THE PATTERN OF VOCAL SIGNALS AND THE INFORMATION THEY CONVEY

by

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It is generally accepted in studies of vocalizations that vocal signals convey information on the motivation of the signaller (DARWIN, 1872; ROWELL, 1962; ROWELL & HINDE, 1962; SMITH, 1963). Searching for the mechanisms which modifies the vocal signal to represent the motivation GREEN (1975) suggested that "if the configuration and dynamics of the (vocal) mechanism have strict neurophysiological determinations then vocalizations are direct representations of the motivational status of the vocalizing animal". This would be the case "if the same neuro-anatomical structures functioning in emotional behavior... yield in general co-varying changes in the vocal activity depending on arousal". However, neither GREEN nor others (*e.g.* LIEBERMAN, 1967) explained why the nerves which produce the emotions should co-function with the nerves which produce the vocal signal. ROWELL (1962) suggested that the variation in the signal which conveys the information about the exact motivation of the signaller is produced by the movements of the whole body and not only by the movements of the vocal apparatus. SCHERER (1979) reviewed the evidence on the correlation between psychological stress and vocal signals in man. He concluded that stress affects vocal signals in a specific way. He suggested that because the psychological changes and the physiological changes which accompany stress must be adaptive, even the tension in body muscles under stress and the changes in respiration are adaptive. The effect of these physiological changes on the vocal signal necessarily display the state of stress of the signaller.

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"Respiration is likely to affect the subglottal pressure in phonation where general muscle tone will affect the operation of the extra and intralaryngeal mechanisms involved in phonation as well as the characteristics of the vocal tract resonance walls and the articulatory mechanisms". With this suggestion SCHERER (in press) pointed to the evolutionary reasons which link the information encoded in a particular vocal signal with a specific internal adaptive state so as to provide the specific signal with evolutionary stability. This suggestion implies that any attempt by a signaller to conceal stress by changing its vocalization would necessitate a deviation from adaptive changes in its body muscles, its respiration pattern etc.

In the following I shall further develop the idea that vocal signals are analogues of the postures and movements of the signaller at the time the signal is produced. I shall cite some observations on the intimate relationship between posture, movements and vocalizations in man and other animals. I shall analyse the logic of threat and fright strategies to deduce the factors which select for movement signals and consequently for vocal signals which communicate threat and fright. I shall also suggest why certain motivations are displayed by particular signal patterns and not others.

THE EFFECTS OF BODY POSTURES AND MOVEMENTS ON THE VOCAL SIGNAL

The effects of body posture and movements (P.M.) on vocal signals are well known to singers and actors. Singers invest much time and effort in learning correct postures and how to move in order to produce particular vocal qualities. It is generally known among singers that even small changes in P.M. affect the quality of their song. Actors on stage are trained to talk in a way appropriate to a particular motivation by imitating the P.M. of the person possessed with that motivation (N. NATIV, pers. comm.). Although I do not know of scientific publications which provide evidence for the intimate correlation between the P.M. of the body in man and tonal quality of his voice I believe that the experience of the audience which discriminate between good and bad actors and the attempt of actors to produce a particular quality to their voice by a particular P.M. is good evidence for the connection between the two.

Some observations suggest that such a relationship between vocal quality and P.M. exists also in animals. LORENZ (1966) observed that a jackdaw which imitated various vocalizations was performing at the same

time the movements which usually accompany motivations advertised by these vocalizations. ROWELL (1962) observed that she could follow the progress of an encounter by listening to the vocalizations. She did not have to see what the monkeys were doing at the time they vocalized to know what they were doing.

An interesting observation on the relationship between P.M. and vocalization has been related to me by L. HERMAN, D. RICHARD and J. WOLZ who study the vocalization of the bottlenosed dolphins (*Tursiops truncatus*). They have observed that: "the aerial squawks, the dolphins produced on command, were always accompanied by head shaking and what appeared to be a tenseness of the body". These bodily postures and movements were typical of agonistic behaviors. In other contexts the squawk is heard during chases between animals and may have agonistic components" (pers. comm.). I suggest that the dolphins were only able to produce the desired quality of the "squawk" while performing the aerial display of head shaking.

The connection between P.M. and vocalizations could also be derived from purely logical considerations. Consider the body of the signaller as a musical wind instrument. The quality of the notes of such instruments is determined by the shape and material of the instrument and the pressures applied to the air passing through it. Changes in the shape of the instrument or pressures applied to it should produce a change in the quality of the note. Hence an experienced listener may be able to determine from the sound pattern, the shape of the instrument and which pressures were applied to it. The vocal signal may thus contain information concerning the P.M. of the signaller. If certain P.M.s are always associated with certain motivations then the vocal signal may display the motivation.

THE RELATION BETWEEN P.M., MOTIVATION AND THE VOCAL SIGNAL

The motivation of an animal may be defined as the likelihood that the animal would perform a certain behavior. It is reasonable to expect that certain P.M.s are better starting points than other, for performing certain activities. Hence, the observer may recognize the motivation of the animal by observing its P.M. An animal attempting to conceal its motivation by changing its P.M. would not be able to behave as efficiently as it would have behaved without concealing its motivation. The animals might also advertise their motivation by exaggerating the P.M.

used as a starting point for the behavior under a particular motivation. Displays described as "intention movements" by DAANJE (1951) are in fact examples of such P.M. displays. If a vocal signal is given at a time the animal behaves in a way which displays a certain motivation, the quality of that vocal signal should disclose the activity of the signaller and consequently its motivation. To the experienced listener the voice may be a good indicator of the P.M. (ROWELL, 1962). The reliability of the vocal signal as an indicator of body movement can easily be appreciated in one's own body. It is impossible to relax in an arm chair and imitate a startled voice, or to get up from the chair while imitating a relaxed sigh. In the case of actors on stage the actor may imitate a vocal signal of a motivation it does not possess, but in order to do so convincingly he must imitate the P.M. which usually accompanies the vocal signal which he intends to produce. Hence also in this case the voice is an analogue to the P.M. of the body. Later I shall discuss the circumstances which allow actors to imitate on stage but select against such cheating in real life.

THE STRATEGY OF THREAT AND THE USE OF THREAT VOCAL SIGNALS

MORTON (1977) pointed at the convergence which exists among the pattern of threat and fright calls of many unrelated species. Threat calls are usually low in frequency and harsh. They stand in contrast to fright and appeasement calls which are higher in frequency and of tonal quality. He suggested that the adaptive significance of these patterns are consequences of the correlation which usually exists between the size of the signaller and the frequency of its vocalization. A low frequency note reminds the listener that it faces a big rival while a high frequency note displays that a small individual, rather than a big dangerous one, is the rival and consequently high notes reduce aggression. DAVIES & HALLIDAY (1978) also found a correlation between the size of a threatening toad and the pitch of its threat. They also suggested that the pitch of the threat call displays the potential of the threatening toad to win the conflict by displaying its size.

Although there is usually a correlation between the size of the threatening individual and the pitch of its threat, it is obvious that the same individual may vary considerably the pitch of its vocal threat. Hence, why should animals not always use the lowest threat signal they can possibly produce and why do animals not evolve a vocal apparatus which produce even lower pitched signals? DAWKINS & KREBS (1978) have already

pointed out this problem. "What is to stop an individual... from bluffing by means of a high intensity threat". "Our general point is that such signals are actually something of a puzzle. It has usually been assumed that a signaller benefits by conveying its exact motivational state to others (SMITH, 1977) but the nature of the benefit is not obvious".

In the following I shall discuss the information which I believe is conveyed by the threat and fright vocal signals. I shall use for this discussion some principles I have developed to explain the evolution of signals in general (ZAHAVI, 1981).

Conflicts are often resolved without fighting, one party winning the dispute and the other losing it by the exchange of threats alone (MAYNARD-SMITH & PARKER, 1976). If the behavior of both parties has been programmed to fit their individual interests, then it is reasonable to believe that the winning party has been able to signal to the other, in a reliable way, that the signaller is likely to win the fight. If both parties agree as to which of them is likely to win, then it is in the interests of the loser to withdraw from a lost conflict without fighting. How could a threat signal convey in a reliable way the information that the threatening party is likely to win?

During a confrontation a weak individual, or one which is not ready to pay the cost of a surprise attack, should always be on the alert ready to fight back or to flee. A strong individual or one which is more ready to pay the cost of a fight may be more relaxed. Hence this difference could be used to assess the differences in the readiness of the signallers to involve themselves in the fight, *i.e.* their motivation. A display of relaxation during an encounter, which provides the rival with the option to attack first, is a display of confidence which is reliable, because attacks by rivals select against weak individuals which relax in order to deceive their opponents about their confidence.

My experience with human vocalizations, during aggressive encounters, suggests that the same individual threatens with a relaxed vocal signal of a low pitch when confronting an individual which is inferior to him in his fighting potential and raises the pitch of his voice when confronting a superior fighter. An inferior fighter is more likely to lose a fight if it relaxes in the face of its opponent. Hence cheating by the use of a relaxed vocal signal demands a high cost (ZAHAVI, 1975) from the signaller. Unlike in real life, an actor performing on stage does not face an immediate danger from its "rival". Hence he can relax his body muscles to act as an aggressive individual confident in his potential to win the conflict. I suggest that DAVIES & HALLIDAY (1978) found the correla-

tion between the size of the threatening toad and the pitch of its voice because it was the bigger toad of the two rivals which threatened. It will be interesting to observe if the pitch of the threat or any other of its parameters changes when facing rivals of different sizes.

Obviously displaying the degree of relaxation is only one way to display threat. Another may be in displaying the strength of the signaller as is the case with the red deer. CLUTTON-BROCK & ALBON (1978) have studied the relationship between the roars of the red deer and its fighting abilities. Stags which invest more energy in roars, emitting frequent and intense roars, are better in intimidating and fighting than stags investing less in roaring. Roaring clearly exhausted the stags. They concluded that since it is likely that the same muscles are used in roaring as in fighting, a stag which can roar better is a better fighter. I consider their findings one of the best cases which support the handicap principle (ZAHAVI, 1975, 1977a). Unfortunately, they do not think so. They believe that signals would evolve to incur the least cost to the signaller, while I believe that it is the cost of the signal which selects for its reliability. The larger the cost, the more reliable the signal. If stags would have whistled while threatening, they would not have been exhausted during a confrontation and the vocal signal would not be correlated to the fighting abilities. It is perhaps important to clarify that the cost of the signal (reduction in fitness) is not easy to observe in honest stags, because they gain from their investment in advertising. However, the cost should be larger than the gain in those individuals who try to cheat. The same investment in energy by different individuals is not necessarily involved with the same cost in fitness (ZAHAVI, 1977b).

THE OPTIMAL PATTERN OF A SIGNAL TO DELIVER A CERTAIN MESSAGE

There are major differences between the strategies of threat and fright, although both strategies aim to reduce fighting. In threat the signaller tries to convince the rival that it is most likely to lose the fight. In signalling fright it tries to convince the rival that the signaller is already aware of the danger and is ready to counter it or flee. The degree of relaxation in the muscles which have to be used in fighting may be used to indicate threat. The degree of tension in the muscles used for quick motion may be used to indicate fright. I suggest that under most circumstances it is not a problem for a confronting rival to find out whether their rivals are threatening or are actually frightened. Whatever they do, fright or con-

fidance would be observed anyhow in the quality of their voice. However, when they wish to convince their rivals about their potential to gain in the conflict they must display how good they are in the use of the strategy they have decided to follow. Threat may require a signal which will reveal differences in relaxation, while fright may require an abrupt short signal to reveal differences in response time and the intensity of a quick reaction. They should choose a signal which would display best the smallest difference in the potential of individuals to succeed in following a particular strategy.

A frightened individual which uses a vocal signal of a threat pattern would be losing in two ways. It would necessarily display that it is frightened by the tension of its voice, but because it did not use a signal adapted to display differences in motion it would not be able to convince its rival that it is good at fleeing or counteracting in a fight. Hence if it is really frightened it had better either stay silent or vocalize in the pattern of a fright call.

SUMMARY

1. The vocal signal is an indicator of the posture and movement (P.M.) of the signaller at the time of vocalization, hence it reveals, by an additional modality, information about the P.M. of the signaller.

2. The vocal signal is a reliable indicator of the motivation of the signaller because cheating would incur the cost of changing the P.M. away from the optimal P.M. for the real motivation.

3. Certain vocal patterns discriminate better than others small differences in the motivation of individuals.

4. The vocal signal which conveys a certain motivation is dependent on a) the strategy used to solve a particular conflict; b) the kind of reliable information which may resolve the conflict; c) the P.M. which conveys best such information; d) the vocal pattern which enables the listener to distinguish between signallers which differ slightly in their motivation.

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ZUSAMMENFASSUNG

1. Lautsignale weisen auf Stellung und Bewegung (P.M.) des Signalisierenden im Moment der Lautgebung hin. Daher geben sie zusätzliche Information über die P. M. des Signalisierenden.

2. Das Lautsignal ist ein zuverlässiger Anzeiger für die Motivierung des Signalisierenden. Wenn der Signalisierende betrügen würde, müsste er die Kosten für die Änderung des optimalen P.M. der wirklichen Motivation tragen.

3. Bestimmte Lausmuster geben besser als andere kleine Unterschiede in der Motivation von Individuen zu erkennen.

4. Das Lautsignal, das eine bestimmte Motivation übermittelt, hängt ab von: a) der Strategie, die benutzt wird um einen bestimmten Konflikt zu lösen; b) der Art der zuverlässigen Information die den Konflikt lösen könnte; c) der P.M., die am besten solche Informtion übermittelt; d) dem Lautmuster, welches es dem Hörer ermöglicht, zwischen Signalisierenden zu unterscheiden, die in ihrer Motivation nur wenig verschieden sind.