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Categorical Responses to Natural and Synthesized Alarm Calls in Goeldi's Monkeys (*Callimico goeldii*)

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ABSTRACT. The responses of Goeldi's monkeys to their natural alarm calls as well as synthesized versions varying in the acoustic parameters that defined the calls were studied. The response patterns, which were subject to a distinct change only with an increase of 0.2 kHz in the frequency range of the modulating sweep, appeared to reflect strict underlying perceptual boundaries. This was analogous to the categorical perception that humans show with speech sounds. Supernormal releaser was found, and the characteristics of its acoustic structure were assessed in terms of the environmental influences of the physical situation in which alarm calls must be emitted.

INTRODUCTION

The problem of how nonhuman species perceive their own communication signals has recently interested ethologists and psychologists. In most Old World and New World primates, among others, numerous categories of vocalizations and visual displays are intergraded with one another and form a continuum. MARLER (1975) has argued that a progressive tendency in vocal grading through primate orders was a prerequisite for the possible evolution of human speech. Labelling of signals as discrete or graded is, however, carried out by the perceptual system of the human observer, not by the conspecifics under study.

The most prevalent method used in investigations related to this question consists of playback and synthesizing techniques. One of the important difficulties of earlier playback experiments with primates (GREEN, 1975; WASER, 1975) concerned the impossibility of separating individual variables from the acoustic parameters in vocalizations which were very complex in their physical structure. Recent developments in synthesizing techniques (PETERS, SERCHY & MARLER, 1980; Zoloth et al., 1980) have enabled us to manipulate the latter variables, independent of the former. By playing back synthesized versions of natural calls which systematically varied in duration, center frequency, band width and modulating sweep, SNOWDON and POLA (1978) reported that graded vocalizations were responded to quite differently, corresponding to slight differences in acoustic parameters in pygmy marmosets. Sharp boundaries between functionally different sounds are indispensable for the accurate transmission of information despite individual variations or environmental noise.

MASATAKA (1982) observed that two different types of responses were released by alarm calls in feral *Callimico* when encountering a predator animal. Each response was not designated by corresponding different vocalizations, being discrete from each other, but fell into a grading continuum. This paper describes the responses of Goeldi's monkeys to five of their natural alarm calls as well as to systematic variants of their synthesized versions along each of the acoustic parameters that define the calls.

METHODS

SUBJECTS

The subjects were a feral-caught male-female adult pair and their offspring who were laboratory-born over the course of 29 months, consisting of two males and a female, kept at the Japan Monkey Centre. They were housed in a large cage (8×7×6 m) divided into two compartments by a wall equipped with a swing door (60×50 cm), through which the animals could pass freely. However, visual communication was interrupted.

ALARM CALLS USED AS STIMULI

Vocal recording, while observing behavioral correlates, had been carried out in a group of Goeldi's monkeys in north-western Bolivia over a six-month period in 1979 (MASATAKA, 1981a, b, 1982). Representative samples of five types of alarm calls, all of which fall into a grading continuum, are shown in Figure 1, and four acoustic parameters for each of them are presented in Table 1. These vocalizations are common in their physical structure consisting of ascending and descending sweeps and a noise burst. The durations of the sweeps range from 0.09 to 0.27 sec, while the band width and center frequency of the noise burst range from 7.2 to 20.0 kHz and 7.8 to 13.2 kHz, respectively.

The Type 1 call is made up of three segments of ascending sweeps with frequencies of 0–2, 5–7 and 11–13 kHz. Having a duration of 0.25 sec, the energy is more concentrated on the central sweep than on the other two sweeps at a duration of approximately 0.12 sec. A noise burst spreads for 0.05 sec across a wide spectrum, 0–20 kHz, occurring subsequently to the inflation of the energy shown by the sweeps. An atonal component, thereafter, accompanies solely the central sweep at a duration of 0.20 sec, while others are absent. Among the five types of alarm calls, the Type 2 call has the shortest duration, 0.09 sec, during which a sweep

Table 1. Four acoustic parameters of five natural alarm calls.

Call type	Duration (sec)	Center frequency (kHz)	Frequency range of modulating sweep (kHz)	Band width of noise burst (kHz)
1	.25	7.8	3.3	20.0
2	.09	8.2	1.8	19.4
3	.27	11.4	2.6±0.5	7.2
4	.16	13.2	3.0	11.9
5	.26	9.5	1.6	11.7

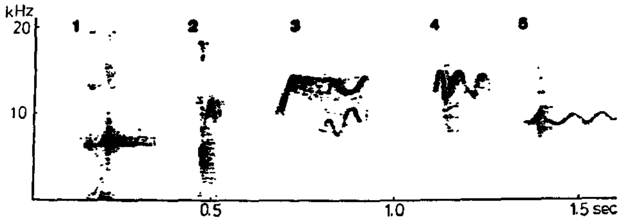

Fig. 1. Sonographs of five types of natural alarm calls.

is modulating from 9 to 11 kHz. A noise burst occurs with lower frequencies, 9.0–0.5 kHz, than that of the sweep, at a duration of 0.06 sec. Although the energy is also distributed at a higher frequency, its structure is scarcely distinguishable. The Type 3 call consists of two sweeps, with the energy concentrated in the higher rather than in the lower one. The former ascends and descends with a frequency of 10–13 kHz at a duration of 0.27 sec. A noisy structure is superimposed on it with a band width of 7.2 kHz. The latter ranges from 8.0 to 10.5 kHz, showing a duration of 0.12 sec, being initiated 0.15 sec later than the appearance of the former sweep and disappearing in accordance with its absence. The Type 4 call shows the highest center frequency among the five vocalizations. 0.04 sec later than the onset of the energy of a single modulating sweep, a noise burst across a wide range of 8–20 kHz occurs at a duration of 0.05 sec. The sweep modulates regularly for 0.16 sec with a frequency range of 3.0 kHz. The acoustic characteristics of the Type 5 call have similarities with those of the Type 4 call in that a sweep repeats ascents and descents at identical intervals. The band width of a noise burst which had its onset at the first inflation of the sweep and spreads for 0.05–0.06 sec, is approximately 12 kHz in both of them. The frequency range of the sweep is 1.6 kHz in the Type 5 call, showing a lower center frequency, 5.6 kHz, than in the Type 4 call.

Field observations have indicated that the responses of *Callimico* to alarm calls were alternative, either emitting warning calls or freezing. In the former case, the group members ran up to the highest strata in the canopy, vocalizing trills, and then hid on the back side of the trunk of a tree by clinging vertically. In the latter case, they climbed down to the ground and kept silent. At 1–3 min after occurrences of freezing, they began to run and climbed up the tree again. In an earlier study (MASATAKA, 1982), the author presented sonagrams of the Type 1 and 3 calls and indicated that both flight patterns were provoked by either of them. The full importance of the relations between the acoustic structures of the alarm calls and the response patterns was not understood at that time. A single category was designated in the earlier paper for alarm calls by illustrating sonographs of those vocalizations that were extremely different from one another in their gross morphology, neglecting a series of intermediates, because it was difficult for field observations and recordings to examine the influences exerted by an acoustic parameter on the behavior correlates. It was also highly probable that elicitation of each flight pattern was determined by unidentified differences, independent of acoustic structures. Explaining the actual circumstances in detail, the Type 1, 3 and 4 calls were observed to be responded to by freezing, and the Types 2 and 5 were responded to by warning calls when they were recorded in the natural settings.

PROCEDURES

Presentations of the stimuli were given by the observer concentrating on a focal animal when he was alone in a compartment, having separated spontaneously from others who were in another compartment. The target animals were observed in a different random sequence. In order to avoid the possibility of the animals localizing and subsequently ignoring the playbacks, two separate speakers were hidden at 3 m outside the cage. The playbacks were directed through either of them, and the speaker location was frequently changed (once per four trials on average). To prevent habituation of the subjects to specific stimuli, the number of presentations on a given day was limited to 15 stimuli. Although the stimuli were played in random orders, four trials for a given stimulus were conducted on every subject throughout the experiment. Any positive response to a playback stimulus was scored when it was shown by an animal within 15 sec of presentation of the stimulus. Differences between the response rates to stimuli were evaluated, using the test for significance between proportions described by FERGUSON (1959).

SYNTHESIS OF VOCALIZATIONS

Vocalizations were synthesized by the method developed by Zoloth et al. (1980). Natural alarm calls were entered through the analogue-to-digital converter of a DEC 11/10 minicomputer and sampled at a rate of 20 kHz. The sequentially digitized samples were stored at 10-bit integers in sequential order in contiguous disk files. The discrete Fourier transform was obtained by applying the fast Fourier transform (FFT) to a digitized representation of a vocalization. Modifications of the signal phase, frequency or duration were made by manipulation of the appropriate Fourier coefficients. An inverse discrete Fourier transform converted the modified spectral data back to a digitized representation of a vocalization suitable for output through a digital-to-analogue converter. The acoustic parameters were varied as follows: frequency range of modulating sweeps, 0.8 to 5.6 kHz; center frequency, 6.0 to 15.0 kHz; duration, 0.05 to 0.40 sec; and band width of noise burst, 3.0 to 14.0 kHz. Each of these four parameters was varied separately.

RESULTS

EXPERIMENT 1: RESPONSES TO NATURAL CALLS

First, five types of natural calls were played in order to determine whether or not captive *Callimico* exhibited identical responses to those of feral *Callimico*. The most consistent be-

Table 2. Occurrence ratios of freezing and warning call responses (%) to natural calls when they were presented with a full spectrum (Experiment 1), and when certain frequency components were filtered out (Experiment 2).

	Experiment 1:					Experiment 2:		
	Call type					Call type		
	1	2	3	4	5	1	2	3
Responses:								
Warning call	10	85	0	5	80	5	90	5
Freezing	80	5	75	85	5	80	5	75

N = 20 in each experiment.

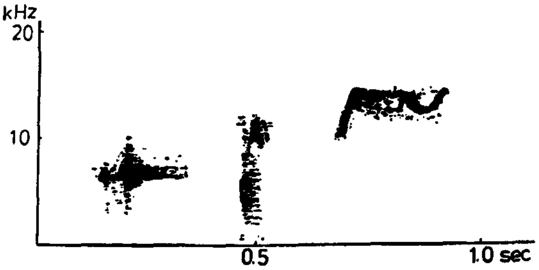

Fig. 2. Sonographs of calls filtered out from natural calls.

havioral response following playbacks of the Type 1, 3 and 4 calls was freezing, the occurrence ratio of which exceeded 75%, while that following playbacks of the Type 2 and 5 calls was emission of warning calls (Table 2). These results agreed with the field observations on behavioral correlates when natural calls were recorded, and it was concluded that freezing and emission of warning calls were good measures of the reaction to playback stimuli.

EXPERIMENT 2: RESPONSES TO CALLS WITH SOME OF THEIR ACOUSTIC COMPONENTS FILTERED OUT

In addition to the modulating sweep and noise burst which are seen commonly in all of the five natural calls, the Type 1, 2 and 3 calls include some other acoustic components. These were filtered out to determine whether they could function as cues for the elicitation of specific responses in the animals (Fig. 2). As shown in Table 2, there were no significant differences between the rates of responses to a natural call and to that after filtering out in each call type.

EXPERIMENT 3: RESPONSES TO SYNTHESIZED VERSIONS VARYING IN FREQUENCY RANGE OF THE MODULATING SWEEP (Fig. 5)

For the purpose of investigating the effects of differences in the frequency range of the modulating sweep on the responses, synthetic calls were played. Since the Type 4 and 5 calls were responded to by the animals as well as other natural calls, being simple in their morphology, they were employed as the standard calls for the synthesis of vocalizations. Representative samples of the synthetic versions used in Experiment 3 are shown in Figure 3A. The frequency range of the modulating sweep was changed from 0.8 kHz to 5.6 kHz by nine steps as shown in Figure 5. The duration, center frequency and band width of the noise burst were kept constant at 0.16 sec, 13.0 kHz and 11.0 kHz, respectively.

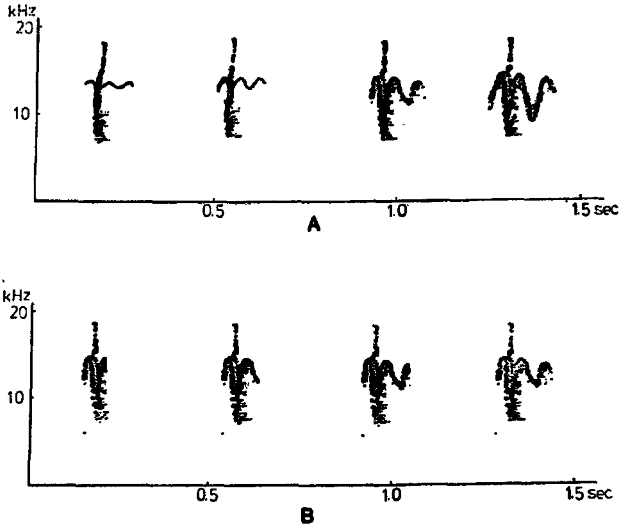

Fig. 3. Representative samples of synthesized versions varying in (A) frequency range of the modulating sweep and (B) duration.

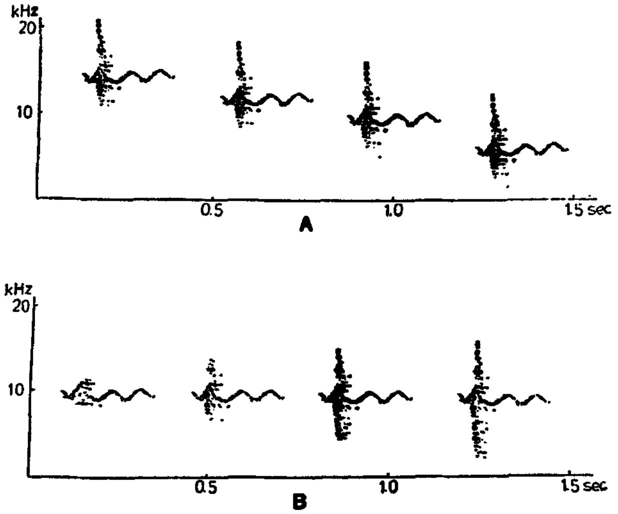

Fig. 4. Representative samples of synthesized versions varying in (A) center frequency and (B) band width of the noise burst.

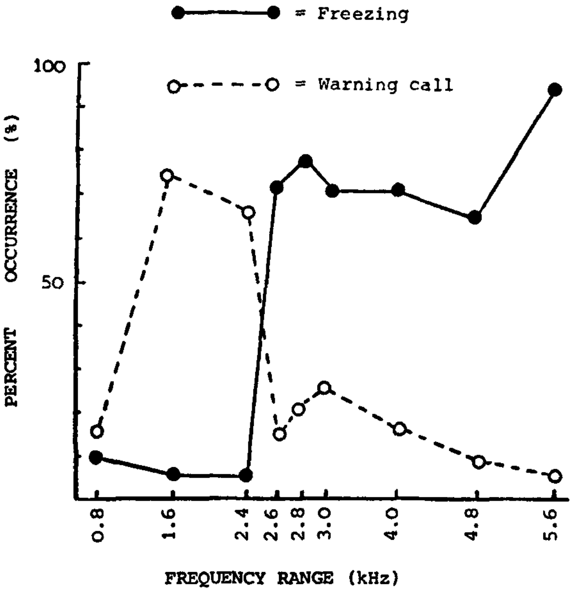

Fig. 5. Response rates to synthesized versions varying in frequency range of the modulating sweep. A significant difference in response ratio occurred only with the 0.2 kHz increase from 2.4 kHz to 2.6 kHz.

The freezing responses to 4.8, 4.0, 3.0, 2.8 and 2.6 kHz stimuli did not differ significantly from one another, whereas the response to a 5.6 kHz stimulus was significantly more frequent (p's<0.05). Compared with these stimulus sounds, others were responded to significantly less often (p's<0.001). Note the significant difference in response ratio that occurred with only a 0.2 kHz increase from 2.4 to 2.6 kHz in the frequency range of the stimulus. The ratios of warning call responses were high when 1.6 and 2.4 kHz stimuli were presented. They differed significantly from those of other stimuli (p's$<$0.001), but did not differ from one another.

EXPERIMENT 4: RESPONSES TO SYNTHESIZED VERSIONS VARYING IN DURATION (Fig. 6)

Synthetic variants in duration from 0.05 to 0.40 sec, of which representative samples are shown in Figure 3B, were presented to determine whether or not they affected the responses. These calls had a frequency range of the modulating sweep of either 1.6 kHz or 3.0 kHz, a center frequency of 13.0 kHz and a band width of the noise burst of 11.0 kHz, changing their duration by six steps as shown in Figure 6. When 3.0 kHz stimuli were played, freezing responses were seen more often than warning call responses except for the case of the 0.40 sec stimulus, which was responded to significantly less frequently than other stimuli (p's$<$0.001) (Fig. 6A). The response rate of the 0.05 sec stimulus was the highest and differed significantly from those of the 0.07, 0.10, 0.16 and 0.30 sec stimuli (p's$<$0.05). On the other hand, warning calls were observed as responses to the 1.6 kHz stimulus on most occasions (Fig. 6B). Only the 0.40 sec stimulus elicited these responses less frequently than other stimuli (p's$<$ 0.001).

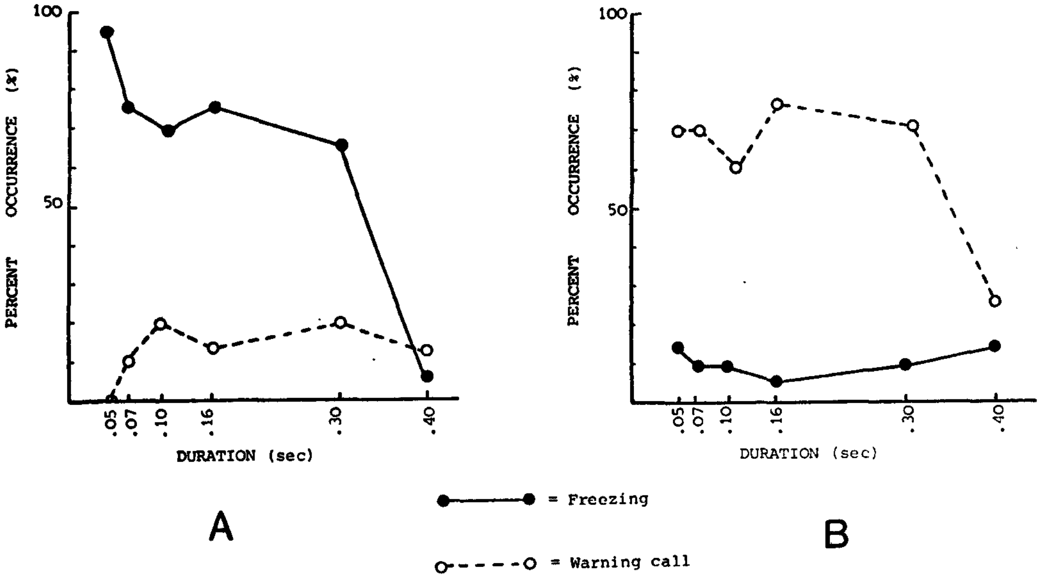

Fig. 6. Response rates to synthesized versions varying in duration, having a frequency range of the modulating sweep of (A) 3.0 kHz and (B) 1.6 kHz. When 3.0 kHz stimuli were played, freezing responses were observed more frequently than warning call responses in most cases, while the opposite was true when 1.6 kHz stimuli were played.

EXPERIMENT 5: RESPONSES TO SYNTHESIZED VERSIONS VARYING IN CENTER FREQUENCY (Fig. 7)

The center frequency was manipulated from 6.0 to 15.0 kHz by five steps as shown in Fig-

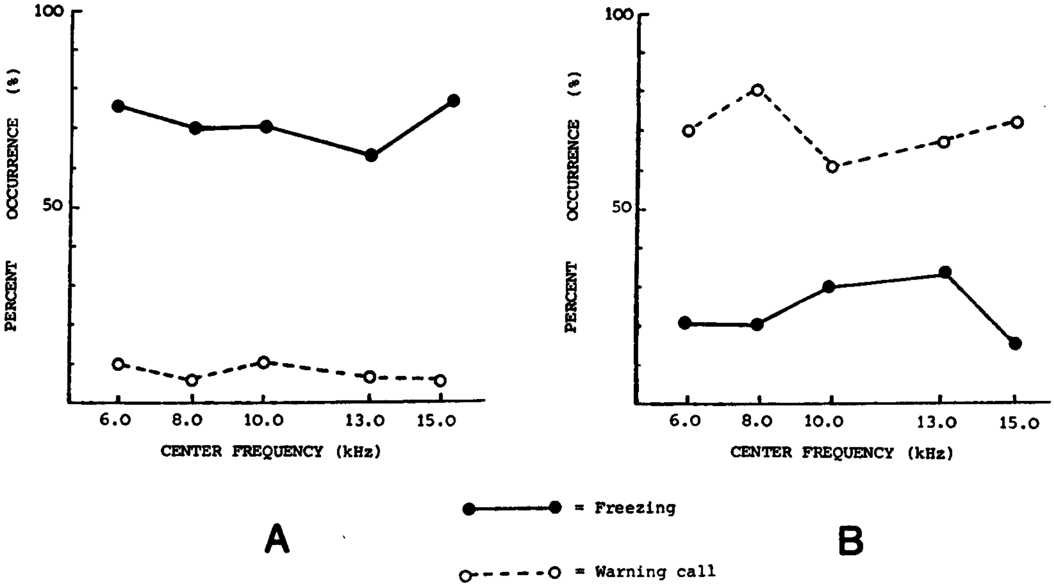

Fig. 7. Response rates to synthesized versions varying in center frequency, having a frequency range of the modulating sweep of (A) 3.0 kHz and (B) 1.6 kHz. All 3.0 kHz stimuli were reacted to by freezing responses more frequently than by warning calls, while 1.6 kHz stimuli were reacted to more frequently by the latter than by the former.

ure 7, with a frequency range of the modulating sweep of either 1.6 kHz or 3.0 kHz, a duration of 0.16 sec, and a band width of the noise burst of 11.0 kHz. Representative samples are shown in Figure 4A. All of the 3.0 kHz stimuli were reacted to by freezing responses more frequently than by warning calls, and the 1.6 kHz stimuli were reacted more frequently by the latter than by the former. There were no significant differences between the rates of responses to the variants.

Experiment 6: Responses to Synthesized Versions Varying in Band Width of the Noise Burst (Fig. 8)

Synthetic calls varying in band width of the noise burst from 3.0 kHz to 14.0 kHz by five steps as shown in Figure 8 were played in order to investigate the differences in responses, with a frequency range of the modulating sweep of either 3.0 kHz or 1.6 kHz, showing a duration of 0.16 sec and a center frequency of 13.0 kHz. Representative samples of the versions are illustrated in Figure 4B. Freezing responses were seen more frequently than warning call responses after all 3.0 kHz stimuli, while the latter responses occurred more often than the former after 1.6 kHz stimuli. No significant differences were found between the ratios of any of the responses to 3.0 kHz stimuli or 1.6 kHz stimuli.

Experiment 7: Responses to the Synthetic Versions, with a Duration of 0.05 sec and a Frequency Range of the Modulating Sweep of 5.6 kHz

From the results of Experiments 3 and 4, it was evident that the freezing responses were

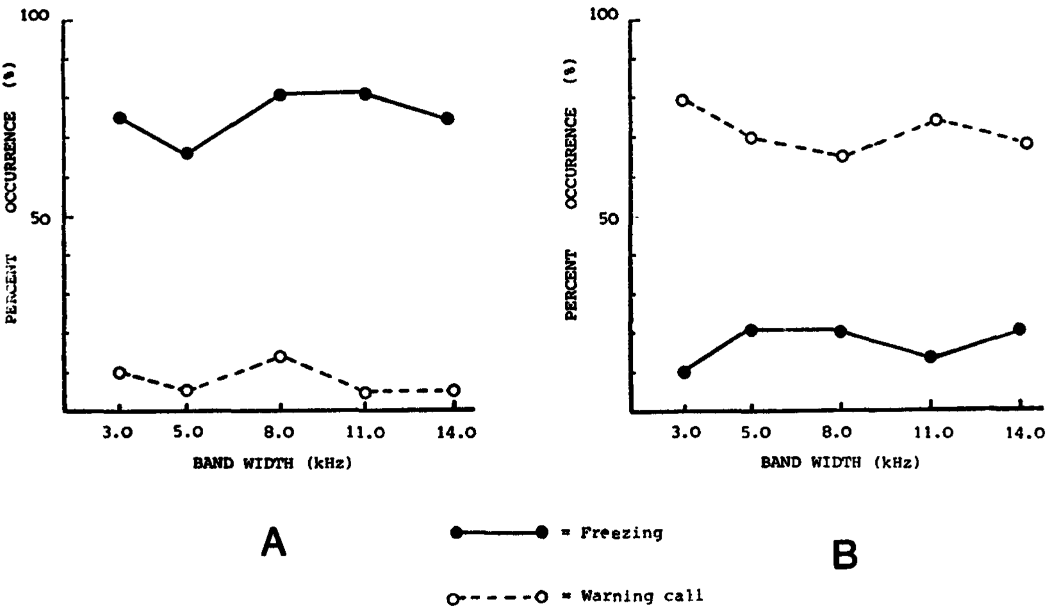

Fig. 8. Response rates to synthesized versions varying in band width of the noise burst, having a frequency range of the modulating sweep of (A) 3.0 kHz and (B) 1.6 kHz. Following all 3.0 kHz stimuli, freezing responses were observed more frequently than warning call responses, while the latter occurred more frequently following 1.6 kHz stimuli.

provoked most effectively when 5.6 kHz stimuli (Fig. 5) or 0.05 sec stimuli (Fig. 6) were presented. Hence, the synthetic version, which had both of them as its acoustic parameters, was played in order to determine whether they could facilitate one another in triggering the responses. When this call was presented, the rate of freezing responses was 100%, i.e., higher than that of any other call previously played.

DISCUSSION

The response patterns which were subject to a distinct change only with an increase of 0.2 kHz in the frequency range of the modulating sweep, appeared to reflect strict underlying perceptual boundaries. This was analogous to the categorical perception that humans show with speech sounds. Similar results have been obtained by Snowdon and Pola (1978) in pygmy marmosets, where the perceptual boundary appeared primarily on the duration continuum when contact calls were played. An association of different responses with correspondingly different alarm calls was also observed by Seyfarth, Cheney and Marler (1980) in vervet monkeys, where each of three types of vocalizations elicited the animals to run up into trees, to look up and run into a dense bush, and to look down at the ground, respectively. This behavioral differentiation corresponded with the types of primary predators of vervet monkeys, i.e., leopards, eagles and snakes. In Goeldi's monkeys, the Type 1, 4 and 5 calls were heard when predator animals, tyras (*Galera barbara*), were perceived by the group members. The Type 2 and 3 calls were provoked as they encountered big birds. Among these instances, however, the Type 1, 3 and 4 calls were emitted, being preceded by predator animals having apparently recognized the group members and attempted to approach them, whereas a tyra or a bird only passed by when other vocalizations were recorded. Freezing responses was a practical option when the distance between the predator and Goeldi's monkeys was too short to permit emission of warning calls. Running down to the ground was considered to occur when they recognized the possible danger as a more urgent one than when they climbed up into the trees, irrespective of the types of predators. The frequency range of the modulating sweep might possibly reflect the magnitude of the flight tendency of a vocalizer when he emits alarm calls.

Variants of duration, center frequency and band width of the noise burst did not elicit sharp differences in response patterns. This does not mean, however, that these parameters are not efficient for the transmission of messages. The Type 2 and 3 calls were emitted by the juveniles, whereas other lower vocalizations were by adult individuals. As pointed out by SNOWDON and POLA (1978), younger individuals with smaller vocal cords would produce calls with correspondingly higher center frequencies. Individual differences can be expressed considerably through this component. Although the response patterns to the Type 1 and 2 calls were different, these two vocalizations were commonly recorded as the group members were cohesive with one another. While foraging, the interindividual distances between the alarmist and other members did not exceed 5 m, in contrast to other cases in which they were at least 10 m. Emission of calls with a shorter duration and distribution of the noise burst across a wider spectrum, is thought to be effective for the precise conveyance of information over a short distance, ensuring the survival of the alarmist against predators by making the time lapse to be localized least. It is highly probable that Goeldi's monkeys are able to make finer discriminations between variants. While sharp boundaries, depending on a single acoustic parameter, determine precisely the response patterns of the signal recipients, individual and contextual differences can be recognized by the members over the broad variability within each category.

Variants which had a duration of 0.40 sec or a frequency range of the sweep of 0.8 kHz were not responded to on most occasions. They were considered not to be perceived as alarm calls. In fact, natural alarm calls common in acoustic parameters with these synthetic versions, have never been recorded. Emission of such a vocalization is not regarded as probable for the animals, which ceased to respond to synthetic calls which were beyond the physical boundaries of the ability to produce the calls.

However, remaining naturally "improbable" calls, which showed a duration of 0.05 sec or a frequency range of the sweep of 5.6 kHz, did not agree with the perceptual boundary. On the other hand, the response ratio was the highest to these stimuli, which are so-called supernormal releasers (KOEHLER & ZAGARUS, 1937) (Fig. 9). Concerning the auditory modality, they were discovered first by SCHUBERT and OEHLER (1971) in siskins, which responded more strongly to their contact calls if certain frequency components of the call were filtered out than when they were presented with the full natural calls. In synthetic calls of *Callimico*, the shorter the duration or wider the frequency range they had, the more effectively were they responded to. The releasing value of the stimuli with each of these acoustic characteristics could be substituted for one another and the call that combined both cues was the most effective (Experiment 7). This has been called stimulus summation by SEITZ (1941).

Although *Cebuella* can vocalize alarm calls similar to this sound (POLA & SNOWDON, 1975), the acoustic structure of the alarm calls of their sympatric species, *S. fuscicollis*, is very different from that of the supernormal releaser. The *Sudden Call* described by MOODY and MENZEL (1976), which was followed subsequently by mobbing responses with the emission of

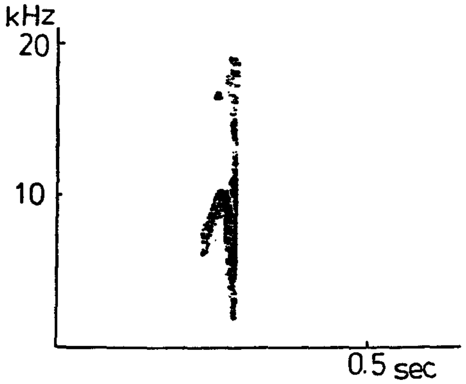

Fig. 9. Sonograph of a synthesized sound functioning as a supernormal releaser.

a *Packaged Trill*, consisted of a tonal segment showing an ambiguous onset and ending and a continuous change in energy distribution which was gradual as possible. Functionally, alarm calls must enable the presumptive signal receiver to establish the location of the sound source in space immediately in order to take refuge from the possible danger. Although vocalizations for a longer duration would be one means of fulfilling the desired function, they are also likely to reveal to predators the position of the calling animal. In order to compromise on this disadvantage, an absence of any discontinuity in phase and intensity differences is found in those calls emitted continuously, which make binaural comparisons of the time of arrival difficult.

On the other hand, another compromising strategy is considered to be to vocalize easily localizable calls, incorporating a time lapse to be localized in space as little as possible, which is adopted by the supernormal releaser, in which the frequency modulation with a sharp onset and sharp ending permits a comparison of phase differences at the presumptive receiver over the short duration (EISENBERG, 1978). Compared with this strategy, the former one is thought to be adapted for aerial predators since such calls tend to sound rather imperceptible to them, whereas even the least time lapse is not likely to prevent them from localizing a sound source once they have perceived the sound.

Since *S. fuscicollis* inhabits higher strata in the canopy than *Callimico* and *Cebuella* (MASATAKA, 1981a; KINZEY, ROSENBERGER & RAMIREZ, 1975), the hunting pressure by flying birds is thought to be higher for the former than for the latter, which are instead likely to be hunted by mammalian predators, from which to escape, the shorter duration is the most effective characteristics of the alarm calls for the animals. Species differences in alarm calls may result from environmental influences which have forced the signal to take on a specific form in accordance with the physical situation in which it must be performed.

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