# Electric fish

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In our theorising about the evolution of mood disorders (1), we have suggested that mania and depression are exaggerations of alternative involuntary agonistic strategies: an escalating strategy which we have called the involuntary dominant strategy (IDS) and a de-escalating strategy which we have called the involuntary subordinate strategy (ISS); and that the choice of strategy depends on the self/other comparison of relative resource-holding potential (RHP). We have pointed out that this new approach of regarding behavioural variation in terms of sets of alternative strategies is something which has been developed in zoology and lends itself to an evolutionary approach. We have examined some examples of strategy sets in animals in order to clarify the model (ASCAP, Nov '92 and April '93). Here I would like to examine another example (2), which is not only a choice between two mutually incompatible alternative strategies, but one in which the choice depends on a self/other comparison. Therefore, although the behaviour concerned (the emission of electric discharges) is one which has not evolved at all in mammals, in formal terms the strategy choice is similar to the one we are interested in, and might repay study. Also, it is the only strategy choice which has been followed in the brain by neuroanatomical study from the stage at which the need for a strategy choice is detected to the final making of the choice.

It is thought that all ancestral fishes were electrosensitive, using ampullary organs in the skin to detect geological electric fields for purposes of navigation and biological electric fields for purposes of prey detection. This capacity has been retained by most present-day cartilaginous fish, but was lost during the evolution of the bony fishes (our ancestors). However, electroreception was regained independently in two lineages of bony fish; and this retrieval of the old capacity to detect electrical fields was associated with the development of the capacity for "weak" electrogenesis, in which electric organ discharges (EODs) are emitted from the muscles in the caudal half of the body and the resulting electric fields are detected by newly evolved tuberous receptors covering the whole body surface. The distortion of the electric field by objects whose impedance differs from the surrounding water allows the fish to "see" these objects, in the way that bats can "see" by echolocation. In this way they are able to navigate through murky water and at night, and to go to depths at which sunlight does not penetrate. They can also use their EODs to communicate with conspecifics. However, the emission of EODs by conspecifics leads to the possibility of "jamming" if the frequencies of two fish are very similar, because the electroreception process depends on the detection of small differences in frequency and amplitude in particular patterns across the body of the fish. This difficulty has favoured the evolution of the jamming avoidance response (JAR) in at least one branch of both lineages. When a fish detects another fish of very similar frequency, it chooses between two mutually incompatible alternative strategies: it either increases its own frequency or it reduces its own frequency.

If we describe our ranking theory in terms of resource-holding potential (RHP), we get a very similar situation. Imagine an agonic social group, one in which symmetrical relationships are not tolerated, as exists in olive baboons and a large number of macaque species. In such groups there is an intolerance of equal RHP, just as in the fish there is an intolerance of equal frequencies. Each baboon struts around emitting signals of absolute RHP; if he meets another baboon signalling clearly higher RHP, he adopts the subordinate basic plan; if he meets a baboon signalling clearly lower RHP, he adopts the dominant basic plan. But if he meets a baboon signalling the same RHP as his own, he cannot adopt either of his customary basic plans, and he has a problem. Or, rather, both baboons have a problem. They have to find some way of developing a difference in RHP, or of detecting and subsequently being able to recognise a difference in RHP. Each has the capacity to alter his own RHP either up or down (or it might be more correct to say that he can alter his own perception of his own RHP up or down - what Hartung (3) has called "deceiving up" and "deceiving down"). We would say that each has a choice of either an escalating or a de-escalating strategy. Each of the pair of equal RHP baboons has an interest in getting the matter settled one way or the other, and also an interest in having it settled in a particular way; i.e., with himself as top baboon. They are in a non-zero sum game, and the choice of strategies has been the subject of much research by game theorists - in fact the concept of RHP was developed by a game theorist (Geoffrey Parker) while tackling just this sort of problem. We can assume that the same problems face a pair of electric fish which happen to have very similar frequencies. They both want to develop a difference in their frequencies, and it may well be that each would prefer to adopt one strategy, such as lowering its frequency, which may involve less energy expenditure than raising its frequency. Each would therefore like the other fish to immediately raise its frequency - and while both are waiting for the other to do so, both are paying the cost of having incapacitated navigation systems.

What the fish do is to examine the frequencies and work out whether their own is slightly higher or slightly lower (they can tell which frequency is emanating from themselves). If theirs is slightly lower, they then lower their frequency further, and vice versa. Presumably they have some plan in the event of the frequencies being exactly the same - some sort of default setting which says, for instance, "if no detectable difference, raise frequency". In the case of baboons evaluating each other's RHP, much the same process seems to be taking place. They explore each other's RHP, using species specific signals (ritualised fighting) which take the form of statements of equal or superior (favourable) relative RHP. When the baboon threatens the other, he is saying "My RHP is greater than yours" and when the other baboon threatens back, it is saying, "No, it isn't". Eventually one baboon decides that its RHP is very slightly lower than the other's, and it then adopts the de-escalation strategy which consists, at least in part, of a lowering of its RHP. In this way a difference in RHP is created where none (or at least no clearly detectable difference) existed before.

It may be instructive to look at the similarities and differences between the situations of the baboons and the fish.

Similarities

There is a population whose well-being depends on all the members having different values of some variable X.

If two members happen to have the same value of X, each can deal with the problem by raising its value of X or by lowering its value of X.

It is in both their interests to create a difference, but their interests conflict over which increases X and which lowers it.

Satisfactory outcomes occur if:

1. One makes an adjustment and the other does nothing.
2. Both make adjustments but in opposite directions.

An unsatisfactory outcome occurs if both make adjustments in the same direction.

They examine the values of X to see if there is a slight difference. If they find a difference, they adopt a strategy which enlarges the difference. If there is no detectable difference, they could randomise the choice of strategy, or they could implement a default strategy which could be either to raise or to lower X. In the latter case the population would be dimorphic, but the morphs would only be apparent when the comparison process was activated, and even then an observer could not know whether a default setting had been activated, or whether a minute difference had been detected. The default strategy could be either genetically determined or it could be contingent on some environmental factor, active either earlier in life or concurrently with the strategy choice. Or it could be randomised. Or it could be a combination. For instance, there could be a genetically determined strategy which read, "if your first social encounter was with an individual of lower X than yourself, activate a default setting of "lower X" if you are feeling hungry, but "raise X" if you have eaten recently; if your first encounter was with an individual of higher X, operate a randomised default strategy, with a frequency of "raise X" of 0.3". In the case of RHP, I think that a default setting of "raise RHP" is what Maynard Smith refers to as a "hawk strategy" and "lower RHP" is what he calls a "dove strategy" (4).

Differences

The baboons explore the difference in RHP by exchanging signals, which are at the same time statements of favourable relative RHP (the fact that the signal is given) and of absolute RHP (the intensity of the signal). We have defined signals of favourable relative RHP (catathetic signals) as signals which lower RHP in the receiver, provided they are not returned in full measure. It is the detection of the fact that it is not returning the adversary's catathetic signals in full measure which convinces the baboon that it is losing the fight and leads to it adopting the de-escalating strategy. Therefore in the case of the baboon, it does not matter whether we say that RHP is lowered by the catathetic signals of the adversary, or as part of its own de-escalating strategy. The two things are part of a systemic dyadic interaction which is recursive in its causative mechanisms.

Likewise, with a pair of baboons it does not matter whether we say that one baboon lowers its RHP or that both baboons look at the RHP scale with much higher definition, and see differences which were previously sub-threshold. However, if we are dealing with a group, the distinction does matter, because in lowering its RHP to create a difference with baboon A, a baboon may alter its RHP difference with previously lower-ranking baboons, either becoming equal in RHP or even lower than those to whom it was formerly superior.

This last situation seems to be the case in many animal species, as a defeated animal may fall to the very bottom of the social hierarchy.

## The comparison of frequencies

The most simple thing would be for the fish to compare the incoming jamming frequency with an "output copy" of its own frequency; and, if the income frequency was higher, to lower its own frequency, and *vice versa*. But they do not do this. They do not appear to have evolved the capacity to retain an output copy. They can tell from the pattern made by the two frequencies on their bodies whether the incoming frequency is higher or lower than their own. Then they alter their own frequency accordingly.

We do not know how animals (or humans) make comparisons of relative RHP. Probably when the capacity to make the comparison first evolved it was based on a single feature like size, although even this comparison cannot have been easy because the representation of one's idea of one's own size, and one's idea of the size of an adversary, use different kinds of information. It is not as simple as comparing two shades of wall-paper placed side by side. At some stage we should make models of the comparison which give different predictions, but at this stage I think it helps just to know that this kind of self/other comparison is made in electric fish, and that the result of the comparison decides between alternative strategies.

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these weak discharges of less than 10 volts can be compared to the electric eels and rays which use electrical discharges of up to 600 volts to stun and kill their prey - the weak discharges are used for locating prey and other objects, and for communication with conspecifics).

They can distinguish between impedance due to capacitance and that due to resistance, so they can sense at least one quality of objects as well as size, shape and direction, in much the same way that we see colour. The frequency of the EODs ranges from a few cycles per second to 1,800 Hz. The fish can detect amplitude modulation of as little as 1%. They can detect phase modulation (the difference in timing of the pulses at two points on the body surface) of a fraction of a millisecond; this compares with the owl threshold of several milliseconds (in the fish, whereas the synapse between receptor cell and afferent nerve is chemically mediated, all the interneuronal synapses are electrically mediated, whereas in the owl all synapses are chemically mediated, and the greater rapidity of electrical transmission is thought to account for the greater power of phase detection in the fish).

## The jamming avoidance response

However, the emission of EODs by conspecifics leads to the possibility of "jamming" if the frequencies of two fish are very similar, because the electrodetection process depends on the summation of small differences in phase and amplitude in repeated pulses in particular patterns across the body of the fish. Coincidence in a single pulse does not matter, because that information can be discarded; but coincidence in a whole series of pulses scrambles the usual location information. This difficulty has favoured the evolution of the jamming avoidance response (JAR). When a fish detects another fish of very similar frequency, it chooses between two mutually incompatible alternative strategies: it either increases its own frequency or it reduces its own frequency.

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## Electric fish: a harmonious model for asymmetrical relationships

When I recently wrote to Ascap about electric fish, and later about authoritarian personality, I little thought that I would soon be sitting down and writing about authoritarian personality in electric fish. And yet, having got more fish material from the library (1), that is what I find myself doing. Let me start with some general information about the evolution of electric fish.

## Evolution of electro-receptivity

It is thought that electro-receptivity evolved several times and shows parallel evolution. Most cartilaginous fishes are electroreceptive. Only two lineages of bony fishes are, and they are the African mormorids and the South American gymnotiforms, both being freshwater fish and therefore likely to very distant relations. Evidence from the receptor organs and brain nuclei suggests that these three lineages developed the capacity independently, but in each case from the tissues of the lateral line system.

They all have ampullary organs which are used to detect external electric fields (such as those given off by prey), and the fields created when the fish moves in relation to the earth's magnetic field. Only the bony fish have tuberous organs which are used to receive their own electric organ discharges (EODs) and those of conspecifics, and these are adapted to receive only the frequencies that it has been adaptive for them to receive during evolution.

## Evolution of electrogenesis

The capacity to create electric fields in the surrounding water is also thought to have evolved several times. Bullock (2) says, (p. 670) "...it appears most likely that electric organs were invented repeatedly, independently, in species already possessed of electroreception, in unrelated orders of elasmobranch and teleost. Only in one case, the stargazers (Uranoscopidae), is it doubtful whether electroreception coexists with the electric organs.....nothing is known about electroreception in invertebrates, reptiles or birds" [it occurs in urodele amphibians and one mammal (the duck-billed platypus)].

There are two distinct forms of weak EOD, wave forms and pulse forms, and both occur in both African and American families. Strong EODs are used for stunning and killing prey, and for defence, and they occur in the torpedines. The weak EODs are used for navigation and communication. The receptors detect alterations in impedance in the electric field, and they can distinguish whether such alterations are due to capacitance or resistance, so these fish have the capacity for "seeing' an environment which would be very strange to us.

The electric organs are evolved from striated muscle (which has lost the capacity for contraction). Therefore the discharges can be abolished with curare (very useful in experimentation). Larvae also have electric organs, which may or may not be homologous with the adult forms. Most organs are developed from trunk musculature and are innervated by spinal electromotoneurones, but some are developed from the extraocular muscles and innervated by cranial nerves. Some fish have accessory electric organs which may discharge at a different rate from the main organ. One group (Apteronotidae) has a "neurogenic" organ developed from spinal motor nerves (probably from the nerves which innervate its larval myogenic organ) and this can reach a frequency of 1,700 cycles per second (and of course it is not affected by curare). One fish has an electric organ developed from sensory nerves.

## Sex differences in frequency

In wave form species (which emit an almost sinusoidal wave of alternating current) the frequency of the discharge is the most important information. There is a tonic or background frequency which is used for species, sex and possibly individual recognition. This is given off 24 hours a day, so the electric fish is par excellence an individual who "cannot not communicate". In some species, the frequencies of the two sexes differ but overlap, in most cases the male has a lower frequency, but in a few species the female has a lower frequency. It is interesting that when the males have a lower average frequency, the male will only mate with a female having a higher frequency, even though many of the females it meets have a lower frequency.

## Wave form and sex hormones

In many species the wave form of females differs from that of males, and this is due to the nature of the electrocytes in the electric organ, and to their arrangement and their number. In most of these cases the female wave form can be converted to the male form by androgens (by changing the electrocytes into male form) and in these cases the electrocyte is a target tissue for androgens like the syrinx of songbirds and the penile bone of the rat (2). Wave forms which do not differ between the sexes are not affected by androgens. In some cases when males are kept in captivity, their EOD wave forms alter to the female type, and this may reflect a change in sex, since we know that sex in fish is often socially determined.

## Frequency modulation and agonistic behaviour

Modulation of the tonic frequency is used in both reproductive and agonistic behaviour. Short interruptions in the tonic discharge (< 1 second) are used as threat displays and courtship displays; they may cause rivals and subordinates to flee. Long interruptions (> 1 second, extending to total electrical silence) serve as submissive displays, and reduce attack by rivals and dominants. These conventions apply to both pulse and wave forms of both mormyrids and gymnotiforms, in fact to all electric fish except the Apteronotids (which have the neurogenic electric organ) and so represent a remarkable case of parallel evolution.

Short increases in frequency (< 1 second) of 10 to 50 Hz also act as threat signals, while long rises (5 to 40 seconds) of 2 to 20 Hz signify submission. It is not known how the significance of rises differs from that of interruptions. Other threat signals in electric fish are antiparallel swimming and head butting.

## Frequency and social rank

In those species of electric fish which form social hierarchies, frequency also varies with dominance. In some species the dominant fish has a higher frequency, in some species lower. In the latter, if a fish becomes dominant, its frequency becomes lower. In some species in which dominant males have lower frequencies than other males, dominant females have higher frequencies than other females.

When two fish of the same species are paired together, they tend to develop frequencies which differ by exactly an octave (1, p. 514). So far this has only been reported for opposite sexed pairs, so it is not known whether it is a reflection of dominance relations or pair bonding. Nor is it known how the regulation is achieved. However, the formal similarity to the adjustment of RHP in complementary marital relationships is striking (3):

> What seems more likely, from what we know clinically, is that the "one- up" husband (or wife) tries to keep his spouse's exercise of control [RHP] a constant amount below his own exercise of control [RHP]. What is maintained homeostatically is not the absolute level of control but the difference in control between husband and wife, what might be called the "control gap" [RHP gap).
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> More generally, the "one-up" spouse maintains a gap on what Birtchnell (1987) has called the "vertical dimension" which describes a number of correlated variables such as mood, rank, self-esteem, self-confidence, dominance, and, in the last resort, the capacity to define the relationship rather than accept the definition provided by the other. Colloquially, we might say he tries to maintain a constant level of "one-upness"; more technically he tries to maintain a constant vertical-gap setting between what he feels to be his own position on the vertical dimension and what he perceives his wife's to be. This "gap" model has the advantage of embracing the phenomena of redirected aggression; if the husband's mood is lowered after receiving punishment from his boss at work, he restores the vertical gap at home by putting his wife down (or omitting to boost her). The feedback loop is probably below conscious awareness: even though he may be aware that he is putting his wife down, he does not understand why he is doing it; and many signals intended as boosting signals are received as putting-down signals, especially in the case of "constructive" criticism (MacLean, 1976).

I am not sure how many situations there are in which one vertebrate compares itself with a conspecific, and then makes a decision which depends on the comparison. There is the comparison of RHP which determines the decision whether to attack of flee in agonistic behaviour, and this is widespread among vertebrates. Then there are these two instances in electric fish, the jamming avoidance response which I discussed last time, and this pair-bonding situation, in which a fish either selects another with a complementary frequency, or creates a desired frequency gap by altering its own or its partner's frequency. And there is mate selection in the herring gull, which, substituting size for frequency, is similar to mate selection in the electric fish. Tinbergen (4) observed in herring gulls that, although the range of sizes of male and female overlapped considerably, he never observed a mated pair in which the female was larger than the male. This means that the gulls must compare their sizes during courtship, and desist if the female is larger than the male.

Is there a basic vertebrate plan for self-other comparisons, which has been drawn on for all these four, and possibly other, comparisons? Or did the self/other comparison evolve separately in each situation? We can do no more than speculate. In the case of RHP and size in gulls, there could well be a common comparison process, as the RHP comparison may well have started off as a simple size comparison. But it is less likely with the electric fish, in which the whole plan for electrogenesis and communication by electric fields evolved independently (our own ancestors are thought to have been electroreceptive but not to have had electrogenetic powers). It is more likely that the capacity for self-other comparison evolved as part of this new system, rather than that an existing self/other comparison system was brought in from somewhere else in the brain, rather as someone developing an aeroplane might have used an engine designed for powering a car.

Of course RHP does not work like the harmonic scale, so there is no obvious size of RHP gap to match the octave of frequency gap. In fact, the variability of RHP gap is probably important, in that it is likely to vary with the "insecurity" of the dominant authoritarian partner. The more secure he feels, the less gap he needs. Therapeutically, this means that one can aim at reducing the gap, short of achieving total symmetry. One could not do this with electric fish, because the system would tend to return the gap to the octave (perhaps one could reduce a gap from two octaves to one octave!). Means of reducing the RHP gap involve educating the dominant partner that gap reduction brings benefits rather than costs: his more powerful wife will use her power to further his interests rather than her own competing interests; a more sociable wife will use her capacity to cultivate his friends rather than fill the house with her own; a more highly sexed wife will increasingly satisfy him rather than give her favours to others (etc., etc.).

For completeness, to the above one must add two categories of self/other comparison with which we are very familiar in humans. There is comparison of what Paul Gilbert has called social attention-holding power (SAHP), in which the comparison asks the question, "am I more attractive than he/she?" in the hedonic competition for prestige. And there is the group membership comparison which asks the question, "Is he/she the same as me?". This latter comparison occurs in insects and rodents in which groups of the same species differ in smell.

## Insensitivity of brain to electric fields

It has been suggested that the human brain might be sensitive to electric fields. But to me, to envisage this possibility persuades exactly the opposite, and emphasises how very insensitive the human brain is to either direct or alternating electric fields. Humans by now must have been exposed to a fantastic variety of fields, including a range of frequencies of alternating current that must include the capacity of any imaginable receptor systems. And yet no behavioural changes have been produced. It seems as if the brain were specifically protected from electrical disturbance. Look at the difficulty we have in inducing seizures in giving ECT. Lightning affects the body but not the mind. It looks as though electroreception has been thoroughly bred out of our systems, possibly because those of our ancestors who remained electrosensitive were at some disadvantage, possibly from the electric discharges of some predatorial dinosaur.

Possibly we did this by evolving chemical neurotransmission, which seems otherwise to be an extraordinarily cumbersome addition to a system which is based on purely electrical transmission. But in requiring chemicals for nerve to nerve transmission we made ourselves invulnerable to outside electrostimulation, and myelin did the rest.

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