Long and Short-term Memory use for Frequency Discrimination in the Barn Owl

by

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Abstract

Two barn owls (*Tyto alba*) were trained in a two-tone frequency discrimination task that allowed for short-term and long-term memory imprinting to the constant cue frequency. The owls performed very similarly to owls of an analogous experiment (Quine and Konishi, 1974) that presented only a single tone and thus allowed only for long-term memory frequency discrimination, implying the equal or greater accuracy of long-term memory than short-term memory for use in frequency discrimination. One owl was then trained in a two-tone delayed matching-to-sample frequency discrimination task that selected only for short-term memory imprinting of an arbitrary cue frequency. The owl demonstrated poorer frequency discrimination skills when compared to results from the first paradigm and to those of Quine and Konishi's (1974) experiment, indicating the decreased acuity of short-term memory frequency selectivity over that of long-term memory. A possible explanation for the difference in acuity may be that prolonged exposure to a constant cue frequency induces a selective increase in acuity and sharpening of the auditory system's tuning curve to that frequency. In contrast, exposure to many cue frequencies of equal relevance did not provide an opportunity for frequency-specific modification in the auditory systems.

Introduction

The interactions between an animal and its environment are regulated by the central nervous system. External stimuli are sensed by peripheral input organs (i.e. ears, eyes, skin, etc.), then transmitted to the brain, which processes this information and ultimately causes a behavioral response. The integration of sounds into the vertebrate ear, and subsequent analysis of their acoustic properties by the auditory system is very complex, involving millions of neurons and many specialized brain regions. Scientific investigators have begun to unmask the highly organized auditory system, and are discovering how the brain first separates sound into its simplest properties for evaluation. We still do not fully understand, however, how the brain interprets a sound or how hearing a sound under different conditions affects the brain's perception of that sound.

To help learn how an organism perceives its acoustical environment, one can study its brain's deliberate responses to specific environmental conditions. The study of an animal's responses in a controlled acoustic environment gives insight into how different sounds affect the brain. Furthermore, if the animal's behavioral intent for a specific sound is understood, one can learn how accurately it detects that sound and how precisely it can distinguish that sound from another sound that represents a different behavioral response. This sort of analysis can be conducted on a trained animal. One can compare the animal's intention (the brain's trained response for a stimulus) to that of its actual behavior. The brain is accurately interpreting a sound when the sound's meaning and the animal's behavior correctly correlate. Conversely, the animal's behavior deviates from the trained procedure if the brain incorrectly interprets a

sound. This concept is the basis for my research. My study involves the training of two barn owls (*Tyto alba*) in two frequency discrimination tasks: one that allows for the short-term and long-term memory storage of a frequency of sound, and another that allows only for the short-term storage of a frequency of sound. This difference in available mental resources enabled me to compare the owls' performances in the two tasks and postulate the relative importance of short-term and long-term memory for frequency discrimination.

Barn owls are ideal subjects for an ethological study of auditory perception because they depend heavily on sounds in their nocturnal hunting behavior. These highly specialized birds can detect, locate, track, and capture a rodent solely by sounds the unsuspecting prey makes. The fact that excellent listening skills are essential to the barn owl's survival has inspired the thorough investigation of their auditory system. Today, the barn owl is a well established animal model of hearing. Similar auditory pathways and brain structures exist in all vertebrates, thus our increased understanding of the owl's hearing further educates us about the ways in which humans and many other animals interact with their acoustic environment.

The barn owl's acoustical recognition of prey is based on the owl's ability to detect, remember, and distinguish prey noises from other sounds. My neuroethological experiment mimics and simplifies this natural behavior, then tests the owl's ability to detect a "prey" frequency, and distinguish it from other frequencies of sound. In the first behavioral paradigm, both owls were trained to associate a food reward ("prey") with a 6,000 Hertz frequency tone. Upon hearing a 6,000-Hz "cue" tone, followed by a "probe" tone of the same frequency, the owls were trained

to fly to a feeder next to the speaker and receive a food reward (Figure 1). A probe tone of any other frequency was not associated with food and, if correctly detected, did not elicit any response from the owls. The owls had two related, but slightly different cognitive processes available to help them determine if the probe tone equalled 6,000 Hz. Using their short-term memories, each owl could compare the probe tone's frequency to that of the cue tone heard a moment earlier. Additionally, it could compare the probe frequency to the 6,000 Hz that, through continued exposure in every trial, had been stored in its long-term memory. In both processes, the owls are determining if the probe tone frequency matches the 6,000 Hz that is imprinted on their memory's mental template.

A similar experiment to the one described above was conducted by Quine and Konishi in 1974. The greatest difference between the two paradigms is that Quine and Konishi did not remind their owls of the food frequency, as I always did with the cue tone, but instead, presented only a single probe tone in every trial. The comparison of the owls' performances in these two paradigms gave me insight into the importance of a reminder stimulus in the detection of a memorized frequency. I hypothesized that my owls would demonstrate better frequency discrimination skills than Quine and Konishi's owls, suggesting that the activation of short-term memory by a reminder stimulus would beneficially supplement long-term memory frequency discrimination skills.

In the second paradigm, I trained one of the owls, Masa, to generalize the discrimination task to any arbitrary cue tone between 4,000 Hz and 9,000 Hz. If the first and second tones were of the same frequency, Masa was trained to fly to the feeder for a reward. A pair of

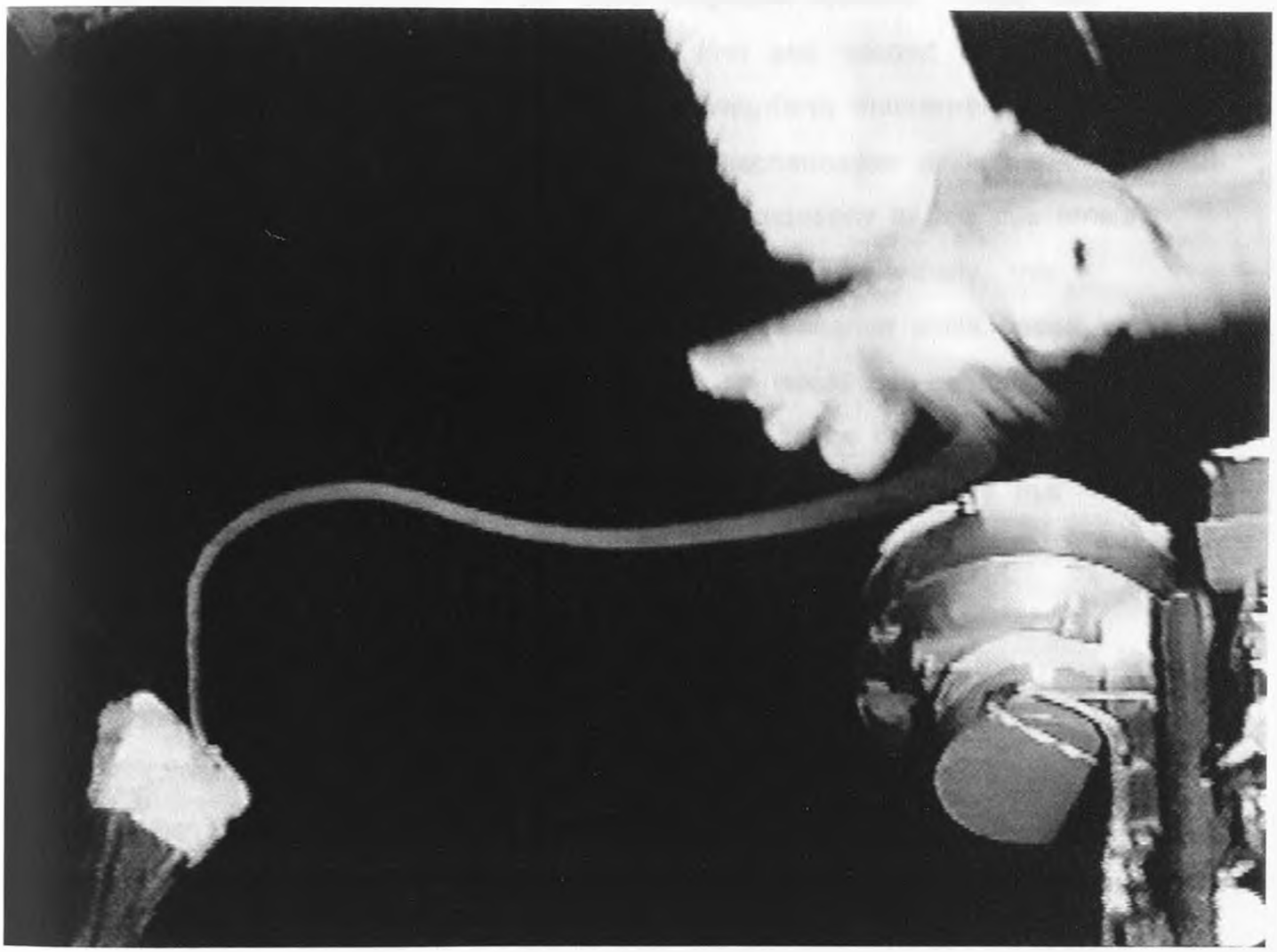


Figure 1. Owl pouncing on feeder plate.

mismatched tones represented no food, and Masa behaviorally acknowledged this by staying on his perch. This is known as a delayed matching-to-sample task, in which the subject must attend to a novel stimulus and detect the same stimulus when presented a moment later. In contrast to the first paradigm, this task did not give an opportunity to store any single frequency in the owl's long-term memory. Thus, the owl's ability to discriminate between the first and second tone frequencies could not be reinforced by a long-term memorable impression of the "prey" frequency. Instead, Masa's discrimination skills depended solely on his comparison of the probe tone's frequency to the cue tone's frequency stored in his short-term memory. Consequentially, this paradigm enabled me to measure Masa's discrimination skills based solely on short-term memory. I hypothesized that he would not be able to detect as small a frequency difference between tones as he did in the first paradigm, or as did Quine and Konishi's owls - a circumstance that suggests the dominating importance of long-term memory over short-term memory for frequency discrimination.

The comparison of my owls' performances in the first paradigm to that of Quine and Konishi's owls revealed that an owl's frequency discrimination ability does not improve when hearing a recently presented reminder tone. This proved my first hypothesis incorrect. The comparison of the first paradigm and Quine and Konishi's results to that of Masa's performance in the delayed matching-to-sample paradigm demonstrated the decreased acuity of short-term memory frequency discrimination over that of long-term memory discrimination. This finding supports my second hypothesis that long-term memory is more precise for frequency discrimination than short-term memory.

Materials and Methods

Preparation. Data were collected from two captive bred adult barn owls (*Tyto alba*) bred from the University of Oregon owl colony. The two owls, Beaker (female) and Masa (male), were 4 yrs, 710 g and 6 yrs, 432 g, respectively at the start of training. Each was tested individually in a room 4.9 m long by 3.2 m wide by 2.7 m high, lined with sound-dampening foam. A perch and remotely controlled food-dispenser connected to a 3.8 cm diameter Alpine speaker were placed in the approximate center of the room (Figure 2). The food dispenser was a plastic rotating circular carousel (16.5 cm diameter) with 20 food depressions evenly spaced around the edge of the top of the disc. A hole in the lid restricted access to only one depository at a time. A wooden block was glued on top of the lid to serve as a perch. The rest was covered in leather to provide grip for the owls' feet. A leash was fed through an eyelet screwed into the side of the home perch facing the feeder, and then through grommet holes securing leather cuffs to each of the owls' legs. A knot at the end of the leash restricted the owl's reachable landing platforms to the home and food perch. An infrared video camera (Canon IR-20W) was mounted in line with the perches on the wall behind the speaker. Cables from the video camera, the food dispenser, and speaker were led under floor tiles to an adjacent room. The camera image was observed and recorded with a black and white 22 cm diameter video monitor and sVHS Hi-Fi MTS broadcast stereo VCR. The dispenser was rotated bi-directionally with a manual switch. The sound type and timing was dictated by software (Microsoft QuickBasic v. 4.5) on a 80 386-chip based microcomputer connected to a tone generator (Hewlett Packard 3245A Universal Source).

Pre-training. Owls were individually brought to the experimental

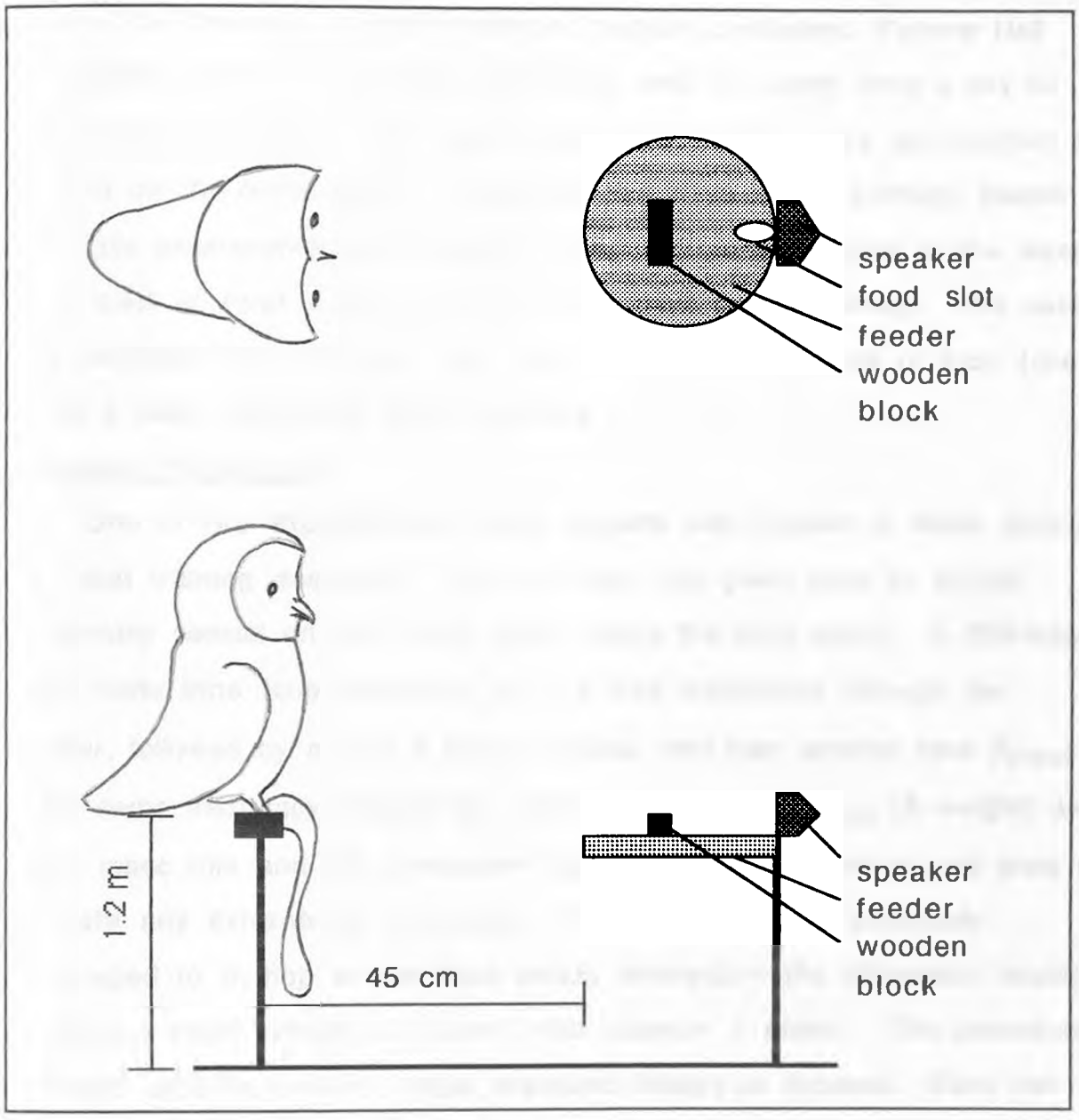


Figure 2. View of experimental set-up. The owl is sitting at the home perch facing the food perch, which consists of a wooden block, circular feeder and loudspeaker. *Top.* Overhead view. *Bottom.* Side view.

room in the company of their imprinted human caretakers, Yvonne Hall with Beaker and Dr. C. H. Keller with Masa, and me nearly once a day for 15 days before the start of the training sessions. They were acclimatized to standing on the home perch. Beginning five days before training, Beaker and Masa permanently wore leather cuffs, and were attached to the leash for at least an hour a day in the last four days before training. The owls were isolated from all other owls and given smaller rations of food (one mouse a day) three days before training.

Behavioral Paradigm A

One or two experimenters were present with Beaker or Masa during the initial training sessions. The owl was first given time to appear comfortably seated on the home perch facing the food perch. A 250-msec 6,000 Hertz tone (cue frequency or f_{cue}) was introduced through the speaker, followed by a 2 to 4 second pause, and then another tone (f_{probe}) at the same frequency (Figure 3). Both tones were 60 dB_{spl} (A weight) and had 5 msec rise and fall attenuation ramps at their beginnings and ends to eliminate any extraneous harmonics. The owl was then physically encouraged to fly/hop to the food perch, whereupon the dispenser rotated revealing a small reward of mouse meat (approx. 1 gram). This procedure continued until the owl no longer appeared hungry or focused. Each owl participated in a training session each day for at minimum 5 days a week.

Once the owl appeared to understand the testing concept (hear two tones > fly to food perch > reward), integer frequency tones between 4 - 9 kHz were occasionally played in place of the second tone (Figure 3). In this case, the owl was not encouraged to move, nor offered any food. If the owl did fly to the feeder after a set of mismatched tones (f_{cue} = 6,000 Hz $\neq f_{probe}$), the lights in the experimental room were turned off for thirty

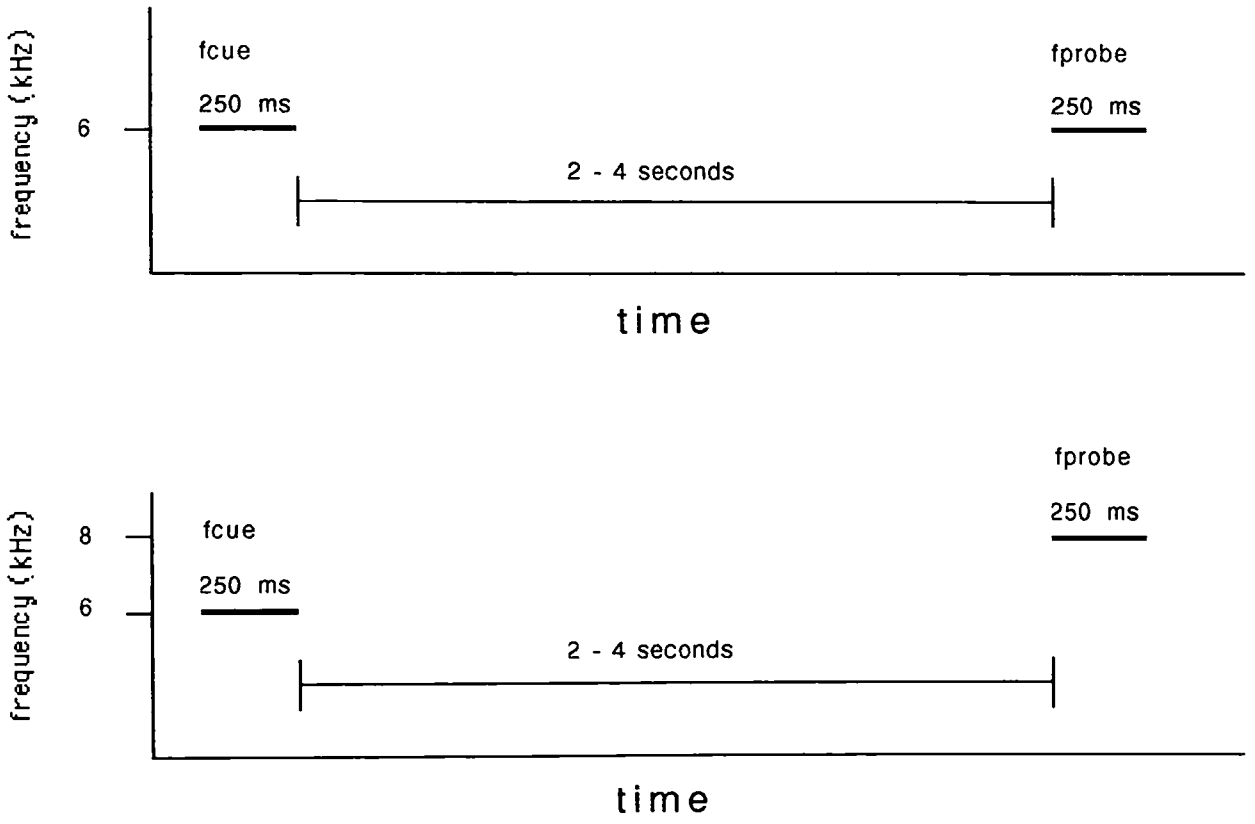


Figure 3. Pictoral representation of sound stimulus in single trials. *Top.* A matched trial in which the owl was rewarded for flying. *Bottom.* An unmatched trial in which the owl was trained to stay.

seconds. This restricted the owl from seeing and flying to the home perch, thus serving as negative reinforcement that delayed the next opportunity the owl could potentially obtain food. When the owl correctly stayed at the perch after mismatched tones, the next trial was initiated after approximately fifteen seconds. Otherwise, the next trial began after the owl had returned home and appeared focused on the speaker. This procedure was repeated for 17 sessions (Masa) and 23 sessions (Beaker) until the owls correctly responded to at least 85% of the matched (fly) and unmatched (stay) trials with probe frequencies differing from the cue frequency by at least 2,000 Hz.

Testing. Probe frequencies more similar to the cue frequency were then played - first within 750 Hz and 500 Hz of 6,000 Hz. As each owl grew accustomed to discriminating between such frequencies, new f_{probe} tones of $\Delta f = \pm 250$ Hz and $\Delta f = \pm 125$ Hz were introduced.

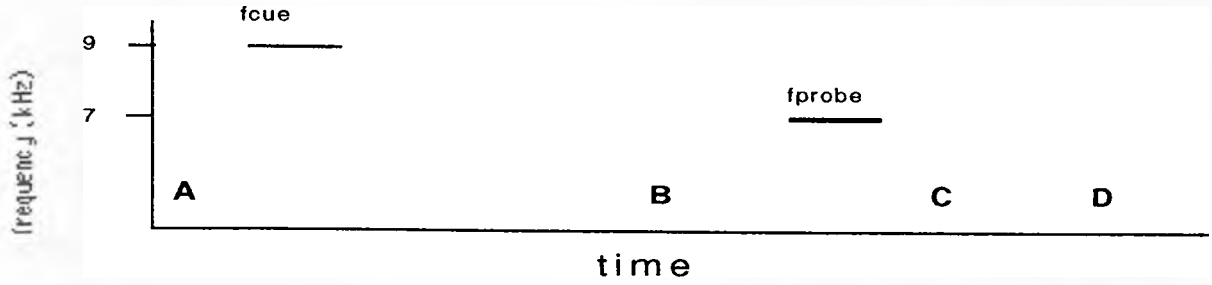
To ensure that each owl was performing optimally, thus reflecting an accurate discrimination ability, data for each new Δf were recorded only after the owl had been exposed to ten trials containing the new f_{probe}. This seemed to allow the owl to attain and sustain its peak Δf detection capability. Furthermore, in each session, the owls had to respond correctly to ten sequential trials, including at least three mismatched tones, to illustrate its willingness to cooperate with the experimental paradigm. Data from the successful completion of these test trials and all following trails in that day's session were used for calculation. Occasionally the owl flew to the feeder before the probe tone had yet been played. Such premature responses did not reflect discrimination ability and were not used to evaluate data. An owl's stayed response to two sequential trail having $f_{probe} = 6{,}000$ Hz indicated its unwillingness to

cooperate with the paradigm. No data was thus used from those trials or any following trials in that session for evaluation.

Behavioral Paradigm B

Masa was then trained to generalize the task to any arbitrary f_{cue} in a delayed matching-to-sample attention task. The experimental set-up was the same as in paradigm A with a few changes; the first and second frequency tones were each 500 msec with an inter-tone delay randomly between 0.5 second and 1.5 seconds long. Initially, only integer cue and probe frequencies between and including 4 kHz and 9 kHz were played. Masa was encouraged to fly to the feeder upon hearing two matched cue and probe frequencies in a single trial. Conversely, he was persuaded to return to the home perch when he flew after mismatched tones. Training proceeded until Masa responded correctly to at least 80% of the matched and mismatched trials with frequency differences equal to or greater than 2,000 Hz (25 days), after which he was left to perform by himself.

I noticed during training that Masa consistently turned his head to the side if he detected that the cue and probe tones did not match, and used this behavior as an operational definition of Masa's decision not to fly. The next trial thus began after he "signalled" that the previous trial was mismatched (figure 4). The utilization of this natural behavior allowed me to play more mismatched trials in a row without overcoming Masa's patience threshold, after which he would invariably fly. If Masa did not signal with a head-turn, the next trial was then initiated after fifteen seconds. I also shortened the thirty second lights-out punishment to a brief flash of darkness immediately after Masa incorrectly took flight on a mismatched trial. Although this procedure induced less punishment, it was sufficient because Masa appeared to already associate the darkness



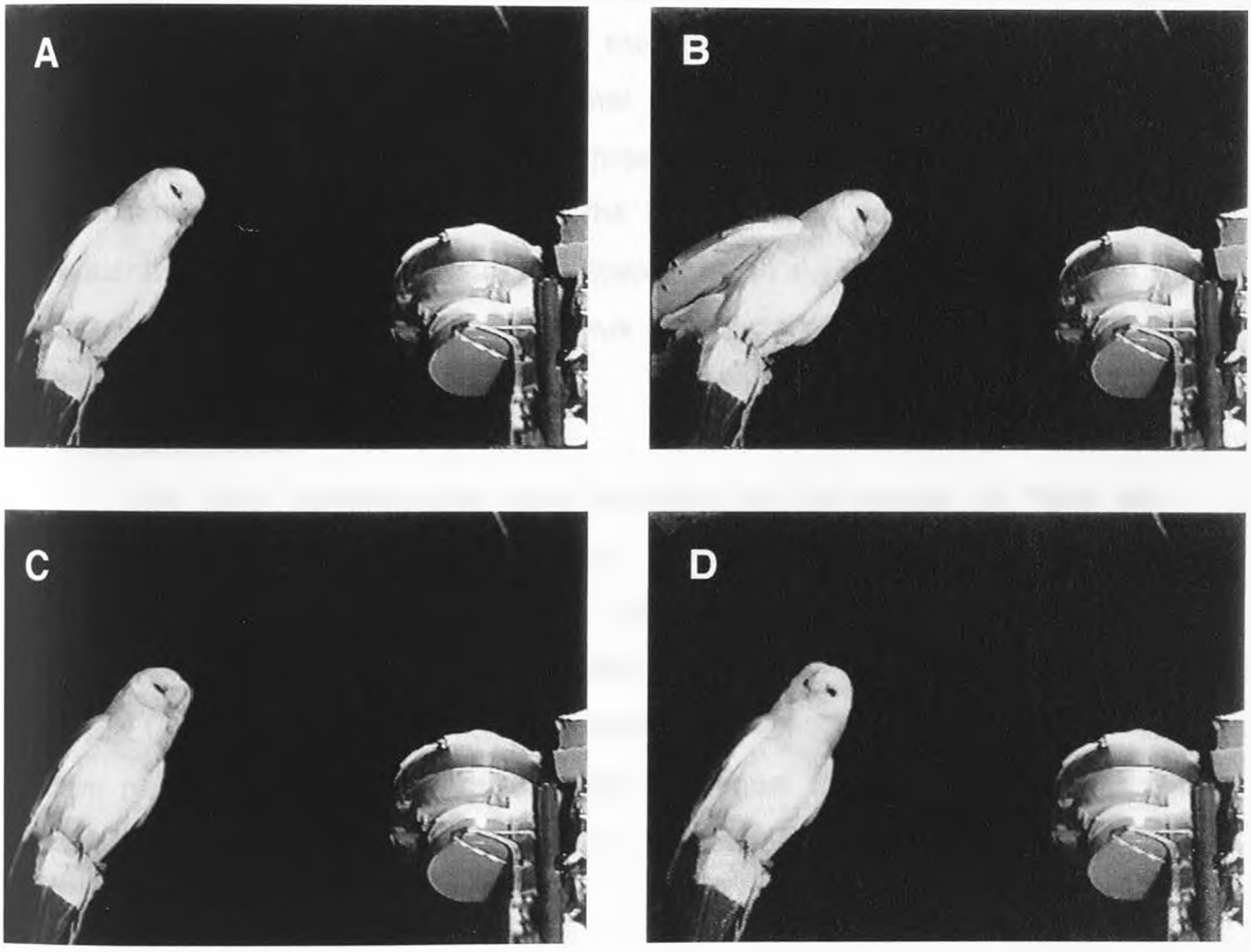


Figure 4: Masa exhibiting head-turn signal after a mismatched trial in paradigm B. Letters correspond to time positions indicated in sonogram.

with an incorrect behavioral response.

Testing. Smaller frequency differences were now introduced - first $\Delta f = \pm 1000$ Hz, then ± 500 Hz, ± 250 Hz, and finally ± 125 Hz for those testing frequencies Masa could most accurately discriminate.

To ensure adequate cooperation in each session, data was once again collected only after Masa correctly stayed on three sequential mismatched trials. In contrast to paradigm A, though, these initial qualification trials did not need to span at least ten total trials, but only as many trial as necessary to correctly stay on the three mismatched trials. Once again, premature flights were not used in the evaluation of data. Staying on two sequential matched trials again indicated Masa's unwillingness to cooperate with the paradigm, and thus data was not collected for evaluation on or after these trials.

Analysis of data

The owls' performances were recorded as the number of flights per total trials for each tested frequency. These ratios were then converted into percent correct performances. The ratios representing each tested frequency were also compared to their corresponding reference frequency ($f_{cue} = f_{probe}$) performance ratios by means of Chi-squared analysis. Data from paradigm B was also divided into two equal (19 day) sections of sequential testing sessions in order to observe a learning trend.

Results

Paradigm A

Beaker and Masa were considered trained to the paradigm once they responded correctly to at least 85% of the matched and unmatched trails with $\Delta f \geq 2{,}000$ Hz, after which testing began. At this point it was apparent that an owl's decision to stay at the home perch was due solely to the fact that it detected a frequency other than 6,000 Hz (figure 5). Figure 6 plots the percent correct responses as a function of the probe frequency. At 6,000 Hz, when cue and probe frequencies were matched, both birds performed nearly perfectly, flying to the feeder in 95% to 98% of the trials. Similarly, when the cue and probe frequencies were widely different ($\Delta f \geq 500$ Hz), the birds also performed nearly perfectly, staying at the home perch at least 87% of the time. At smaller frequency differences, the bird's percent correct performances declined. Both owl's percent correct responses dropped more rapidly at Δf = -250 Hz and -125 Hz, than at corresponding positive frequency difference values.

Data for each owl were analyzed statistically using Chi square and found to not be different from each other at six of the eight testing frequencies (table 1). In comparison to their performances at f_{probe} = 6,000 Hz, Chi square analysis determined significant discrimination behaviors for both birds at all probe frequencies (table 2).

Paradigm B

Masa was successfully trained to generalize paradigm A to any arbitrary cue frequency (minimum 80% correct responses at matched and unmatched [$\Delta f \geq 2{,}000$ Hz] trials at start of testing). Thus, he learned to fly to the feeder when the cue tone of any frequency matched the frequency of the probe tone. The results in figure 7 plot his percent

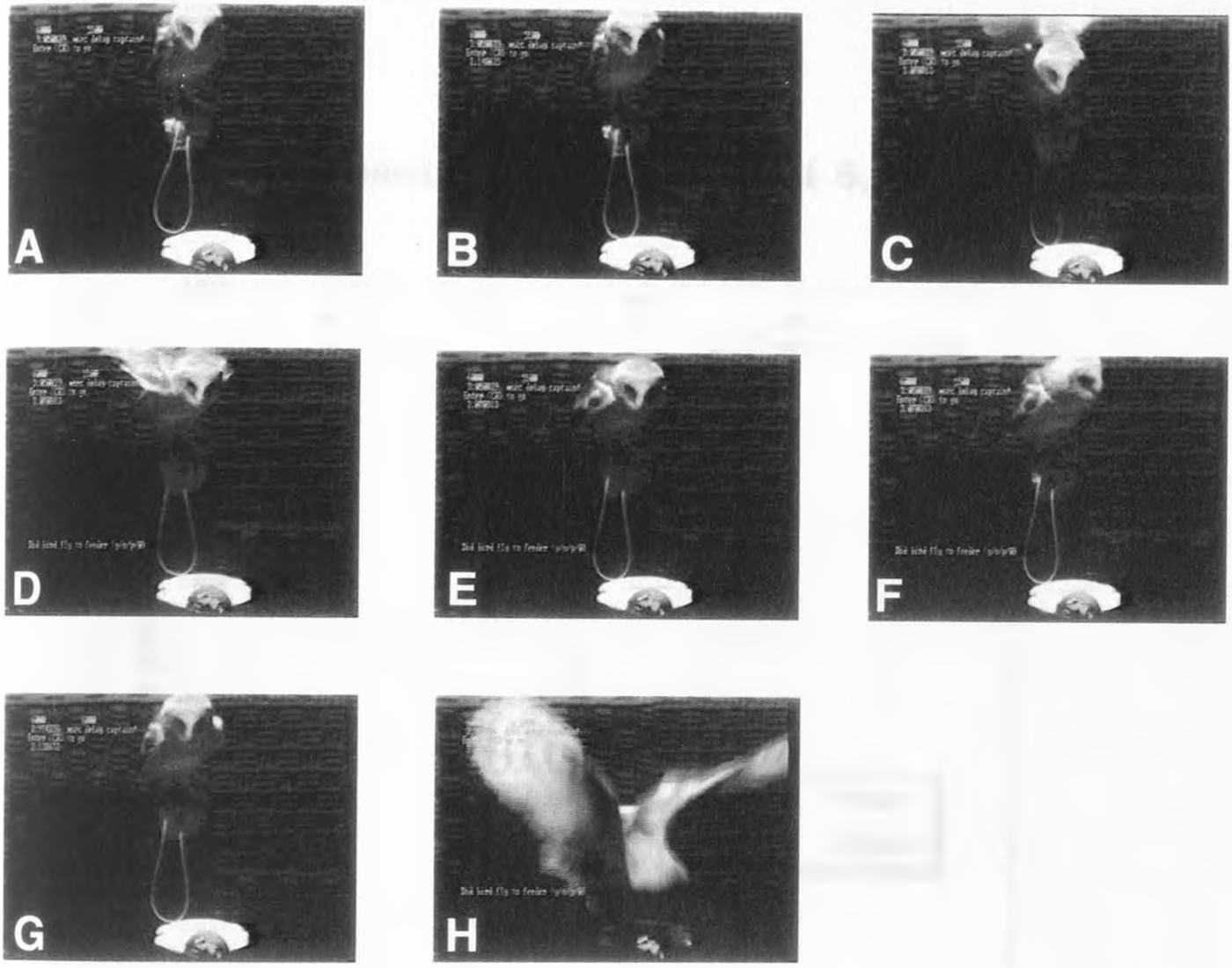
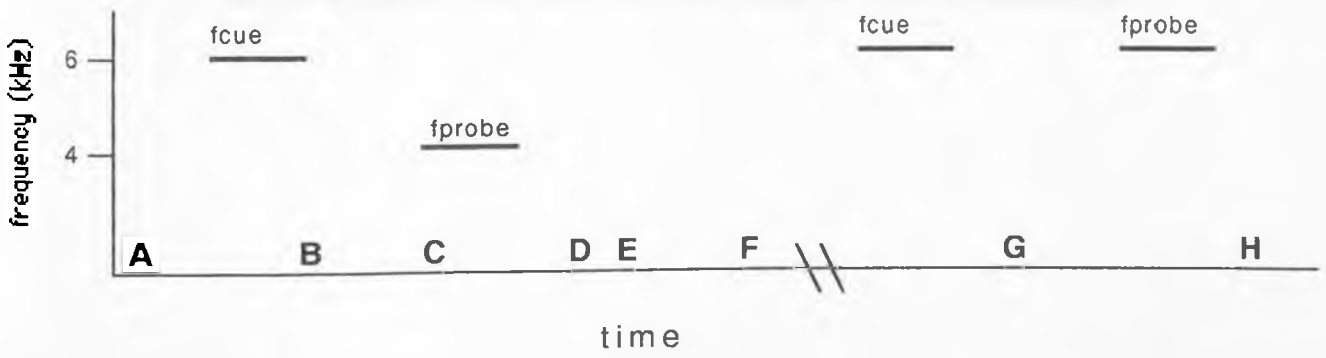


Figure 5: Beaker's behavior in two consecutive trials in paradigm A. The first trial (plates A - F) contains mismatched cue and probe frequencies. Notice that she spreads her wings in preparation for flight (plate C), then retracts them and momentarily looks away after deciding not to fly (plates D - F). The second trial (plates G and H) contains a 6,000 Hz probe tone. Letters correspond to time positions indicated in sonogram below.



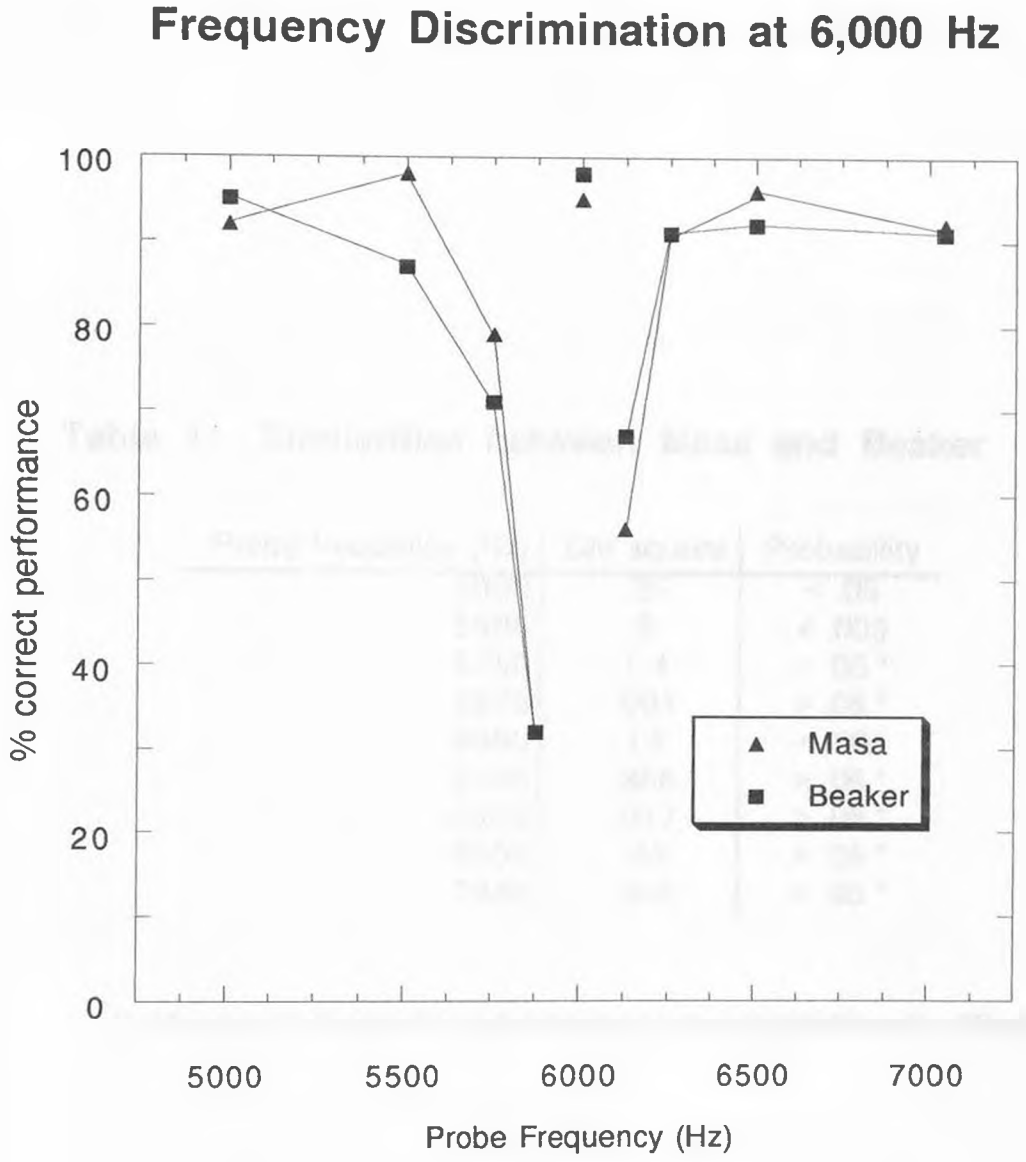


Figure 6: Masa and Beaker's performances in paradigm A. Points indicate each birds % correct responses at that probe frequency (fly on 6,000 Hz; stay on other frequencies).

Table 1: Similarities between Masa and Beaker

Probe frequency (Hz)	Chi square	Probability
5000	.35	< .05
5500	9	< .005
5750	1.4	> .05 *
5875	.004	> .05 *
6000	12	< .001
6125	.866	> .05 *
6250	.017	> .05 *
6500	.63	> .05 *
7042	.048	> .05 *

(*) Masa and Beaker's performances are not significantly different.

Table 2: Differential responses to 6,000 Hz and nearby frequencies

Beaker

Probe frequency	# trials	% correct	Chi square	Probability
5000	59	95	311	<<.001
5500	98	87	406	<<.001
5750	93	71	283	<<.001
5875	37	32	36	<.001
6000	959	98		reference
6125	27	67	80	<.001
6250	22	91	107	<<.001
6500	36	92	47	<.001
7042	32	91	159	<<.001

Masa

Probe frequency	# trials	% correct	Chi square	Probability
5000	51	92	215	<<.001
5500	100	98	459	<<.001
5750	63	79	199	<<.001
5875	66	32	40	<.001
6000	1241	95		reference
6125	45	56	76	<.001
6250	49	92	209	<<.001
6500	67	96	302	<<.001
7042	38	92	257	<<.001

Probe frequency Chi square probabilities are determined in comparison to the owl's performance at the reference frequency (6,000 Hz). All probabilities indicate significant discrimination behaviors.

Frequency Discrimination (4 - 9 kHz)

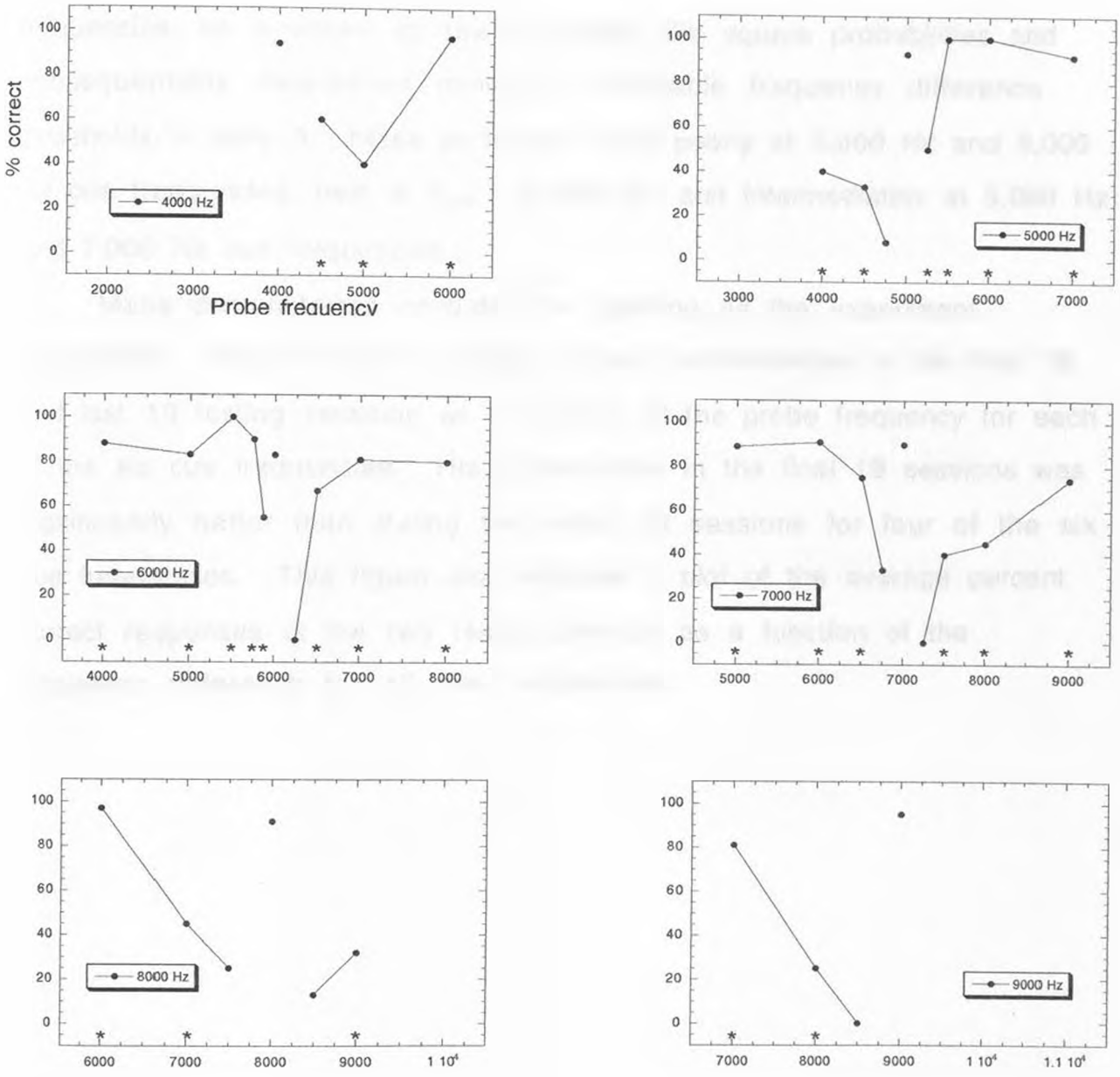


Figure 7: Masa's performance in paradigm B. Points indicate % correct responses as a function of the probe frequency. (*) significant ($p < .05$) discrimination ability when compared to performance at reference frequency.

correct responses as a function of the probe frequency for each of the six tested cue frequencies. Masa's performance varied at different cue frequencies, as is shown by the calculated Chi square probabilities and subsequentially determined minimum detectable frequency difference thresholds in table 3. Masa performed most poorly at 8,000 Hz and 9,000 Hz cue frequencies, best at f_{cue} = 6,000 Hz, and intermediately at 5,000 Hz and 7,000 Hz cue frequencies.

Masa demonstrated considerable learning as the experiment progressed. Figure 8 plots percent correct performances in the first 19 and last 19 testing sessions as a function of the probe frequency for each of the six cue frequencies. His performance in the final 19 sessions was significantly better than during the initial 19 sessions for four of the six cue frequencies. This figure also includes a plot of the average percent correct responses of the two testing periods as a function of the frequency difference for all cue frequencies.

Table 3: Differential responses to reference and nearby frequencies

Cue freq (Hz)	Frequency difference: probe - cue										Threshold	
4000	-2000	-1000	-500	-250	-125	0	250	500	1000	2000	lower	upper
# trials						178		16	52	31		
% correct						94		60	40	97		
Chi square								48	77	123		
Probability						ref		< .001 *	< .001 *	<< .001 *		< 500 Hz †
5000												
# trials		40	15	12		160	8	16	27	25		
% correct		40	33	8		93	50	100	100	92		
Chi square		28	10	.011			16	93	119	101		
Probability		< .001 *	< .005 *	> .05		ref	< .001 *	< .001 *	<< .001 *	<< .001 *	< 500 Hz	< 250 Hz †
6000												
# trials	32	24	10	10	11	135	5	9	32	20		
% correct	88	83	100	90	55	83	0	67	81	80		
Chi square	61	39	36	29	9		1.019	13	51	37		
Probability	< .001 *	< .001 *	< .001 *	< .001 *	< .005 *	ref	> .05	< .001 *	< .001 *	< .001 *	< 125 Hz†	< 500 Hz
7000												
# trials	28	35	14	6		163	3	10	44	50		
% correct	89	91	75	33		90	0	40	45	74		
Chi square	87	102	12	3			.35	8	29	82		
Probability	< .001 *	< .001 *	< .001 *	> .05		ref	> .05	< .005 *	< .001 *	< .001 *	< 500 Hz	< 500 Hz
8000												
# trials	38	49	4			182		8	22			
% correct	97	45	25			91		13	32			
Chi square	132	35	1.09					.089	10			
Probability	<< .001 *	< .001 *	> .05			ref		> .05	< .005 *		< 1000 Hz	< 1000 Hz
9000												
# trials	42	20	3			98						
% correct	81	25	0			95						
Chi square	84	8	.16									
Probability	< .001 *	< .005 *	> .05			ref					< 1000 Hz	

* Significant discrimination ability when compared to performance at reference frequency.

† Threshold may be less than the indicated value because frequency differences closer to the cue were not tested and thus a below-threshold probability was not determined.

Improvement over Time

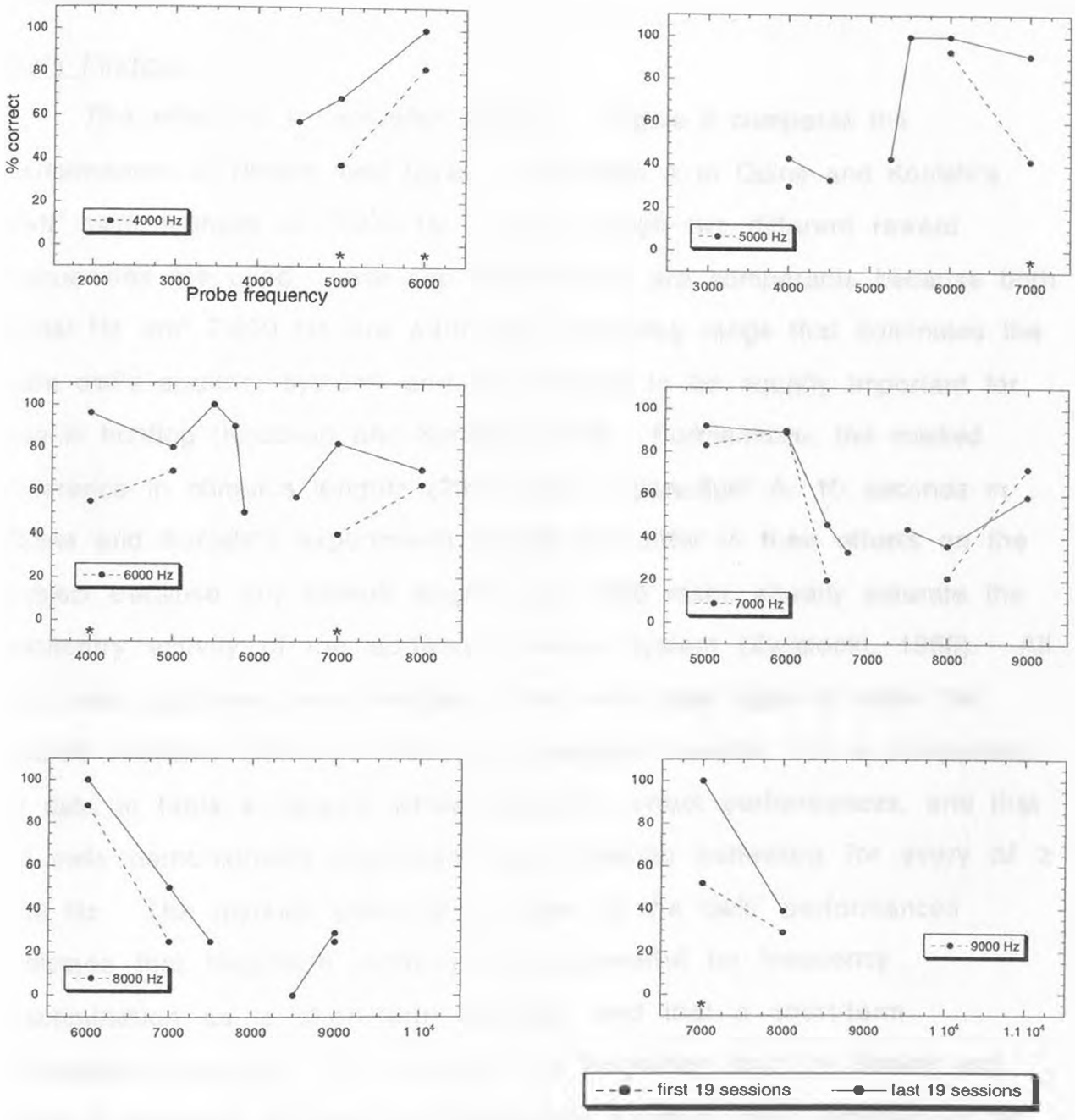
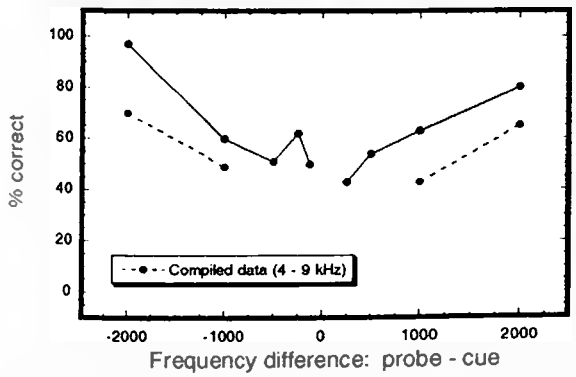


Figure 8: Masa's performance in paradigm B during two sequential time intervals (6/9 - 7/2 and 7/3 - 7/22). Points indicate % correct responses in relation to the testing context.
(*) significant ($p < .05$) difference between two sessions' performances.



Discussion

Main Findings

The effect of a reminder stimulus. Figure 9 compares the performances of Beaker and Masa in paradigm A to Quine and Konishi's owls' performances at 7,000 Hz. Even though two different reward frequencies are used, these two experiments are comparable because both 6,000 Hz and 7,000 Hz are within the frequency range that dominates the barn owl's auditory system, and are thought to be equally important for use in hunting (Knudsen and Konishi, 1978). Furthermore, the marked difference in stimulus lengths (250 msec in paradigm A, 10 seconds in Quine and Konishi's experiment) should not differ in their effects on the subject because any stimuli lengths over 200 msec equally saturate the excitatory activity of the auditory nervous system (Zwislocki, 1960). All four owls performed very similarly. Not only does figure 9 show the overall similarity between the two paradigms' results, but a comparison of data in table 4 reveals similar percent correct performances, and that all owls demonstrated significant discrimination behaviors for every $\Delta f \geq$ 100 Hz. The marked similarity between all the owls' performances indicates that long-term memory is as powerful for frequency discrimination as is short-term memory, and that a short-term memorable impression of a constant cue frequency (held by Beaker and Masa in paradigm A) does not necessarily improve one's detection of the memorized frequency. This finding contradicts my hypothesis and with the proposal by Quine and Konishi (1974) that a test similar to theirs, but with a smaller time difference between cue and probe frequencies (up to several trials long in their experiment; 2 - 4 seconds in mine), would allow for the detection of smaller frequency differences.

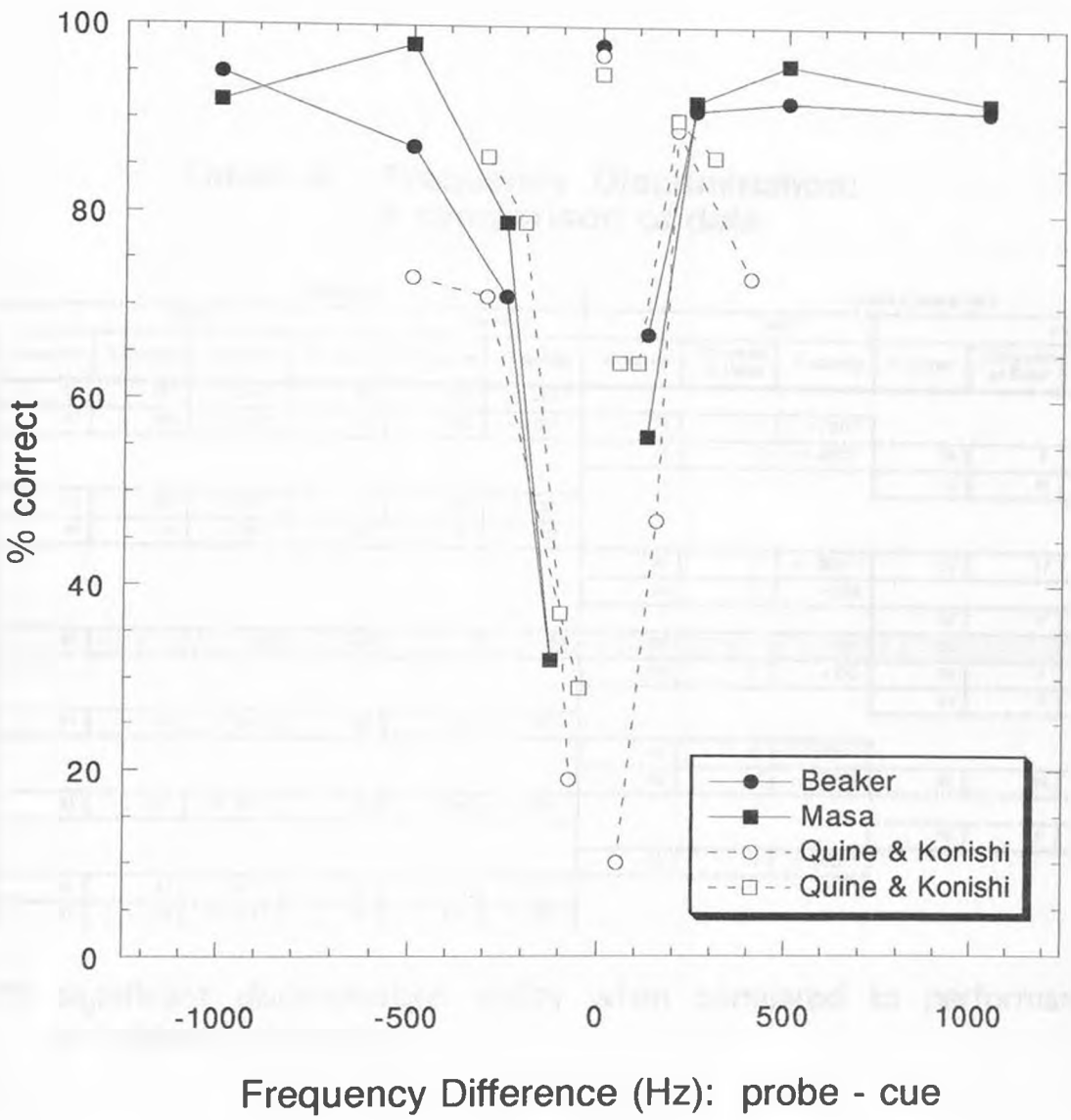


Figure 9: A comparison of Beaker and Masa's performances in paradigm A (ref. freq. = 6,000 Hz), to two owls' performances in a similar experiment conducted by Quine and Konishi in 1974 (ref. freq. = 7,000 Hz).

Table 4: Frequency Discrimination: a comparison of data

	Paradigm A						Quine & Konishi 1974					
	Beaker			Masa			owl 5			owl 6		
Freq Diff.	% correct	Chi square	Probability	% correct	Chi square	Probability	% correct	Chi square or Fisher	Probability	% correct	Chi square or Fisher	Probability
-1000	95	311	<< .001 *	92	215	<< .001 *						
-500	87	406	<< .002 *	98	459	<< .001 *	73	F	<< .001 *			
-300							71	F	<< .0001 *	86	F	<< .0001 *
-200										79	81	< .0005 *
-250	71	283	<< .001 *	79	199	<< .001 *						
-125	32	36	< .001 *	32	40	< .001 *						
-100							37	F	<< .0001 *	37	17	< .0005 *
-75							19	F	=.108			
-50										29	F	=.013
0	98		ref	95		ref	97		ref	95		ref
50							10	F	=.315	64	F	<< .0001 *
100										64	F	< .0005 *
125	67	80	< .001 *	56	76	< .001 *						
150							47	F	<< .0001 *			
200							89	67	< .0005 *	90	94	< .0005 *
250	91	107	<< .001 *	92	209	<< .001 *						
300										86	F	<< .0001 *
400							73	54	< .0005 *			
500	92	47	< .001 *	96	302	<< .001 *						
1042	91	159	<< .001 *	92	257	<< .001 *						

(*) significant discrimination ability when compared to performance at reference frequency.

Delayed matching-to-sample task. Masa met training criteria to demonstrate his understanding of the delayed matching-to-sample frequency discrimination task. Matching acoustic relations is natural for humans and Chimpanzees (*Pan troglodytes*), and, amongst birds, the common pigeon (*Columba livia*) has been trained to match visual stimuli (Thompson, 1997; Roberts, 1996; Zental, 1993). No owl has before been taught a delayed matching-to-sample task. Masa's ability to compare two tones separated in time, then deliberately chose to fly or stay in response to the relative frequencies of the tones, demonstrates a cognitive ability to receive, compare, and respond differentially to acoustic stimuli.

The relative effects of long-term memory versus short-term memory on frequency discrimination. Although Masa's significant discrimination ability at f_{probe} = 5,875 Hz suggests that he can detect as small frequency differences by short-term memory as by long-term memory, other convincing characteristics of his delayed matching-to-sample performances indicate that frequency discrimination in this task is more difficult than that of paradigm A or Quine and Konishi's paradigm. A fundamental theory of frequency discrimination, $\Delta f/f_{cue}$ = constant, suggests that Masa would perform very well at low frequencies (Pickles, 1988). Testing at 4,000 Hz and at 5,000 Hz should yield small (possibly the smallest) Δf's of the entire testing range. At 5,000 Hz, he was tested with Δf = ±250 Hz, and demonstrated difficulty discriminating 4,750 Hz from 5,000 Hz. If $\Delta f/f_{cue}$ is constant, this performance indicates that he would only be able to detect frequency differences equal to or greater than ±250 Hz at higher cue frequencies. Furthermore, a comparison of Masa's performance at 7,000 Hz to Quine and Konishi's owls again indicates the increased difficulty of frequency discrimination in a delayed

matching-to-sample attention task. Figure 10 plots the percent correct performances of Masa and Quine and Konishi's owls as a function of the probe frequency. Masa's threshold at Δf = 500 Hz far exceeds those of the owls in the earlier study.

The discussed characteristics of Masa's performance in the delayed matching-to-sample task and comparisons of his performances to those of paradigm A and Quine and Konishi's results cumulatively illustrate that it is more difficult to match two arbitrary frequencies separated in brief time, than to match one frequency with its representation in long-term memory. These results support my hypothesis that long-term memory of a repetitively presented cue tone allows for better frequency discrimination skills than short-term memory of an arbitrary tone.

A Possible Explanation for the Decreased Performance in Paradigm B

Weinberger and colleagues (1993) investigated the effects of acoustic classical conditioning on neurons within the auditory cortex of adult guinea-pigs. They recorded from cells tuned to a specific frequency before and after exposing the anesthetized guinea-pig to a different specific frequency accompanied by a mild electric shock to the foot. In response, the neurons decreased in their sensitivity to the previous best-frequency, and increased in sensitivity to the new, conditioned frequency. Their investigation shows that prolonged exposure to a stimulus can lead to changes in the nervous system that represent long-term memory imprinting. It is possible that Masa and Beaker's (and Quine and Konishi's owls') neuronal sensitivity to the reward frequency was similarly modified. Their prolonged exposure to a behaviorally important frequency (6,000 Hz or 7,000 Hz) probably induced changes in the frequency selectivity of neurons at and around that frequency's receptive field in the

A Comparison of Long-term and Short-term Memory Frequency Discrimination Skills

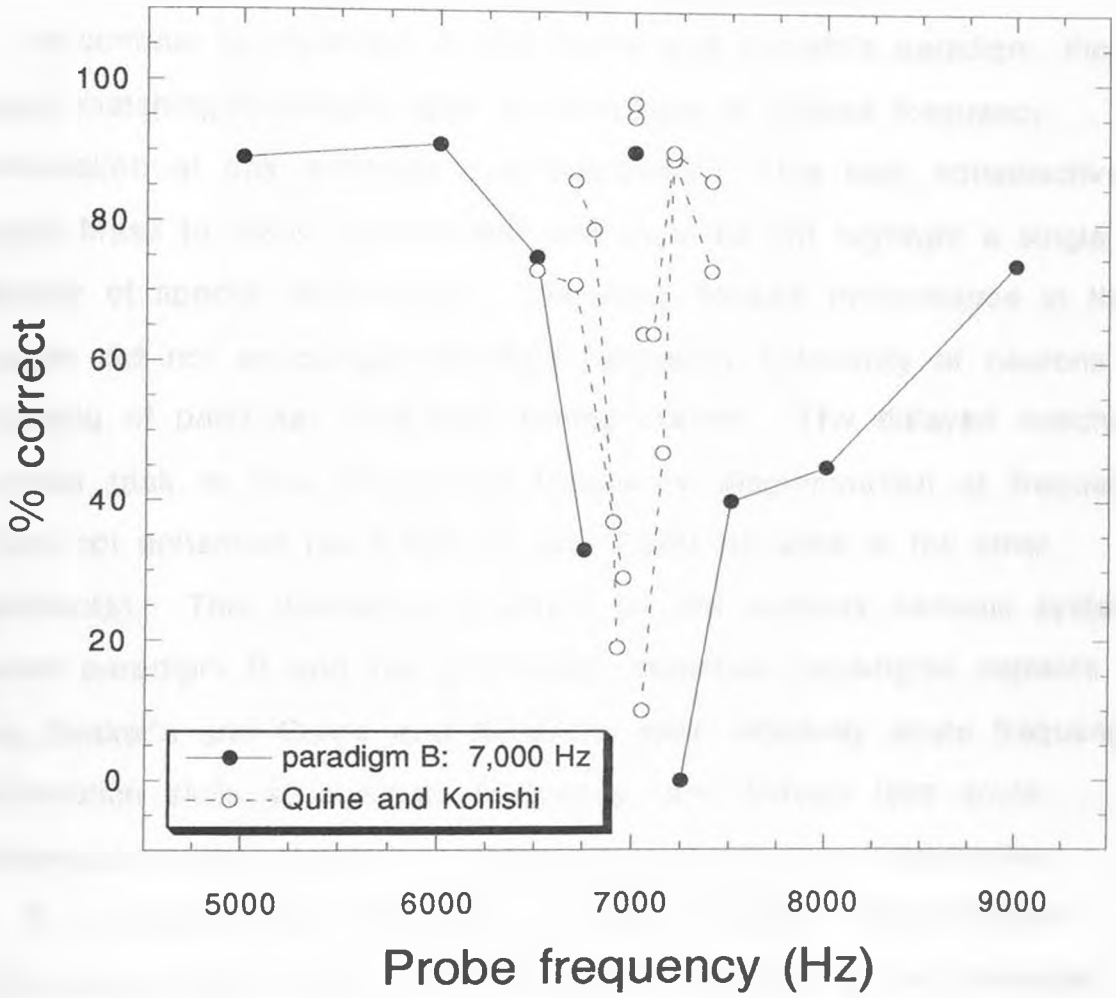


Figure 10: A comparison of Masa's performance at 7,000 Hz in paradigm B to Quine and Konishi's owls' performances at 7,000 Hz. Points indicate % correct at that frequency.

auditory system, so as to ultimately sharpen the tuning curve at that frequency. Such an occurrence would help improve frequency discrimination at and around the conditioned frequency.

In contrast to paradigm A and Quine and Konishi's paradigm, the delayed matching-to-sample task of paradigm B probed frequency discrimination at any arbitrary cue frequency. This task nonselectively exposed Masa to many frequencies, and thus did not highlight a single frequency of special importance. Therefore, Masa's performance in the paradigm did not encourage modified frequency selectivity of neurons or sharpening of particular frequency tuning curves. The delayed matching-to-sample task is thus measuring frequency discrimination at frequencies that are not enhanced (as 6,000 Hz and 7,000 Hz were in the other experiments). This difference in effect on the auditory nervous system between paradigm B and the previously described paradigms explains Masa, Beaker's and Quine and Konishi's owls' relatively acute frequency discrimination skills at a single frequency, and Masa's less acute discrimination skills at each of several arbitrary cue frequencies.

It is possible that Masa's increased frequency discrimination performances around 6,000 Hz in paradigm B are due to his prolonged sensitivity to 6,000 Hz from paradigm A. Weinberger *et al.*'s (1993) study discovered long-term retention of the auditory cortex's frequency-specific sensitivity for up to eight weeks after he ceased to condition that frequency with a foot shock. Considering that the time between the last paradigm A session and the first paradigm B testing session was 27 days, it is possible that Masa's auditory system contained residual heightened sensitivity to those frequencies used in paradigm A. His sensitivity may even have been maintained through paradigm B, because

the correct detection of those frequencies once again benefitted the owl (though not necessarily to the same degree). This phenomena may explain why Masa did so well at f_{probe} = 5,875 Hz, and at all other testing frequencies around 6,000 Hz except f_{probe} = 6,250 Hz (perhaps he would have done better at this frequency had I tested there more thoroughly [n = 5]). It may also explain why he performed better below the 7,000 Hz cue frequency (at f_{probe} = 5,000 Hz, 6,000 Hz, and 6,500 Hz - all frequencies introduced in paradigm A), than above 7,000 Hz; and why, conversely, his detection skills were significantly better above the 5,000 Hz cue frequency than below it.

In such an experiment as paradigm B that asks the subject to match probe tones to one of six constant cue tones, it is possible that the subject would eventually memorize all six cue frequencies. In the 38 testing sessions, Masa already demonstrated improved frequency discrimination skills, as is depicted in figure 8. His improvement in the last 19 sessions over that shown in the initial 19 sessions suggests that the auditory system has already begun to sharpen its tuning curves for each of the selected cue frequencies. It is possible that prolonged exposure to the paradigm would eventually allow the auditory system to develop peak selective sensitivity to the cue frequencies, a circumstance that might give rise to frequency discrimination performances comparable to those demonstrated in paradigm A.

It is of interest to note that, if the owls' auditory systems have undergone similar modifications to those shown in Weinberger's guinea-pigs, such neuronal plasticity could not have occurred in the auditory cortex because a 6 - layered neocortical structure is absent in birds. Instead, such changes may have happened within the field of the

telencephalon. Although this region represents the avian analogue to the mammalian neocortex, the telencephalon's cellular architecture is uniquely different. If neuronal changes did occur within this structure, it demonstrates that, in spite of birds and mammals having separately diverged from the reptiles long before the development of "modern" auditory systems, the avian auditory system can undergo similar modifications using a distinctly different neuronal circuitry.

Future Investigations

To better understand frequency discrimination, it would be helpful to compare a subject's ability to detect a frequency difference (as was revealed in my experiments) to its ability to detect a frequency change. A continuous change from one frequency to another over time, or an FM (frequency modulation) sweep, may prove more or less difficult to detect than two frequencies separated in time. When compared, a subject's performances in these two tasks would help indicate the relative importance of single frequency fragments and the FM sweeps between these fragments in our interpretation of sounds.

A barn owl trained in a delayed matching-to-sample task is potentially an excellent model to help us further understand auditory perception. For any concept the owl is trained to match, its brain's intention to match stimuli would be understood and therefore could be compared to the owl's demonstrated matching behavior. This would, of course, give insight into how well the brain can detect and match the presented stimuli. One could test an owl's ability to match complex noises, sound locations, or other acoustic characteristics.

To understand the neuronal processes underlying a delayed matching-to-sample task, one could conduct an electrophysiological study

on a trained barn owl. One such study could investigate the possible recruitment of neighboring cells, or short-term changes in sensitivity of neurons that have just been stimulated by an arbitrary cue frequency. It is possible that the owl's attention towards the cue frequency, and subsequent anticipation of the same probe frequency, may cause the brief modification of the auditory system's sensitivity to that frequency. If so, this would demonstrate the remarkable flexibility of the brain, and its profound short-term control over its own processes.

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Glossary

Auditory cortex: The final site of acoustic analysis in mammalian brains.

Auditory system: The regions of the central nervous system pertaining to sound reception and evaluation.

Barn owl: A widely distributed owl (*Tyto alba*) that has plumage mottled buff brown and gray above and chiefly white below, frequents barns and other buildings, and preys especially on rodents.

Decibel (dB): A unit for expressing the ratio of two amounts of electric or acoustic signal power equal to 10 times the common logarithm of this ratio. Degree of loudness.

Delayed matching-to-sample task: A paradigm in which the sample stimulus is followed, after a delay, by a test stimulus, and the subject is rewarded for indicating whether it matches the sample.

Ethology: The scientific and objective study of an animal's behavior.

Frequency (of sound): The number of sounds waves per second produced by a sounding body.

Frequency modulation: Modulation of the frequency of the carrier wave in accordance with speech or a signal.

Hertz: A unit of frequency equal to one cycle per second.

Memory: The power or process of reproducing or recalling what has been learned and retained especially through associative mechanisms.

Neuron: A cell with specialized processes that is the fundamental functional unit of nervous tissue.

Telencephalon: The anterior subdivision of the forebrain comprising the cerebral hemispheres and associated structures.

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