was suppressed (harmonic suppressed note). One bird did not reach the criterion after 10,000 trials. We tried to record songs of this bird, but could not, because this bird might tended to sing less frequently than the other birds. The songs of the other birds were recorded successfully. The mean number of notes that included harmonic structure was 3.5 per bird and the mean number of notes showing harmonic suppression was 1.8 per bird. The birds who showed a larger number of harmonic suppressed notes had a tendency to require fewer trials before reaching the learning criterion than those who had a smaller number of harmonic

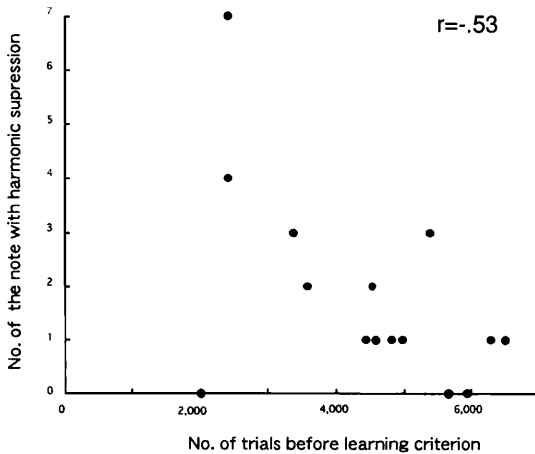


Fig. 5. Correlation of two variables, number of notes including harmonic suppression and the number of trials before the learning criterion was reached. Each dot indicates data from one bird. The correlation was significant ($r = -.53$, $t = 2.24$, $df = 13$, $p < .05$).

suppressed notes (See Fig. 5). The two variables, number of harmonic suppressed notes and number of trials before reaching the learning criterion, correlated significantly ($r = -.53$, $t = 2.24$, $df = 13$, $p < .05$).

Neurophysiological experiment

(1) Normal adult birds

In the IMAN of normal birds, 72 neurons of the 133 encountered along the electrode track were responsive to the auditory stimuli. Response patterns of these neurons were tested using different harmonic suppression patterns (HSPs).

Some neurons (22% of auditory responsive neurons) responded selectively to a single HSP (the single HSP selective neuron) (See Fig. 6A; Table 1). In these neurons, the responses to a single HSP were more than 2.5 times larger than the responses to other HSPs or to the tone burst, or the neurons did not respond to other HSPs or to the tone burst (See Fig. 7A-D). The other neurons (11%) did not respond to the note in

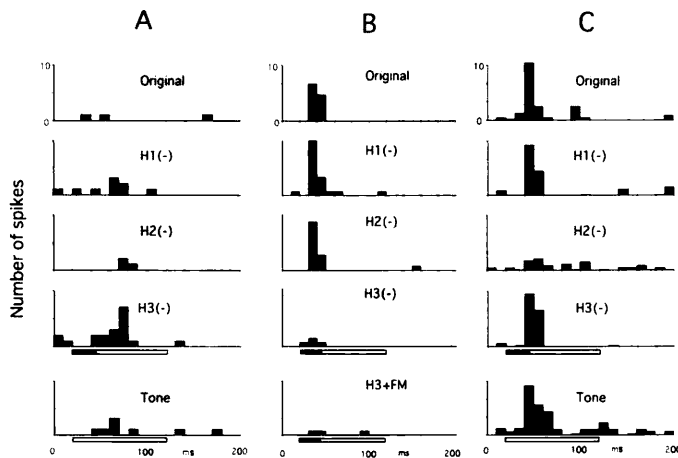


Fig. 6. PSTHs of three different types of IMAN neurons. Responses to the original note, a note with the first (H1(-)), second (H2(-)), or third (H3(-)) harmonic suppressed, and tone burst (Tone) or the third harmonic followed by the FM (H3+FM) are shown from top to bottom in A, B and C. The bars under each histogram indicate the time of stimulus presentation (filled bar=CF, open bar=FM). PSTHs were made from the responses to 25 repetition of the sound stimulation. A Typical examples of responses of a single HSP selective neuron. This neuron responded selectively to the note in which the third harmonic was suppressed, while it did not respond to other patterns nor to a tone burst. B Typical example of responses of a multiple HSP selective neuron. This neuron responded to the note in which the third harmonic was present, but did not respond to the third harmonic. C Typical example of responses from a frequency-dependent neuron. This neuron responded to all harmonic patterns except a note in which the second harmonic was suppressed. The neuron also responded to a tone burst corresponding to the frequency component of the second harmonic.

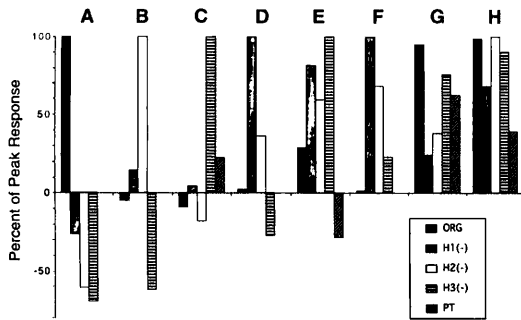


Fig. 7. Relative amplitudes of responses to different HSPs and tone bursts in 8 different neurons in the IMAN. Responses to each stimulus were normalized to the peak response. A-D: Neurons responded preferentially to a single HSP. E-G: Neurons responded to multiple HSPs. G: Neurons responded to the frequency component of the sound. H: Neurons responded to all HSP used in the experiment. In some neurons, discharge rate during some sound stimulation was less than the spontaneous discharge rate (A-E). (ORG=original, PT=tone burst).

which a specific harmonic was suppressed. Otherwise, the neurons responded. However, the neurons did not respond to the corresponding harmonic itself nor to frequency component of the harmonic. Thus, the neurons responded preferentially to the multiple HSPs including specific harmonic (See Fig. 6B). The responses of these neurons to the HSP were 2.5 times larger than the responses to other HSP or to the tone burst, or neurons did not respond to other HSP (See Fig. 7E-F).

Among the single HSP selective neurons, most neurons selectively respond to the note in which fundamental or third harmonic was suppressed (36% for fundamental and 43% for third harmonic), and fewer neurons responded to the original note in which all harmonic were present or to the note in which second harmonic was suppressed (3% for original and 18% for second harmonic) (See Table 2). Eighty eight percent of the multiple HSP sensitive neurons responded to the note in which second harmonic was present.

A few neurons (3%) of auditory responsive

Table 1. Percentages of two different response types among the auditory responsive neurons in the IMAN of normal and isolated adult male zebra finch and the normal adult female zebra finch. Single=single HSP selective neuron, Multi=multiple HSP selective neuron. The single HSP selective neurons were found exclusively in the normal male zebra finch, while the multiple HSP selective neurons were found in the three different animal types.

	Male	Isolate	Female
Single	22%	0%	0%
Multi	11%	17%	4%

auditory neurons n=72 n=53 n=54

Table 2. Classification of the single HSP selective neurons in percentages. The neuronal responses depended on the HSP used. ORG=original note, H1(-)=note with the fundamental being suppressed, H2(-)=note with the second harmonic being suppressed, H3(-)=note with the third harmonic being suppressed. Most neurons responded selectively to the note in which the fundamental or third harmonic was suppressed, and fewer neurons responded to the original note in which all harmonic were present or to the note in which second harmonic was suppressed.

ORG	3
H1(-)	36
H2(-)	18
H3(-)	43

neurons in the IMAN, responded to the frequency component of the stimulus sound (See Fig. 6C, Fig. 7G). They responded to the tone bursts. When the harmonic which included the corresponding frequency was suppressed, they did not respond to HSP. Otherwise, they responded to the HSPs as well as to the tone burst. The other neurons (19%) responded to all the harmonic patterns (See Fig. 7H). The remaining auditory responsive neurons (45%) did not fall

into any of the above mentioned groups, since their response patterns were not consistent during the experiment.

(2) Auditory isolated birds

In the IMAN of the auditory isolated birds, 53 neurons of 107 neurons encountered during experiment were auditory responsive. The response patterns to the different HSPs were recorded in these auditory responsive neurons.

Some (17%) of the auditory responsive neurons responded preferentially to the multiple HSPs (See Table 1). This percentage is similar to that found in the normal birds. However, we could not find the single HSP selective neurons in the isolated birds. As in the normal birds, most (89%) of the multiple HSP neurons responded to the note in which the second harmonic was present.

A few neurons (6%) of the auditory responsive neurons responded to the frequency component of the stimulus sound (not shown). The other neurons (39%) responded to all the harmonic patterns and tone burst (not shown). This neuron type occurred frequently in isolated birds than in normal birds. The remaining auditory responsive neurons (38%) were not classified into any of the above mentioned groups because their response pattern was not consistent during the experiment.

(3) Normal female birds

In the IMAN of the adult female zebra finch, 54 neurons of 98 neurons encountered during the experiment were auditory responsive. The response patterns to the different HSPs were recorded in auditory responsive neurons. We could not find neurons which responded selectively to the single HSP. However, 4 percent of the auditory responsive neurons responded selectively to multiple HSPs (See Table 1). Other neurons could not be classified.

Discussion

We found neurons which selectively responded to a single harmonic suppression pattern (HSP) in the IMAN, one of the vocal control brain nuclei, of the normal adult male zebra finch. However, we could not find these single HSP selective neurons in the IMAN of the birds reared in auditory isolation from 20 days after hatching and in the IMAN of the normal adult

female zebra finch. The isolated birds could not hear and memorize normal zebra finch song, and therefore could not develop normal songs (Price, 1979). The female birds did not vocalize songs, although they heard normal adult song during their youth. Therefore, it appears that the single HSP selective neurons emerge during normal song learning.

The auditory isolated birds could not hear adult song during the sensory phase of their sensitive period. However, these birds are able to develop their own songs by matching to the innate song model during the period of sensori-motor learning (Immelmann, 1967; Price, 1979). On the other hand, because female birds do not sing, although they heard normal songs while young, the sensori-motor learning that normal and isolated male birds undergo is absent from their experience. In the present report, neurons that responded to the multiple harmonic suppression pattern in the IMAN were found in the normal and auditory isolated bird brain, while in the female birds the number of such neurons was smaller than the number in the isolated males. These data suggest that the multiple harmonic suppression pattern's sensitive neurons might be related to sensori-motor learning.

Using conventional GO/NOGO operant conditioning, normal adult male zebra finches were trained to discriminate between two different sounds, a sound that included all five harmonics and a sound with the second harmonic suppressed. The zebra finches used the presence or absence of the second harmonic as a discriminative cue independent of the number of harmonics in the sound. The single HSP selective neurons found in the neurophysiological experiment responded to the absence of a particular harmonic, and the multiple HSP selective neurons responded to the presence of the particular harmonic. The neuronal substrate for the discrimination task used in the experiment might include the single and multiple HSP selective neurons in the IMAN.

When the number of harmonics was small, some birds tended to show GO response to the sound including the fundamental frequency, even though the second harmonic of the sound was suppressed. The birds trained to make NOGO responses to the sound with the second

harmonic suppressed have a tendency to show GO response to the sound when the lower frequency is suppressed.

We showed that birds who vocalize song notes including harmonic suppression with greater frequency tend to require fewer trials before reaching the learning criterion in GO/NOGO operant conditioning training. Williams et al. (1989) showed that harmonic suppression pattern of the song note was acquired during song learning. We suggest that the abilities to discriminate among harmonic patterns is highly related to song learning.

REFERENCES

- Bottjer, S. W., Miesner, E. A., & Arnold, A. P. (1984) Forebrain lesions disrupt development but not maintenance of song in passerine birds. *Science*, *224*, 901-902.
- Bottjer, S. W., Halsema, K. A., Brown, S. A., & Miesner, E. A. (1989) Axonal connections of a forebrain nucleus involved with vocal learning in zebra finches. *Journal of Comparative Neurology*, *279*, 312-326.
- Brenowitz, E. A. (1991) Altered perception of species-specific song by female birds after lesions of a forebrain nucleus. *Science*, *251*, 303-305.
- Cynx, J., Williams, H., & Nottebohm F. (1990) Timbre discrimination in zebra finch (*Taeniopygia guttata*) song syllables. *Journal of Comparative Psychology*, *104*, 303-308.
- Doupe, A. J. (1997) Song- and order-selective neurons in the songbird anterior forebrain and their emergence during vocal development. *Journal of Neuroscience*, *17*, 1147-1167.
- Doupe, A. J., & Konishi, M. (1991) Song-selective auditory circuits in the vocal control system of the zebra finch. *Proceedings of National Academy of Science of U.S.A.*, *88*, 11339-11343.
- Eales, L. A. (1985) Song learning in zebra finches: some effects of song model availability on what is learnt and when. *Animal Behavior*, *33*, 1293-1300.
- Evans, E. F. (1979) Neuroleptanesthesia for the guinea pig; an ideal anesthetic procedure for long-term physiological studies of the cochlea. *Archives of Otolaryngology*, *105*, 185-186.
- Fortune, E. S., & Margoliash, D. (1992) Cytoarchitectonic organization and morphology of cells of the field L complex in male zebra finches (*Taeniopygia guttata*). *Journal of Comparative Neurology*, *325*, 388-404.
- Immelmann, K. (1969) Song development in the zebra finch and other estrildid finches. Hinde, R. A. (ed.) *Bird vocalizations*. Cambridge University Press, Cambridge 64-74.
- Karten, H. J. (1968) The ascending auditory pathway in the pigeon (*Columba livia*). II. telencephalic projections of the nucleus ovoidalis thalami. *Brain Research*, *11*, 134-153.
- Katz, L. C. and Gurney, M. E. (1981) Auditory responses in the zebra finch's motor system for song. *Brain Research*, *211*, 192-197.
- Kelley, D. B. and Nottebohm, F. (1979) Projections of a telencephalic auditory nucleus—Field L—in the canary. *Journal of Comparative Neurology*, *183*, 455-470.
- Konishi, M. (1965) The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Zeitschrift für Tierpsychologie*, *22*, 770-783.
- Lewicki M. S. and Arthur, B. J. (1996) Hierarchical organization of auditory temporal context sensitivity. *Journal of Neuroscience*, *16*, 6987-6998.
- Maekawa, M., & Uno, H. (1996) Difference in selectivity to song note properties between the vocal nuclei of the zebra finch. *Neuroscience Letters*, *218*, 123-126.
- Margoliash, D., & Fortune, E. S. (1992) Temporal and harmonic combination-sensitive neurons in the zebra finch's HVC. *Journal of Neuroscience*, *12*, 4309-4326.
- Price, P. H. (1979) Developmental determinants of structure in zebra finch song. *Journal of Comparative and Physiological Psychology*, *93*, 260-277.
- Marler, P. (1970) A comparative approach to vocal learning: song development in white-crowned sparrows. *Journal of Comparative Physiology and Psychology*, *71*, 1-25.
- Nottebohm, F., Stokes, T. M., & Leonard, C. M. (1976) Central control of song in the canary, *Serinus canaria*. *Journal of Comparative Neurology*, *165*, 457-486.
- Okuhata, S., & Saito, N. (1987) Synaptic connections of thalamocerebral vocal nuclei of the canary. *Brain Research Bulletin*, *18*, 35-44.
- Scharff, C., & Nottebohm, F. (1991) A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: implications for vocal learning. *Journal of Neuroscience*, *11*, 2896-2913.
- Slater, P. J. B., Eales, L. A., & Clayton, N. S. (1988) Song learning in zebra finches (*Taeniopygia guttata*): progress and prospects. *Advances in the Study of Behaviour*, *18*, 1-34.
- Sutter, M. L., & Margoliash, D. (1994) Global synchronous response to autogenous song in zebra finch HVC. *Journal of Neurophysiology*, *72*, 2105-2123.
- Vicario, D. S., & Yohay, K. H. (1993) Song-selective

- auditory input to a forebrain vocal control nucleus in the zebra finch. *Journal of Neurobiology*, 24, 488-505.
- Volman, S. F. (1993) Development of neural selectivity for birdsong during vocal learning. *Journal of Neuroscience*, 13, 4737-4747.
- Volman, S. F. (1996) Quantitative assessment of song-selectivity in the zebra finch high vocal center. *Journal of Comparative Physiology [A]*, 178, 849-862.
- Williams, H. (1989) Multiple representations and auditory-motor interactions in the avian song system. *Annals of New York Academy of Science*, 563, 148-164.
- Williams, H., Cynx, J., & Nottebohm, F. (1989) Timbre control in zebra finch (*Taeniopygia guttata*) song syllables. *Journal of Comparative Psychology*, 103, 366-380.
- Yu, A. C., & Margoliash, D. (1996) Temporal hierarchical control of singing in birds. *Science*, 273, 1871-1875.
- Zann, R. (1985) Ontogeny of the zebra finch distance call: 1. Effects of cross-fostering to bengalese finches. *Zeitschrift für Tierpsychologie*, 68, 1-23.