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MOTIVATIONAL VARIATIONS IN THE SINGING BEHAVIOR OF A SIAMANG PAIR (HYLOBATES SYNDACTYLUS)

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ABSTRACT: Several experiments have shown that engaging in territorial singing is an appetitive and reinforcing activity in gibbons. The present study examined whether the strength of this behavior would vary with changes in motivational conditions in the same manner as does the strength of the consummatory behavior associated with other reinforcers. The subjects were a fully accommodated pair of siamangs. Following baseline. $(\bar{X} \text{ duration} = 34.33 \text{ min})$, song-bout durations were observed under low motivation ($\bar{X} = 20.33 \text{ min}$), then high motivation ($\bar{X} = 36.16 \text{ min}$), then low ($\bar{X} = 22.67 \text{ min}$), then high $(\bar{X} = 32.50 \text{ min})$. Six song bouts were observed under each condition. In the high motivation condition, 5-6 days intervened between song bouts; in the low motivation condition, song bouts were separated by 2 days. Each change in motivation was accompanied by a significant change in song-bout duration (Mann-Whitney U tests; p's < .01). Findings are related to a general conception of species-typical behavior as a source of reinforcement.

The gibbons are small arboreal apes inhabiting the climax forests of Southeast Asia. All species of gibbons live in monogamous family groups on relatively fixed territories, and all perform elaborate, species-specific vocal displays, or songs (Carpenter, 1940; Chivers, 1972, 1974, 1976; Ellefson, 1968, 1974; Haimoff, 1981, 1984; Gittens, 1978; Marshall & Marshall, 1976; Marshall & Sugardjito, 1986; Tenaza, 1976; Whitten, 1982). Gibbon songs are assumed to function as a means of advertising territorial possession and of development and maintenance of cohesion within the family group (Carpenter, 1940; Haimoff, 1984; Marshall & Marshall, 1976).

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Experiments with three species of gibbons (*Hylobates syndactylus*, *Hylobates agilis*, and *Hylobates muelleri*) suggest that their territorial singing, particularly within the natural context of accompanying vocal responses of family members and neighbors, is an appetitive behavior in these animals. In each of the experiments (Haraway, Maples, & Tolson, 1981, 1988; Maples & Haraway, 1982), the duration of the subject's vocal responding increased when tape-recorded accompaniment was made contingent on subject-vocalizations, decreased when this contingency was revoked, and increased again when the contingency was reestablished. In each case, the extinction effect occurred only following a period of persistent high strength in the subject's vocal response, that is, only following resistance to extinction. In the last of these three experiments, it was found that playback of recorded vocalization also served to reinforce locomotor and station-keeping responses, in addition to the subject's *vocal* responding.

What these experiments show, specifically, is that appropriate playback stimulation serves as a positive reinforcer of responses that produce it, particularly if these are singing responses. One interpretation of these findings is that singing behavior in gibbons has reinforcement value, generally, and that its reinforcement value is *enhanced* by the occurrence of appropriate accompanying vocalizations.

Given these demonstrations of the reinforcement value of singing in gibbons, it is reasonable to ask whether the strength of such singing behavior varies with motivational conditions in the same manner as does the strength of consummatory behaviors that are associated with other sources of reinforcement. For example, we know that food deprivation increases the amount of eating behavior which occurs once food becomes available (e.g., Dufort & Wright, 1962; Horenstein, 1951); and, of course, a similar relationship exists between water deprivation and drinking behavior (Adolf, 1950; Siegel, 1947; Stellar & Hill, 1952). The present experiment, then, related the strength of the subjects' singing response to a systematic variation in the length of the interval between successive song bouts. The authors wished, specifically, to determine whether the subjects would perform longer song bouts under conditions when their song bouts were infrequently performed than under conditions when their song bouts were frequently performed.

The subjects of this experiment were a pair of siamang gibbons who, under normal circumstances, were always housed together. There was no readily available way to impose a deprivation on the singing behavior of these subjects, since they could effectively engage in such behavior almost at any time. However, because the male member of this pair would initiate a song bout almost immediately in response to presentation of recorded siamang vocalization; it was possible to arrange for the subjects to vocalize *more frequently* than at their normal interval of song bout initiation. In this way, it was possible to generate a comparison of the relative strength of the subjects' singing behavior under contrasting motivational conditions.

METHOD

Subjects

The subjects, again, were a mated pair of siamang gibbons. The male, approximately 19 years of age, was wild-caught at an early age, and had lived at the Louisiana Purchase Gardens and Zoo in Monroe, Louisiana for the past 18 years. His previous mate had died, and he had lived alone for a period of 12 years. The female, 7½ years of age, had lived with her own parental group at the National Zoological Park in Washington, D.C. until her arrival at Louisiana Purchase Gardens and Zoo. The pair had been living together for approximately 18 months at the beginning of the experiment and were housed indoors in adjoining and connecting cages, each measuring 10 m x 4 m x 4 m high. During the period of this experiment, the animals remained in the same cage together at almost all times. Coordinated performance of the species great call had been achieved by this pair by approximately 12 weeks following their introduction to one another (Maples, Haraway, & Hutto, 1989). Copulation was first observed in the pair at approximately 10 months after their introduction.

PROCEDURE

On each experimental day, experimenters were present at the zoo from approximately 8:30 a.m. to 11:00 a.m. to observe the subjects' singing behavior. All song bouts that occurred during this period of the morning were recorded on audio tape, and the duration of each song bout was determined. In addition, zookeepers monitored the occurrence of singing behavior by the subjects at other times of the day. Zookeeper's reports were considered in determining the timing of procedural events during the controlled (nonbaseline) portions of the experiment, although these bouts, which were relatively few in number, were not audio-recorded and were not timed. The data for this study consist of 27 song bouts recorded between January, 1987, and October, 1987.

The experiment began with the recording of three song bouts under baseline conditions. Experimenters simply appeared at the zoo every morning and recorded any song bouts that occurred.

Next, the duration of the subjects' song bout was observed under a condition of relatively low motivation. For the purpose of this experi-

ment, degree of motivation was defined by the number of days that had passed since the subjects' most recent song bout. Extensive observation of these subjects had shown that their usual rate of song initiation was one song bout approximately every 5 days. During the low motivation condition, a song bout was stimulated by our recorded vocalization every other day until six song bouts had been recorded. We may note, here, that while the alternate-day frequency of song initiation was a relatively high rate of occurrence for this particular pair of siamangs, it is not a very high rate of song occurrence for this species, generally considered (Chivers, 1976). The male typically responded to recorded stimulation almost immediately, and the stimulation was terminated following the male's second vocal phrase.

After six song bouts were observed under the low motivation condition, song bout duration was observed under a condition of relatively high motivation. During this phase of the experiment, song bouts were stimulated only if six days had passed since the previous song bout. In addition, any song bouts which occurred on the fifth day following the previous song bout also were counted for data analysis. Two such song bouts occurred during the experiment. If a song bout occurred, or was reported by zookeepers, closer in time than 5 days from

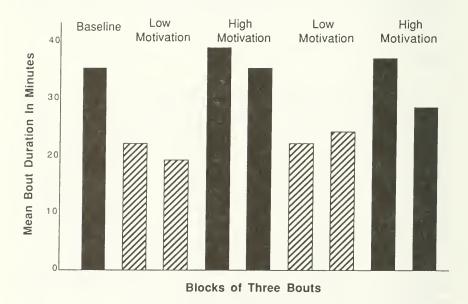


FIGURE 1

Mean song-bout duration under the various motivational conditions.

the preceding song bout, that song bout was excluded from consideration, and the experimenters waited 6 more days before stimulating the next song bout. During the high motivation condition, then, the interval between successive song bouts was approximately three times what it was during the low motivation condition. Finally, six additional song bouts were observed under the low motivation condition, and then six more bouts were observed under the high motivation condition.

RESULTS

It can be seen in figure 1 that song bout duration varied systematically with the variations in motivational conditions employed in this study. Mean song-bout duration changed from 34.33 min during baseline to 20.33 min under low motivation, then to 36.16 min during high motivation, then to 22.67 min during low motivation, and finally to 32.50 min during high motivation. The overall \bar{X} duration under low motivation was 21.50 min, and under the combined conditions of baseline and high motivation, \bar{X} was 34.33.

Mann-Whitney U-Tests were used to compare song-bout durations observed before and after each of these changes in motivational condition. Each change was accompanied by a significant variation in song bout duration; U-values ranged from 0 to 3, and all probabilities were less than .01, two-tailed.

The authors wish to emphasize that formal inferences from these statistical comparisons are limited to the behavior of these two subjects. Within the parameters of the present experiment, however, we may conclude that these subjects perform longer song bouts under conditions of high motivation than under conditions of low motivation.

DISCUSSION

The findings of the present study demonstrate that singing behavior in a pair of siamang gibbons varies systematically with motivational conditions in the same manner as do consummatory responses associated with such traditional reinforcers as food and water. Earlier studies (Haraway, et al., 1981, 1988; Maples & Haraway, 1982) have demonstrated the reinforcing value of stimuli (tape-recorded playbacks of gibbon songs) which provide a context for the occurrence of gibbon song. Taken together, these studies provide evidence of a functional similarity between singing behavior in gibbons and traditional and archetypical sources of appetitive reinforcement. Selective benefits potentially gained by the evolutional investment of gibbon song with reinforcement value were discussed in an earlier paper (Haraway, et al., 1988). Glickman and Schiff (1967) proposed that species-typical behaviors, generally, constitute an important source of reinforcement. They suggested that the physiological substrates which underlie reinforcement functions may have evolved originally as means of facilitating the appropriate occurrence of species-typical behaviors. A survey of the literature on reinforcement in animal behavior reveals a surprisingly large number of research findings which may be interpreted as support for Glickman and Schiff's hypothesis.

A number of studies have achieved formal demonstration of reinforcement effects by using what may be regarded as species-typical behaviors in the role of reinforcers. These behaviors have included running behavior in rats and mice (Hill, 1956; Kagan & Berkun, 1954; Kavanau, 1966), sand-digging in mice (King & Weisman, 1964), social play in juvenile rats (Crowder & Hutto, 1988; Humphreys & Einon, 1981; Panksepp, Siviy, & Normansell, 1984), and exploratory behavior in a variety of species (Butler, 1953; Butler & Harlow, 1954; Butler & Wollpy, 1963; Chapman & Levy, 1957; Montgomery, 1954; Montgomery & Segall, 1955; Mote & Finger, 1942; Nissen, 1930; Schneider & Gross, 1965). Obviously, the great number of studies illustrating the reinforcement value of eating food, drinking water, and engaging in sexual behavior could be readily interpreted in the same manner.

In addition, a number of studies have demonstrated the reinforcing effectiveness of stimuli which establish an appropriate context for the occurrence of species-typical behaviors. Stimuli that have been shown effective in this fashion include an "imprinted" object, with chicks (Hoffman, Searle, Toffey, & Kozma, 1966); a rival male, with nesting sticklebacks (Sevenster, 1968), Siamese fighting fish (Melvin, 1985; Thompson, 1963), and domestic roosters (Thompson, 1964); and the song of another male, with chaffinches (Stevenson, 1967). Of course, the previously mentioned demonstrations of the reinforcement value of recorded gibbon song (Haraway, et al., 1981, 1988; Maples & Haraway, 1982) also fit into this category.

As we have seen, much evidence exists to support the generality that many species-typical behaviors are reinforcing in themselves, with the capability to serve as activity reinforcers for other behaviors which enable their occurrence. Much empirical work remains to be done in determining the proper parameters of this generality. It may be that few, if any, simple reflexes are reinforcing in this manner; and many speciestypical behaviors involving defense from predators and from noxious stimuli may be sources of negative rather than positive reinforcement (Glickman & Schiff, 1967; Siminov, 1983). Whatever appropriate parameters are eventually established, species-typical behaviors appear to be a potent source of reinforcement in animals—and a source that often has been ignored.

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