RITUALIZATION AND THE EVOLUTION OF MOVEMENT SIGNALS

by

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Huxley (1914) termed as ritualization the evolution of movements which lost their original function to serve as signals. Lorenz (1966) pointed out that the ritualized display which functions as a signal in communication is more stereotyped than the original movement from which it has been derived. The evolution of signals has been considered to result from the common interest of the communicating parties to communicate as clearly as possible. The ritualization process has been considered as the process by which the clarity of the signal is increased. Morris (1957) believed that a stereotyped signal provides less information concerning the motivation of the communicating parties. "The reduction on the amount of information provided by the signal about the exact state of the signaller, that is involved with this stereotyping, is apparently more than compensated for by the elimination of signal ambiguity. A signal that is constant in form cannot be mistaken". Morris suggested that in order to compensate for the loss of information, signals evolve variance in their duration, intensity or repetetivness.

Considering the evolution of signals in general (Zahavi, 1977) it was suggested that it is reasonable to assume that signals evolve if they increase the transfer of reliable information, concerning differential quality of individuals or differences in motivation. Otherwise, signals may do more harm than good to individuals who respond to them. While Morris was faced with the problem of reconciling the demand for clarity in signals with the need for variation in order to maximize information transfer, I was faced with the problem of reconciling the demand for signals to pass on more reliable information differences (Zahavi, 1975), with the observations that signals tend to evolve stereotype. In the following I propose to resolve the

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conflict, suggesting that signals evolve out of competition rather as a result of the importance to communicate clearly.

Is there really a loss of information in the process of ritualization of signals? To the best of my knowledge, besides the intuitive feeling that there is a loss of information involved in the stereotyping of signals there has not been any direct evidence to support it. An alternative possibility is that much of the variance of a movement, before it has evolved to be a signal, did not add to the information sought by its observer. Obviously a ritualized movement is less variable than a non-ritualized movement, hence it seems to possess a smaller potential to transfer information. Nevertheless I suggest that to the experienced observer a ritualized movement may increase the information relevant to the message encoded in the signal by increasing the reliability of the information. I further suggest that the apparent clear ritualized signal is a byproduct of the selection for reliable information.

My suggestion may be illustrated by the following. It is possible for the observer to people walking in the street to predict from the way they move which of them can hardly ru nat all and which of them are good runners. But in order to classify people exactly according to their quality as runners, it is necessary that they display their ability to run in a standardized way. Such a display is both in the interests of the runner claiming his or her running ability and that of the observer who is interested in determining the ability proclaimed. Unless we are aware that the split second difference at the end of the run is the important variance for which the whole display has evolved, we may be misled by the long synchronized and ritualized run which forms the main part of the display. Although the overall variance in a running competition is smaller than the variance in ordinary movements of people, the meaningful variance which separates clearly the ability of one runner from another is more reliable in a standard competition. The performance of the runner has not come about as a consequence of his or her motivation to display clearly, that he or she is a runner, but as a consequence of the drive to display his or her personal claim to be the best runner.

SIMPSON (1968) studied the threat display of the Siamese fighting fish. Most of the variation in the threat display concerning the likelihood of the individual to win a conflict is displayed at the end of the display when the loser displays less erection of its gill covers. Unless the observer looked for the difference in that part of the display he might have concluded that the rivals were equal in displaying threat. It is not impossible that important information in displays of other animals, in which individuals seem to display in a standard way with no meaningful variance, may be found to display a variance after some more careful study. The untrained observer is often

impressed by the common pattern in the display rather than by a subtle variance which the common pattern is of help to expose.

The theory that signals always display a difference between individuals suggested a search for differences in signals which seem to be given alike by different individuals like species specific signals. Sometimes the differences may exist in a modality unsuspected by the observer. Species specific colour patterns may help to display slight differences in the morphology of individuals (Zahavi, 1978). Standard movement signals may clearly display differences in the dimensions or morphology of certain body parts. The movement may have been selected because of its importance to signal the difference in the structure. Individuals may respond differentially to the threat movement of various individuals because they perceive differences in their dimensions. It is the receiver of the signal who selects the signals according to his best interests. By paying more attention to signals which are displayed according to a standard, the receiver of the signal selects for reliable information. This selection process for reliable information results in the ritualization of signals.

Reliable information is sought under all social circumstances. Even the most complementary social pairs, such as sexual pairs (WILLIAMS, 1966; ZAHAVI, 1975) or a parent and its offspring (TRIVERS, 1974) have a measure of rivalry between their members. Some guarantee of reliability should be an essential component of every signal if signals are to effect the behaviour of a rival (ZAHAVI, 1977).

The present theory which considers reliability as the most important demand on signals suggests a logical connection between the signal and its message content. In order to be reliable, a signal must be designed in a way which will not allow individuals who differ in quality or motivation to display equally well. In that respect a signal may not be just any convention. Certain signals should be superior to others in passing certain information reliably. The following illustrates that point by an example from movement signals. Assume that threat is to be displayed by walking. In order to be effective a threat signal should carry reliable information about the motivation of the threatening individual to fight. Walking away from the opponent is equally possible for an animal ready to fight and one which is not. Hence it is not a good threat signal. On the other hand walking toward the opponent is less costly for an individual ready to fight, not frightened of a clash, while it may be detrimental to an individual not ready to fight by decreasing its chances to escape its rival if a real clash occurs. Hence of all possible threat signals by walking, walking toward the rival is the best threat display.

Like Morris (1957) I suggest that ritualized signals may display differ-

ences in motivation by a variance in their intensity, duration, amplitude, etc. But even when the signal seems to consist of only one bit of a stereotyped movement there is reason to believe that it may still be the best movement to display a certain variation. The stereotypy of the movement while misleading the untrained observer, most probably should provide information to the experienced observer trained to look for the meaningful variance. Unlike Morris who suggested that signals evolve as a byproduct of two opposing selecting factors, one for clarity and the other to display motivation, I suggest that selection for reliability alone may result in ritualized signals. This theory does not necessarily exclude the other. But the theory presented here has the extra advantage of solving the problem of reliability.

SUMMARY

It is suggested that the competition among individuals to display their advantage over others and the interest of individuals to display their motivation in a reliable way have been responsible for the evolution of ritualized signals. Small differences between displays can only be perceived against a standard mode of display. Experience is often needed to determine the nature of the variance which is displayed. It is suggested that the stereotyped ritualized species specific movements have evolved as a byproduct of the competition among individuals to display differences and not because of the advantage of displaying specific differences.

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ZUSAMMENFASSUNG

Er wird vorgeschlagen, dass der Wettbewerb zwischen Individuen einer Art, ihre Vorzüge gegenüber anderen hervorzuheben, sowie der Vorteil für diese Individuen, wenn sie ihre Motivierung auf zuverlässige Weise darzustellen wissen, für die Entwicklung ritualisierter Signale verantwortlich sind.

Geringe Unterschiede im Imponierverhalten können nur im Vergleich mit standardisierten Imponierverhalten wahrgenommen werden. Ohne Erfahrung ist die Qualität der Verhaltensunterschiede oft nicht festzustellen.

Ausserdem wird angenommen, dass sich stereotype artspezifische Bewegungen als Nebenergebnis des Wettbewerbs zwischen Individuen entwickelt haben, die ihre Unterscheide zur Schau tragen, und nicht als Folge des möglichen Vorteiles, der ihnen aus diesen Unterschieden erwachsen könnte.