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The fallacy of conventional signalling

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SUMMARY

All signals, with the exception of very special ones such as human verbal communication, evolve to be reliable. Communication systems that have been considered as systems of conventional signalling are reinterpreted as reliable systems by indicating the investment which increases their reliability. Examples are given from decorative patterns and set specific signals, such as status signals. The general importance of reliability is further discussed for cases such as the chemical signals within the multicellular organism, in which there is no conflict between the communicating parties. The reliability of signals which display symmetry, as is measured by the 'fluctuating asymmetry', is interpreted as a consequence of the investment required of signals that coordinate development.

1. RELIABLE SIGNALS AND CONVENTIONAL SIGNALS

Reliability is crucial for the functioning of signals, as there is an inherent potential for conflict in all social interactions and the communicating parties may use the signals to cheat. Trivers (1972) indicated the conflict between mates and the conflict between parents and offspring (Trivers 1974). The conditions for conflict among groups of collaborators were described by Zahavi (1976, 1990) and Emlen (1984). It is difficult to imagine any social interaction in which there is no potential for conflict at some time or other. Hence, receivers of signals act in their own best interests if they check the reliability of information encoded in all signals they receive, and do not respond to signals which do not carry a component of reliability. The idea that investment in signals increases their reliability, the 'handicap principle' (Zahavi 1975, 1987), has received recent support from models (Grafen 1990*a,b*), though earlier models have rejected it (Maynard Smith 1976; Davies & O'donald 1976; Kirkpatrick 1986). The larger the investment, the more reliable the signal, although obviously the investment in a signal cannot be greater than the potential gain from using it properly. A signal is reliable when the investment required for its use is greater than the potential gain a cheater would make from using it improperly. The investment should be acceptable to an honest signaller and prohibitive to a cheater.

The handicap principle creates a logical connection between the detailed pattern of a signal and the message encoded in it. It suggests that for every message there is an optimal signal, which best amplifies the asymmetry between an honest signaller and a cheater. For example, wasting money is a reliable signal for wealth because a cheater, a poor individual claiming to be rich, does not have money to throw

away; the message of strength may be displayed reliably by bearing heavy loads; and confidence may be displayed by providing an advantage to a rival.

The special mechanism by which signals evolve to be reliable was described in my theory of signal selection. The theory suggests (Zahavi 1981, 1987) that signals are selected by a different evolutionary mechanism than all other characters, for which an investment is an unavoidable evil. For signals, an investment is necessary, because it ensures the reliability of the message encoded in the signal. The larger the investment the more reliable is the message. The theory of signal selection, like Darwin's theory of sexual selection (1874), deals with the dichotomy in the selection processes: both theories suggest that there are two distinct and opposing selection processes in evolution. The theory of signal selection separates the two processes cleanly along a line which divides all signals from non-signals. Mate choice and rival deterrence belong with all other signals, whoever their receivers may be. On the other hand, physical fighting and other adaptations for reproduction that Darwin encompassed in the set of sexually selected characters are not a part of signal selection (Zahavi 1991).

(a) *What about conventional signals?*

Human verbal language is a good example of conventional signalling. Very different signals (words) are used to convey the same message in different languages and often even in the same language (verbal synonyms), and similar sounds like 'see' and 'sea', may have completely different meanings. The concept of conventional signals suggests that signals are selected to be specific and efficient in order to be perceived clearly. In conventional signals no evolutionary mechanism relates the pattern of the signal to their messages. Any signal pattern, which is efficiently

clear and is understood by the communicating parties, may serve as a conventional signal. There is nothing in conventional signals that prevents cheating, except for the notion that these signals serve the common interest of the communicating parties and may not function if cheating prevails (but see Dawkins (this symposium) for an alternative view). This is an argument based on group selection. Like its parent concept, group selection, conventional signalling is a logical model. However, it is a very unlikely one, because of its susceptibility to social parasites, that is, cheaters (Maynard Smith 1976).

Because conventional signalling is still a logical possibility, the only way to demonstrate its absence in biological communication systems is to show that the most likely contenders to conventional signals are better interpreted as reliable signals. I shall attempt to demonstrate this by discussing the following: (i) set-specific signals; (ii) signals with a very low cost; and (iii) signals within the multicellular organism.

2. SET-SPECIFIC SIGNALS

In the following I suggest how so-called 'set-specific' decorations, which have been interpreted as conventional signals for identifying the species, age or gender of an individual, may serve as standard patterns which are of help to the receiver in assessing the quality of the signaller.

Very simple decorations such as a line along the body of a fish may function as a reliable advertisement for its length (Zahavi 1979). I suggest that the information provided by the decorative line is not the presence or absence of the specific decoration but the line's actual length, which differs for each individual signaller. Length is an important component of the size of the fish, and thus a line can be used to deter rivals or attract mates. The message thus serves competitive interests rather than functioning as a marker common to the species. Barlow (1972) pointed out the correlation of decorative patterns to body shape in fishes: fishes with long bodies are usually decorated with horizontal lines, whereas fishes with tall bodies are decorated with vertical bars. I suggest that such decorations provide reliable information about specific body dimensions important in competition among members of these species, each revealing by the pattern of its decorations dimensions of the adaptations important for its success: fast fish display their length while fish with a high body demonstrate their adaptation to swimming within the coral reef.

Once one realizes that decorative patterns common to a set may serve to demonstrate differences in particular qualities which exist among members of the set, the door is wide open for reinterpretation of all decorative patterns as components of competitive messages which require reliability. A dot in the middle of a round structure may help to assess its radial symmetry, and a median line may display the degree of bilateral symmetry. A line along the edge of a structure may provide evidence for the fact that the structure is complete and its edge has not deteriorated. A conspicuous color covering a structure such as a

nail, or the tip of a bill, displays clearly the perfection of its shape. The complex patterns of 'eyes' on the peacock's train of feathers and their degree of perfection, may serve as evidence for physiological events which happened during their development (Parsons 1990). In all these cases the decorations reveal the qualities of body parts. Such decorations bring out the degree of perfection, often by bringing into focus defects which would be much less detectable without the decorations. Therefore, as in all honest signals, the investment in these decorations is differential. A high quality individual can develop a symmetrical body or any other perfect structure, which the decoration helps to display, but a low quality individual may face difficulties in doing so because it may not grow a perfect structure (see below).

Decorations may also function to display the variation in movement signals. Crests and horns, as well as facial decorations such as eye lines, help their bearers display at a distance the direction of their gaze. But by displaying the direction of their attention, they also provide information as to which directions they are not observing. This information endangers individuals of a low quality more than it endangers dominants or high quality individuals. A strong individual, sure of itself and of its dominance over its neighbours, does not fear a surprise attack from behind, and thus loses little from disclosing the direction it is not facing, while a weak individual cannot afford such a handicap. I suggest that this is the handicap involved in some of the facial decorations that have previously been considered as badges of status (Fugel *et al.* 1989). Subordinates and low quality individuals have to keep looking around lest they miss vital information. If a subordinate were to assume decorative patterns which disclosed the direction of its attention, it would display clearly that it was looking around frequently, in order to obtain information. This is probably the reason why facial decorations are more pronounced in adult or dominant males than in young or females. The 'status signal' is a mechanism which helps members of the same status class to compete better with one another rather than to specify the set. The fact that there are two modes of competition, each making use of a particular decorative pattern, is not evidence that the different decorations have evolved to advertise the fact that a certain individual belongs to one of these two sets. In a series of papers on the evolution of movement signals (Zahavi 1978), vocal signals (Zahavi 1980) and decorative patterns (Zahavi 1979), and in my paper on the general theory of signal selection (Zahavi 1987), I indicated this general principle: a signal which seems to be performed alike by all individuals in a set is in fact a 'standard' against which the quality of different individuals of the same set is judged. The same is true for signals which advertise motivation. Their pattern evolves to display in the most reliable way the smallest difference between two levels of motivation. Common patterns evolve due to competition to display more clearly variability among individuals rather than a common denominator. Once a common pattern evolves it may be used by conspecifics or by other organisms as

means of identification, just like other characteristics that may be used for the same purpose, such as the body shape or gait. As an example, assume that kangaroos can identify other kangaroos at a distance by observing their typical motion. Can we assume therefore that the gait of kangaroos has evolved and is maintained by the use other kangaroos make of it for identifying kangaroos?

3. SIGNALS THAT REQUIRE A VERY SMALL INVESTMENT IN THEIR RELIABILITY

Recently, Guilford & Dawkins (1991) and Dawkins & Guilford (1991), suggested that the investment of the receiver of signals in checking their reliability, and the investment of the signaller in the reliability of its signals, can create a selection process that reduces the investment in signalling reliability to the extent that signals evolve to be efficient rather than reliable, thus becoming conventional signals. They also suggested that such conventional signals may increase the scope for cheating. I claim that reducing the investment either by the signaller or by the receiver of the signal will reduce the amount of information transferred by the signal, but will not necessarily lead to conventional signaling or to cheating. Even a small amount of information may be reliable. Communication starts evolving because there is a potential receiver trying to collect certain information about the signaller (Fisher 1930, p. 129). Signals evolve only if it is in the interest of the signaller to supply that information, and only if the information thus supplied is reliable enough for the receiver to take it into account. Hence it is reasonable to assume that once the reliability of the signal is gone the signals will be selected out rather than become conventional.

4. CHEMICAL SIGNALS WITHIN THE MULTICELLULAR ORGANISM

I would like to use this opportunity to suggest that even signals used in the most collaborative systems, those that function within the body of a multicellular organism, are not conventional signals, and require investment to assure their reliability. I shall support this claim by presenting a logical argument as well as by some observations on chemical signals. What is the advantage of using reliable signals within the body, in a system in which cheating does not carry any advantage? Messages within the body are concerned with signals which one cell sends to another in order to change the receiver's functioning. The signalling cell is expected to collect information about certain happenings within itself or on its membrane. These observations are assessed and the decision of the signaller is encoded in the signal. It is important to note that the receiver of the message cannot assess the information which had caused the signal to be sent. Hence, if signals were of conventional molecular patterns, such as simple polypeptides and proteins, the receiver would not be able to detect mistakes resulting from the production of the signal by a wrong cell or at the

wrong time, because all the cells in the body are of the same genotype and have the same machinery to produce the polypeptides that are encoded in their DNA. Mistakes in such communication systems could therefore be common. The best way to avoid mistakes is to design the signal molecule in such a way that only cell phenotypes destined to be the signallers would be able to produce the signal, at the right stage of their phenotypic development. Within the body the differences between signalling cells and non signallers are phenotypic, hence the signal should include components that represent the phenotypic peculiarities of the signaller. This could be achieved if the chemical signal would be a molecule, or a component of a molecule, that could be produced only by the correct phenotype. The same principle that is used to increase the reliability of signals between organisms, i.e. the handicap principle, can also function to avoid or eliminate mistakes inside the multicellular body.

I stated above that a signal is reliable when the investment required for its use is greater than the potential gain a cheater would make from using it improperly. This may be rephrased for the case of signals within the body as follows: signals within the body may be reliable when the wrong cells would be unable to produce them. In fact, intercellular communications within the body often use the same molecules such as glycoproteins, c-AMP, etc., that are used for chemical signaling between unrelated organisms.

Signal molecules are often modified polypeptides, or other molecules that may attest to the phenotypic quality of the cell producing them. These modifications often decrease the specificity of the signal, because they display considerable variation, such as the microvariations of the sugar components on glycoproteins (Sharon 1984). They are often involved with much investment, such as sugars, that does not add to the efficiency of signal production. There is ample evidence to show that the essential messages encoded in chemical signals are often present in the modifications rather than in the polypeptide backbone, i.e. peptides without the modifications often do not function, or function to a different degree (Kalyan & Bahl 1983). It may be useful therefore to consider the modifications as conveying the contents of the message, and consider the polypeptides as no more than the carriers of the signals, transmitting the message from the sender cell to a receptor on the surface of the receiving cell. We have lately suggested that when signals are unmodified polypeptides, the important information may reside in their precursor, a protein which is usually loaded with the modifications (Nahon *et al.* 1993).

The recent findings that nitric oxide and carbon monoxide (Snyder & Brecht 1992), function as neurotransmitters, seem to lend support to my suggestion that the investment in reliability, rather than specificity, is the most important component of signals even within the body. These small molecules have no specific receptors on the surface of the receiving cell and hence show a low degree of specificity. They are also very harmful, and hence require a high investment of the cells which use them.

5. THE INVESTMENT REQUIRED TO PRODUCE SYMMETRY

Recently, the degree of symmetry has been suggested as a measure of the quality of the signaller (Moller 1990; Parson 1990) (although recent papers use the term 'fluctuating asymmetry', I suggest that the simple term 'symmetry' should be preferred). Indeed, it has been shown that females prefer more symmetrical males (Moler 1992; Thornhill 1992). I have already suggested (Zahavi 1979; and above), that certain decorations help to assess the symmetry of the signaller. However, if asymmetry advertises low quality, what limits low quality individuals from developing a more symmetrical body? If it is the lack of energy or resources why should it result in asymmetry rather than in a symmetrical reduction in body dimensions? It is more probable to assume that the communication system which regulates the development of both sides of the body does not function well in times of stress.

I suggest that what is lacking in times of stress is the considerable investment required for the reliability of the signalling systems. The body may do better by developing without coordination than by developing in response to unreliable signals.

6. CONCLUSION

I have shown how simple decorations such as a dot and a line may impose handicaps on their bearers – handicaps which may eliminate cheating – and suggested that signals that have been interpreted as set specific conventions are more meaningful when interpreted as competitive signals. I have also suggested that even in the most cooperative systems, those of the multicellular organism where there is no conflict between the communicating parties, signals require an investment in order to be reliable, in order to eliminate mistakes. This leaves practically no scope for conventional signalling.

The understanding that the selection for reliability creates a logical connection between the signal pattern and its message content, opens up the option to recognize the beauty of adaptations in signal patterns.

This paper was written after I delivered my talk. It presents all the topics of my talk but not necessarily in the same order or with the same examples. I am much indebted to Avishag Zahavi and Naama Zahavi-Ely and Naomi Paz, for their comments. Contribution of the Institute of Nature Conservation research INCR 12/92.

REFERENCES

- Barlow, J.W. 1972 The attitude of fish eye-lines in relation to body shape and to stripes and bars. *Copeia* 1972, 4–11.
- Darwin, C.R. 1874 *The descent of man and the selection in relation to sex*, 2nd edn. (1031 pages.) London: J. Murray.
- Davis, G.W.F. & O'donald, P. 1976 Sexual selection for a handicap. A critical analysis of Zahavi's model. *J. theor. Biol.* **57**, 345–354.
- Dawkins, M.S. & Guilford, T.C. 1991 The corruption of honest signalling. *Anim. Behav.* **41**, 865–873.
- Emlen, S.T. 1984 Cooperative breeding in birds and mammals. In *Behavioural ecology an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 305–359. Oxford: Blackwell Scientific Publications.
- Fisher, R.A. 1930 *The genetical theory of natural selection*. Oxford: Clarendon press.
- Fugle, G.N., Rothstein S.I. Osenberg, C.W., & McGinley, M.A. 1984 Signals of status in wintering white-crowned sparrows (*Zonotrichia leucophrys gambelii*). *Anim. Behav.* **32**, 86–93.
- Grafen, A. 1990a Sexual selection unhandicapped by the Fisher process. *J. theor. Biol.* **144**, 473–516.
- Grafen, A. 1990b Biological signals as handicaps. *J. theor. Biol.* **144**, 517–546.
- Guilford, T.C. & Dawkins, M.S. 1991 Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42**, 1–14.
- Kalyan, N.K. & Bahl, O.P. 1983 Role of carbohydrate in human chorionic gonadotropin. *J. biol. Chem.* **258**, 67–74.
- Kirkpatrick, M. 1986 The handicap mechanism of sexual selection does not work. *Am. Nat.* **127**, 222–240.
- Maynard Smith, J. 1976 Sexual selection and the handicap principle. *J. theor. Biol.* **57**, 239–242.
- Maynard Smith, J. 1976 Group selection. *Q. Rev. Biol.* **51**, 277–283.
- Maynard Smith, J. 1991 Theories of sexual selection. *Trends Ecol. Evol.* **6**, 146–151.
- Moller, A.P. 1990 Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Anim. Behav.* **40**, 1185–1187.
- Moller, A.P. 1992 Female swallow preferences for symmetrical male sexual ornaments. *Nature, Lond.* **357**, 238–240.
- Nahon, E., Atzmony, D., Zahavi, A. & Granot, D. 1993 Mate selection in yeast: a consideration of the signals and the message encoded by them. (In preparation.)
- Parsons, P.A. 1990 Fluctuating asymmetry an epigenetic measure of stress. *Biol. Rev.* **65**, 131–145.
- Sharon, N. 1984 Glycoproteins. *Trends Biochem. Sci.* **9**, 198–202.
- Snyder, H.S. & Brecht, D.S. 1992 Biological roles of nitric oxide. *Scient Am.* **266**, 28–35.
- Thornhill, R. 1992 Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*, Mecoptera). *Behav. Ecol.* **3**, 277–283.
- Trivers, R. 1972 Parental investment sexual selection. In *Sexual selection and the descent of man 1871–1971* (ed. B. Campbell), pp. 180–230. Chicago: Aldine.
- Trivers, R. 1974 Parent offspring conflict. *Am. Zool.* **14**, 249–264.
- Zahavi, A. 1975 Mate selection a selection for a handicap. *J. theor. Biol.* **53**, 205–214.
- Zahavi, A. 1976 Co-operative nesting in Eurasian birds. In *Proc. 16th Int. Ornith. Congr.*, pp. 685–693. Canberra.
- Zahavi, A. 1979 Decorative patterns and the evolution of art. *New Scient.* **80**, 182–184.
- Zahavi, A. 1980 Ritualisation and the evolution of movement signals. *Behaviour* **72**, 77–81.
- Zahavi, A. 1982 The pattern of the vocal signal and the message encoded in it. *Behaviour* **80**, 1–8.
- Zahavi, A. 1981 Natural selection, sexual selection and the selection of signals. In *Evolution today* (ed. G. G. E. Scudder & J. H. Reavell) pp. 133–138. Pittsburgh: Carengie-Mellon University Press.
- Zahavi, A. 1987 The theory of signal selection. In *Proc. Int. symp. on Biol. Evol.* (ed. V. P. Delfino), pp. 305–325. Bari: Adriatica Editrice.
- Zahavi, A. 1990 Arabian babblers: the quest for social status in a cooperative breeder. In *Cooperating breeding in birds* (ed. P. B. Stacey & W. D. Koenig), pp. 105–130. Cambridge University Press.
- Zahavi, A. 1991 On the definition of sexual selection, Fisher's model, and the evolution of waste and of signals in general. *Anim. Behav.* **42**, 501–503.