

dersten Europäer? Es wäre vielmehr zu erwarten dass die Selektion bei der schwarzen Bevölkerung eine erhöhte Immunität begünstigt hätte.

HALDANE, I. I agree with Dr. Montalenti's project. Another possibility is

that (by analogy with the advantage possessed by vermilion *Drosophila* on media deficient in tryptophan) microcythemic heterozygotes may be at an advantage on diets deficient in iron or other substances, thus leading to anaemia.

2. Perhaps the theory that most diseases evolve into symbioses is somewhat panglossist. I doubt if it occurs as a general rule, though it may do so. The position for the original host is however best.

Animal communication and the origin of human language*

J. B. S. Haldane

Weldon Professor of Biometry in the University of London, University College

If we accept the theory of evolution, we must face the problem of the evolution of human language. We cannot yet solve this problem, but we are nearer to solving it because a great deal has been learned about animal communication in the last twenty years. The greatest discovery in this field is von Frisch's analysis of bee communication, but bees' methods are so unlike our own that his work throws little direct light on the human problem.

I say that animal X communicates with animal Y if it produces a signal S describable in the language of physics or chemistry which alters Y's behaviour. "Telepathic" or "paranormal" co-ordination of the activities of X and Y, if it occurs, is not necessarily communication between X and Y. Bee Y might imitate the actions of X because both were controlled by the "spirit of the hive." In the case of bees at least, von Frisch's observations make any such hypothesis unnecessary. We cannot draw a sharp line between communication and other forms of intercourse, but we can say that the signal usually involves little expenditure of energy by X, and has a large positive or negative effect on

Y's energy expenditure. We can classify these signals in many ways.

The most obvious is by their physical nature, or what comes to the same thing, the receptor organ by which Y receives the signal. A classification by X's effector organ yields a quite different and less useful picture. For example, a production of skin pigment, a contraction of chromatophores, and a muscular movement can all start visual signals. Our rough classification is: Chemical (olfactory), optical (visual), vibratory (acoustic), mechanical (tactile or kinaesthetic), and electrical (receptor not yet fully described). The type of reception is bracketed. There is some overlap between auditory and tactile reception.

We can also classify signals as transient or persistent (perhaps dynamical and statical). A peacock's feathers last for some months, his erection of them for a few seconds or minutes. Chemical signals are always somewhat persistent. An animal can sometimes turn an odour on suddenly. It can rarely turn it off suddenly. Only chemical and optical signals can be persistent.

When we consider the function of a communication our most obvious classification is into communication within a species and between members of different species. (We might also, of course, consider communication between cells in an organism, and even within a cell.) Communication within a species appears, usually at least, to be advantageous to the species, and quite often to both the individuals X and Y,

though it is not a simple matter to define the word "advantageous." Communication between two species may be advantageous to both, but is often harmful to one. We shall see that it includes "negative communication" (Spurway, 1955b) or hiding, and the equivalent of human lying. Members of one species may "understand," that is to say react appropriately to, the signals of another. Thus many of our small song birds are alarmed by the alarm calls of other species.

Within a species we can distinguish (again with some uncertainty) between the signals repeated by the recipient, and those which are not. A signal by X, as we shall see, always predicts X's behaviour. If it evokes a quite different, but biologically complementary, behaviour by Y, it is not repeated by Y. Thus some adult birds X signal to their chicks Y with coloured patches on the beaks, and appropriate movements. The chick does not repeat these signals. It commonly emits quite different ones, such as a characteristic sound, and opening its beak to show coloured throat patches. When the signal results in Y performing a similar activity to X, it is commonly repeated. Thus when dog X growls at dog Y, Y commonly growls back, and they proceed to "threatening" gestures. When finch X emits the alarm call appropriate to a hawk, it takes cover. If finch Y hears it, it repeats the note, and takes cover too. Thus the alarm is rapidly spread through a flock.

*A summary of lectures given at the Royal Institution on November 30th, December 2nd, and December 7th, 1954. If any of the ideas here put forward are novel, they are as much due to my wife (Dr. H. Spurway) as to myself.

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We can study the ontogeny of communication, and in particular ask whether the production of the signal by X, on the one hand, and Y's response to it on the other, are learnt or unlearnt activities. Of the European song-birds so far investigated, about half sing fairly normally, when reared by human beings out of earshot of their own species. The other half must have heard the song at some stage in their lives. If reared in isolation they produce a grossly abnormal song. This shows that there is no simple answer to the question. What is worse, on almost any evolutionary theory, some of these species must have passed through a stage where the song was learnt by some individuals and was instinctive in others. As a geneticist I think that it is quite impossible to make a sharp distinction between learnt and unlearnt behaviour. Later on I shall remark on the instinctive basis of human speech.

We can speculate on the phylogeny of communication. When several related species have very similar codes, it is at least plausible that their common ancestor had a code of this type, and Whitman (1919) and Lorenz (1941) have used the mating signals of birds as an aid to phylogenetic taxonomy. Aristotle was of course responsible for the use of such behavioural traits as the drinking method of the Columbidae, as taxonomic characters. We can also speculate on their derivation from other activities, as Tinbergen (1952) has done. Clearly, for example, most sound production by land vertebrates is performed with the breathing apparatus. Insects, which breathe with tracheae and not lungs, make acoustic signals in other ways, as do some land vertebrates, for example rabbits by stamping, and male guinea-pigs by chattering their teeth. More surprisingly, we may speculate on the transformation of communication into other activities. For example anal scent glands are communicatory in many mammals. In the skunk they have become a formidable weapon. Still further speculations deal with the nervous "mechanisms" responsible for the production of the signal and the response to it. In view of our ignorance of the precise process which goes on even in the simplest conditioned reflex, I cannot take them quite as seriously as do their authors, who are not generally neurologists.

Before describing some communications in detail, I enunciate two principles, one which is generally accepted, and one which, though anticipated by William Shakespeare and William James, has recently been applied by my wife and myself (Haldane, 1953, 1954; Haldane and Spurway, 1954) to a group of animal communications, but has not yet stood the test of criticism. A signal by X is always a sign of some physiological or psychological condition of X. We say without hesitation that this female cat is "calling" because she is on heat, this dog growls, snarls, and raises his hair because he is angry. When, however, we say that the dog is angry, we do not know telepathically that it has this emotion. We have learned that these signals often precede an attack. The code is to some extent arbitrary. Tail movements in a dog are a sign of friendship, in a cat of hostility, in a horse of the presence of flies. To sum up, a signal by X predicts some activity or inactivity of X. This is generally accepted. It is not so generally realised that the response to the signal may indicate a physiological state of Y. I shall give examples later.

Now most animal activities have some observable prelude. Many insects and birds "rev up" by flapping their wings before beginning to fly. This is not a signal in non-social insects. It is clearly a signal in some large sea birds. The cat's tail movement may be regarded as the prelude to a leap, in which the tail will be used for balancing. Newts resting on the bottom often raise their heads before coming up for a breath of air. Other newts pay no attention. But if it were biologically advantageous for a number of newts to come up together, they would perhaps come to notice such movements. A human being generally gives some signs of his psychological state, and therefore his future conduct, unwittingly. A good actor or actress can imitate these signs consciously. If it is advantageous that animal Y should co-ordinate its conduct with that of animal X, two things can, and frequently do, happen in the course of evolution. The prelude performed by X before an action is ritualised and often exaggerated. And Y comes to respond to it appropriately (Tinbergen; 1952).

Quite often, in my opinion, the performance of a prelude facilitates the subsequent action, not merely in a

simple physiological way, for example by warming up insect flight muscles, but by throwing the nervous system into a suitable "mood." Shakespeare's *King Henry V* (Act III, Scene 1) commands his soldiers to perform a variety of muscular contractions before an assault. Some may be regarded as mere preparations for a sprint. Most of them were designed to get them into the correct mood to kill Frenchmen. If the prelude facilitates the subsequent action, then when the prelude becomes a signal its repetition by Y will get Y into the mood to do whatever X is going to do, in other words it will facilitate unanimous action by a group. A final point of some importance is this. The investigation is not complete until we have tried a series of artificial signals S_1, S_2, S_3 , etc., to determine Y's response. The signal S will be common to them. Animal signals, like human words, have a good deal of redundancy. And a signal which to human senses agrees with X's signal may have a different effect, if any, on Y, often because Y's senses are different from our own; for example it may see ultraviolet radiation, hear supersonic vibrations, and so on.

With these preliminaries I pass to the consideration of chemical signals. I have discussed protozoan communication elsewhere (Haldane, 1954). This was, I think, a necessary preliminary to the formation of metazoa. A mass of mutually adherent cells is not an organism unless they can influence one another. In fact cells in a metazoan communicate chemically by two types of signals. Some, such as acetyl-choline, are destroyed in a small fraction of a second. Others, like the thyroid hormone, last for several days.

The odorous sexual signals of mammals are often chemically related to the steroid sex hormones, one of which, testosterone, has a distinctly musky smell when warmed. I have given reasons to think that the vertebrate sex hormones began as inter-individual signals (Haldane, 1954). Simultaneous spawning occurs in various invertebrate groups including some lower chordates. It appears to be due to chemical signals discharged into the water with the gametes. In tunicates the receptor organ is the ciliated pit which is believed to be homologous with part of the vertebrate pituitary. The vertebrate pituitary responds to chemical changes in the blood. I

suggest that its precursor responded to changes in water. I give another argument here. A female bitterling (*Rhodeus amarus*) develops an ovipositor when placed in water in which a male of her own or at least one related species has been swimming. Several of the steroid sex hormones have the same effect when added to the water (Bretschneider and de Witt, 1947). Butler (1944) has described the chemical communication between the queen honey bee and the workers. The cuticle of a mated queen secretes a compound or group of compounds called the queen substance, which can be wiped off with cotton wool. It contains an odorous signal. The workers eat it and pass it on to one another by the food exchange process. In the absence of this substance they quickly become excited, within twelve hours or less they start building queen cells on the brood comb, and later begin to lay eggs. It is not known whether the hormone-like substance inhibiting egg-laying is the same as the odorous signal substance. Virgin queens secrete a substance which has a similar effect on workers if no mated queen is present, but may release hostile behaviour in presence of a fertile queen. Other social insects communicate in a similar way.

Chemical, or odorous, signals are particularly important in most of the mammalian orders. Man has, on the whole, a poor sense of smell, but is fairly competent in recognising the volatile substances produced by plants, in many cases as signals to animals which disperse their pollen or seeds. In the ground-living mammals odour is probably the most important means of social recognition. It is unimportant in monkeys or men. This is one reason why we men understand the social behaviour of birds better than that of mammals. Birds, like ourselves, rely mainly on visual and auditory signals, and we can record these and produce dummies such as coloured models and gramophone records. We cannot record smells by any objective method such as photography, nor can we produce dummy smells, except to a small extent by the synthesis of animal odorous products or compounds which may be found to have similar effects. Moncrieff (1954) claims that smells recognised by humans as similar show a similar pattern of adsorption by surface-active substances. He may have done for smell what Newton did for colour. If so an objective

study of mammalian social behaviour will become possible.

Communication by smell has many disadvantages. The signal can convey the information that it comes from animal X_1 rather than X_2 or X_3 , or in the case of bees, from hive X_1 rather than X_2 or X_3 . It can convey some information as to the physiological state of X . In many Lepidoptera and mammals it can convey the information that female X is in a sexually receptive state. But the message cannot be altered rapidly, so far as we know. This, however, gives chemical signals their one great advantage. X can signal to Y in his absence. Many male mammals mark out a territory by depositing odorous substances within it. This instinctive behaviour in male cats often embarrasses their human owners. Male Y is chary of entering a territory so marked by male X . And male X shows characteristic behaviour which we interpret as showing satisfaction, on smelling his own chemical signals. The signal is often secreted by glands near the excretory organs, and deposited along with the excreta. But many ungulates, such as the chamois, and some carnivores, such as the hyaena have scent glands on the head, whose secretions they smear on rocks, branches, and even the walls of their cages, in some cases making marks visually recognisable by human observers (Hediger, 1949).

Thus chemical communication can be communication by X to Y in the future, and more remarkably, by X to X in the future. So its function is that of human writing rather than of human speech. A closer human parallel is with the persistent visual signals affixed to trees by Polynesians to indicate that their fruit is "tabu" for trespassers.

I shall pass very lightly over the topic of visual communication, because Tinbergen (1951, 1953, 1954) has recently published three books which are largely concerned with it, and might be regarded as a lexicon of the visual signals used by a number of animal species. The greatest contribution which Tinbergen and his school have made to scientific method is, I think, the systematic use of series of dummies or models of persistent visual signals, following the example of Lissmann (1932) and others. By presenting a series of such models to a group of animals they have been able to discover which features in the animals'

visual field are signals, and which are irrelevant. The most extensive research has been on the visual signals which elicit pecking in newly hatched seagulls. The herring gull has a yellow beak with a red spot near the tip. Tinbergen and Perdeck showed that a yellow model beak with a terminal red patch elicited more pecking responses than one with a patch of any other colour. But the colour of the head to which the beak is attached is irrelevant. It is not part of the signal any more than the shape or colour of the post carrying a traffic signal is relevant to a motorist.

It might have been expected that the brain or mind of the chick was nicely adapted to the persistent visual signal furnished by its parents' beaks. This is not so. Tinbergen was able to produce visual signals which elicit a greater response from the chick than do models which resemble the parental beak. This phenomenon is quite widespread. Many birds prefer eggs considerably larger than those which they lay themselves, a fact of which cuckoos take advantage. In our own species liquids such as beer and tea elicit a supernormal drinking response, that is to say we not only drink them in preference to water, but we drink more of them than we should of water. An appreciable fraction of our national income is devoted to the purchase of objects which are believed by females of the human species to act as supernormal sexual signals, both visual and olfactory. The latter, at least, often have an inhibitory effect on some males, of whom I am one.

Tinbergen and his colleagues have not gone so far in their analysis of transient visual signals, such as movements and postures. They have described them in great detail, and have been able to imitate some of them with dummies. Tinbergen can imitate the zigzag movements of a male stickleback luring a female to his nest with a dummy on a wire. This is a matter of personal manual skill. He has not quantified the effect on the female of oscillations of varying period and amplitude, which is a difficult but ultimately necessary task. The only quantitative analysis of signals given by bodily movement is that of von Frisch, and here, as we shall see, the signals are not visual. Lorenz' (1941) descriptions of the movements of ducks when courting are of great interest, but almost unintelligible unless one has

spent many days in watching ducks. And it is quite uncertain which features in these movements are signals, and which are as irrelevant as the colour of the dummy seagulls' heads. Armstrong's (1947) *Bird Display* covers an extremely wide field, and is the most comprehensive study of visual signals made for any group. Dr. Thorpe and his colleagues, including Hinde (1954), at Cambridge are studying the movements and postures of British birds, particularly finches, in relation to their signal functions, and are coming nearer to a quantitative analysis. But, as they fully recognise, they have a long way to go.

Auditory signals are particularly interesting to men, because our most important signals are auditory, as appears from the elementary fact that a child born deaf is very hard to socialise, whilst one born blind fits into society with less difficulty. They have been studied extensively in birds, and to some extent in Orthoptera. But there are two serious pitfalls in their study. We have sharply different signals for graded series of qualities or actions, such as "run," "walk," "halt," or "hot," "warm," "cool," "cold." *Animal signals grade into one another.* This is most obvious in the bee "language," but Lorenz (1949) gives an excellent example in geese (*Anser anser*). A group of geese produce phrases of about ten "honks" when at rest. If moving on the ground the number diminishes as the speed increases, until during flight the "honk" is monosyllabic. Its pitch also alters. Tinbergen (1954) notes how the sounds produced by gulls in different contexts grade into one another. The second pitfall is technical. A grasshopper's sound signal reproduced by a gramophone or through a loudspeaker by magnetic recording may seem very like the original to a human ear, but may have no effect on a grasshopper which hears it. Conversely a human being may be able to call grasshoppers, as Loher (Busnel and Loher, 1954) can, by making a sound which to a human ear is quite unlike a grasshopper's chirp. This is presumably because grasshoppers hear supersonic notes of which some are inaudible to us, and others are heard as an unmusical SSSS, or FFFF. Busnel and Loher found that they would not respond to most mechanical reproductions from a magnetic tape record. This is because loudspeakers have diaphragms with too

much inertia to move freely at supersonic frequencies. The problem was solved by Klein's (1954) invention of the ionophone, which has no solid or liquid moving parts. A stream of gas is thermally ionised and passed through an oscillating electric field generated by the tape record. Grasshoppers are lured by a record played through the ionophone. The accuracy of our reproductions of bird sounds in the high part of the register is a matter on which we must bow to the responses of birds. In fact they do respond to some at least of the reproductions made by Dr. Thorpe and his colleagues.

Human beings can easily distinguish some bird cries, for example the song, the call note, and the alarm cry of the chaffinch. They have meanings for other chaffinches. Are they arbitrary in the sense that the sounds which mean "father" and "even" in French are close to those which mean a fruit or two of a kind in English? Marler, in work still unpublished, which he most generously allows me to quote, has proved the contrary. When a male chaffinch sings, other males tend to keep away, while unmated females approach. They react in the same way to reproductions of the song. Both activities are advantageous for the species. When a chaffinch utters the alarm note on seeing a hawk, other chaffinches repeat the note, hide under leaves, and scan the sky with characteristic eye movements. It is advantageous that the direction of a singing chaffinch should be readily localised, and that the direction of one uttering the alarm note should not.*

Now an animal discovers the direction from which a sound comes because the messages received by its two ears are different. If the wave-length is very small the waves do not readily travel round the head. There is a "sound shadow" on one side. If the wavelength and therefore the interval between pressure maxima is large, there is a difference of phase between the messages picked up by the two ears. Again if the sound begins or ends abruptly it may reach one ear appreciably before the other. A note is hardest to localise when it rises and falls slowly, and has a wavelength not too different from the diameter of the hearer's head. The shrill,

*Dr. Marler's records of the song and alarm call were reproduced at the Royal Institution

slowly rising and falling, alarm note is hard for a predatory bird to localise. If elephants ate chaffinches on a large scale, the alarm cry would presumably be a much lower note. On the other hand the song is easy to localise because it is broken up into syllables, mostly of a lower pitch than the alarm cry. The human alarm cry, the shriek of fear, is somewhat lower than the chaffinch's and perhaps adapted to the larger heads of wolves, lions, and bears.

Lorenz (1952, p. 76), in a book which has been widely read, makes the amazing remark about the vocal signals of birds that "this purely innate signal code of an animal species differs fundamentally from human language, every word of which must be learned laboriously by the human child." In fact Barrington (1773) discovered that many species of birds have to learn their song, and it was not till about 1910 that Heinroth (v. Heinroth and Heinroth, 1924-1926) discovered that other species sang it untaught. Lorenz goes on to state that "this so-called language is, for every animal species, ubiquitous in its distribution." In fact Promptov has discovered differences of song in chaffinches, and Marler (1952) has found at least three dialects in the British Isles. The Scottish birds have, on an average, the most complex phrase, but those of the Thames valley are more variable, and include some birds producing a more complex song than any of the Scots. Von Frisch, Hein, Tschumi, and others have found similar differences in bees (v. Haldane and Spurway, 1954).

To mention three familiar British birds, the blackbird does not have to learn its song, but the song of an untaught cock chaffinch is said to resemble that of a lesser white-throat, though vaguely like that of a normal chaffinch. That of an untaught skylark is quite unrecognisable. Call notes are less often learnt, but are usually learnt among the finches. The most detailed study of this question is probably that of Promptov and Lukina (1945) on tits. They distinguish about twenty different calls by the great tit, of which all but three, the alarm, fighting, and long-distance calls, must be learned. Learning a phrase implies imitation. Imitation is rather rare in animals, for an obvious reason. Animals do not have mirrors. A dog cannot see itself snatching, and a cockatoo can barely see itself raise its

crest. If it does so it looks as unlike another cockatoo's crest, as my nose looks unlike anyone else's to myself, until I use a mirror. But a sound made by Y produces sensations in Y like a sound made by X. Y also imitates X's dance, on the ground or in air or water, by simply following X. If we accept the theory that when Y imitates X's signal it tends to bring itself into the mood to perform the action predicted by X's signal, it is clear that the instinct to imitate signals is a help, if not a prerequisite, to unanimous action in social animals. Lorenz (1952, p. 89) writes, "We ask ourselves vainly what it is there for." Here is a hypothesis which is at least worth testing.

Some birds, then, may be said to have a language in the sense of a learnt repertory of vocal signals, each, on the whole, made in appropriate situations by X and evoking appropriate reactions in Y. It differs essentially from human language in being predictive and evocative, as human language can be, but never descriptive. Birds may be called idealists. They have symbols for their own internal states, but not for external objects.

Bees can attract other members of their hive by producing scent from a gland in their backs, but I regard their communication as mainly kinaesthetic and partly tactile, for the following reason. A bee which has found food at a distance and is about to return for more frequently performs a "dance," usually on a vertical comb. Other bees follow it, and those which have done so may then fly out in a direction and to a distance indicated by the dance. There is no doubt that the dance carries information. A human observer can interpret it. It may take place in total darkness. Visual signalling is excluded. It is doubtful whether bees can hear. If so there are innumerable noises in a hive. Those which follow the dancer feel it with their antennae. But they must also receive much the same kinaesthetic sensations (or nervous impulses, if you regard their consciousness as hypothetical) as the dancer. Von Frisch (1954 and earlier) has described the dances in great detail. I shall summarise his work on the directive waggle dance, and my wife's and my interpretation of it (Haldane and Spurway, 1954).*

*Von Frisch's film of these dances was shown at the Royal Institution.

dance consists of a series of rapid runs in a particular direction, during which the abdomen is wagged. The bee then turns alternately right and left, comes back in a semicircle without wagging, and repeats the "waggle run." If the dance is on a horizontal surface, the waggle run is in the direction of the food source. The analogy with a pointer dog is obvious. If it is on a vertical surface, its direction makes the same angle with the zenith as that of the food source makes with the direction of the sun. The distance can be read by a human observer in two distinct ways. Between 100 and 700 metres one extra waggle per run is added for every 75 metres. It is not known whether this code holds at higher distances, as counting becomes very difficult. Between 100 and 3000 metres the number of turns made in 10.45 seconds is diminished by unity when the distance is doubled. That is to say the number of turns falls off in a linear manner with the logarithm of the distance. With greater distances it falls off more slowly. Von Frisch believes that the rhythm of the dance is its main signal of distance. My wife and I have given reasons for regarding the number of waggles as more important. Since the rhythm falls off when the wind is blowing towards the hive or the outward flight is uphill, what is signalled is effort needed or time of flight, rather than distance to be travelled.

Von Frisch, perhaps rightly, has avoided speculation as to the evolution of this dance or its nervous mechanism. My wife and I have been less cautious. We start from Darwin's (1878, p. 210) remark as to pointer dogs, that "the act of pointing is probably, as many have thought, only the exaggerated pause of an animal preparing to spring on its prey." If the dance is an exaggerated and ritualised preparation to fly in a given direction for a given time, we can understand how another bee which has executed the same dance may fly in the same direction. Perhaps a human analogy may make this quantitative co-ordination between two sets of movements of different muscles a little more plausible. A tennis player, if and only if he has followed the movements of a ball with his eyes, that is, to say has performed certain contractions of his eye muscles, will be able to hit it. I suggest that if another man could exactly imitate the movements of the

player's eye muscles (which is clearly impossible) he would be able to strike an invisible ball moving in the appropriate path.

Lindauer (1951) has shown that the same code is used in indicating possible sites for a future hive. The swarm is offered a choice of a number of sites, and finally decides on one as the result of a system which may at least be compared with human voting. This is the most remarkable achievement of animal communication so far known to man.

Until recently the electrical organs of fishes were very awkward for evolutionists. Several species of fish have electric organs which are formidable weapons. "How," asked the Duke of Argyll, "could such an organ have evolved by natural selection, as it is useless until it can deliver a severe shock?" Whereas, for example, a very imperfect leg is of some use in crawling, an imperfect wing in gliding, and so on. Romanes (1892) tried to answer him with no great success. Neither of the disputants laid much stress on the small and apparently useless electrical organs of some other fish, which could be explained neither by design, by natural selection, nor by the transmission of acquired characters. Lissmann (1951) discovered that these small electrical organs are constantly sending out pulses with a frequency of the order of 300 per second, which can be recorded, and which enable the fish to locate conductors, such as other fish, in the water. Lissmann has since found that electrical impulses enable fish to shoal in muddy water (Roy, Soc. conversazione, 1952). It is not yet known whether the communicatory or exploratory function is the more primitive, nor (to the general public) what receptor organ interprets the changed pattern of pulses produced by conductors and boundary layers, though Dr. Lissmann informs me that he has probably located the organ in question.

The analogous use of supersonic pulses by bats to locate obstacles from which they are reflected, that is to say to communicate with themselves (Hartridge, 1920), is almost certainly the conversion of an originally communicatory signal into an exploratory one.

Communication between different species may be beneficial to both, in which case it is stabilised by natural selection, or harmful to one, in which

case the species harmed will tend to evolve so as to negate it. The best example of symbiotic communication is furnished by the persistent visual signals (coloured petals and other organs) and the odours by which plants attract insect and occasionally bird pollinators. Only second to these in importance are the brightly coloured, odorous, and often pleasantly tasting fruits with which they attract mammals and birds which disperse their seeds. In each case the animal finds a food source. Less obviously symbiotic is warning coloration. But it is in fact advantageous to a stinging or unpleasantly tasting insect that a bird should not eat it, and it is equally advantageous to the bird that it should be warned. Hostile communication has a component analogous to lying. An angler fish deceives other fish as does an angler with his shining baits and bogus flies. The most striking negation of communication is cryptic coloration, though I prophesy that when we can analyse odours we shall discover cryptic odours.

There must be continual conflict in many species between the needs for more communication between members of a species, and for less communication with other species. Clearly transient signals, or persistent visual signals which can be hidden, offer a partial solution. One can cease to show them when one perceives the enemy. But in fact the conflict is irresolvable, being part of the conflict between predator and prey, or pathogen and patient. It does, however, seem to be usually advantageous to each of two similar and therefore competing species, whose habitats overlap, that they should be distinguishable by their own members. Otherwise they will interbreed. The hybrids may be inviable or sterile, or their progeny ill-adapted. This means that it is advantageous for such species to differ in respect of some external, superficial character, which is readily recognised by their members. A patch of white feathers is much more important for recognition than an extra tooth or lumbar vertebra, or even an extra toe. Members of other species possessing similar sense organs will generally be able to tell them apart. The behaviour of taxonomists (Pantin, 1954, Spurway, 1955a) is thus an example of vertebrate behaviour. If you accuse a taxonomist of distinguishing between two species on the basis of a superficial difference, he

can fairly answer in a number of cases that the biological function of the difference is to make the distinction possible. It is worth pointing out that "species" means "appearance" in Latin.

Taxonomists usually work on visual characters, which, if they are superficial, are or may be persistent visual signals. The exception which proves the rule is that of Gilbert White (1789) who distinguished the willow warbler (*Phylloscopus trochilus*) and the wood warbler (*P. sibilatrix*) from the chiffchaff (*P. collybita*) by their songs. They have since been distinguished by visible differences. But the differences in song must almost certainly help to prevent hybridisation. Occasionally a chiffchaff produces a song like one of the warblers, and conversely. It will be of great interest to find out whether such deviants have difficulty in finding mates, or even mate with the wrong species.

With this background, what can we say about the probable origin of human language? First of all two points are worth making. We communicate by visual and auditory signals other than language. Some of these signals are pretty clearly innate, for example sobbing and blushing. Others are conventional. Nodding the head in the sagittal plane means "Yes" in most parts of Europe, but "No" in Greece. Many of these signals, which are very important in team work, are probably older than language. Secondly, language is instinctive in the sense that a human baby makes a great many sounds which could be words before it imitates anyone else, and that this imitation is instinctive, though later developed by learning. A baby chimpanzee brought up in a human family makes far less speech-like noises, and does not imitate more than a few words at most of human speech. A dog may understand many human words, but does not imitate them. Thirdly, spoken language conveys a great deal more meaning than written words. The different nuances of a single word such as "Yes" are the rule in animal languages. But there are very few "words."

I assume that at some date in the past our ancestors had a fairly rich vocal repertory for expressing emotions, and that some phrases in it were conventionally used in certain situations only. A *Pithecanthropus* child which gave the danger call or the food discovery call without due cause was probably puni-

shed. As men developed technical skills requiring co-operation, for example hunting in groups, digging pitfalls, and making huts, this vocabulary was enlarged. But it was still not essentially different from the language of social birds, where a phrase can be interpreted as "I want to fly home," "Let us fly home," or even "Fly home." We have still a few such expressions, such as those which in various European languages mean "Let us drink together." As culture developed these essentially hortatory phrases became almost descriptive. The phrase meaning "let us hunt the mammoth" presumably called up images of a mammoth rather than a deer or horse, as "tally-ho" calls up visions of a fox rather than a pheasant or a salmon. But the reference was still to the future.

Acoustic signals must have been particularly important where transient visual signals, such as arm movements, were invisible, as in darkness or forests, or impossible, as when the hands were occupied. They may, as Paget and Johansson thought, have developed from visual signals in part. They must have been particularly important when dogs were domesticated. Dogs hear better than men, and see worse.

This is essentially the account of the origin of language given in the nineteenth century by Noiré and by Engels, the friend and collaborator of Karl Marx. Its critics called it the "Yo-heave-ho" theory. No doubt there was a good deal of gesture, even of ritual, in the preparation for some communal activities. By ritual I mean a communal activity in which signals are emitted and often exchanged, and which, if not always, like a war dance, a preparation for some definite act, at least alters the mood of the participants, as religious rituals do. The effect of rituals is greatly enhanced by the belief that signals are received by one or more supernatural beings. But not all human ritual is religious or magical. I agree with Armstrong that birds may properly be said to perform rituals, and that ritual is thus older than language.

The decisive event in the origin of human language was, I suggest, the use of vocal signals to refer to past, rather than future, events. This must have been a very difficult achievement. An attempt to say "There were salmon in this pool last autumn" with sounds only appropriate to preparation for fishing would

have been actively misleading. Perhaps the habit of boasting helped to bridge the gap. The hunter re-enacting "How I killed the mammoth" must have used vocal signals to refer to past events. And in so far as a ritual re-enacted past events, real or imaginary, it helped to bring about this change of reference.

Pumphrey (1951) and Haldane (1952) independently suggested that the origin of language (I would now say "descriptive language") is rather recent, and probably coincidental with the technological revolution of the Upper Palaeolithic. Techniques of flint chipping had altered little over hundreds of thousands of years. The Aurignacian age saw the introduction of new kinds of tool often cruder than the old ones, but adapted to new uses, along with the first known representations of animals. Some of these developments were perhaps foreshadowed in the Perigordian, and we do not know where Aurignacian techniques were invented. The change may have been much slower at the site of their origin than in south-western France. In France this transition coincided with the replacement of *Homo neanderthalensis* by *Homo sapiens*. Pumphrey thinks that their interbreeding gave rise to an outburst of variation, including some unusually intelligent individuals. I think that cultural hybridisation may have been equally important. If one could chip a flint in a dozen different ways for different uses, it became necessary to name them.

Among the first words referring to the past must have been names for persistent objects such as animals and human individuals. Individual human names were doubtless used earlier for calling individuals. In our primitive cultures it is still believed that one cannot utter a person's name without influencing him or her, and for this reason the "true name" is often kept secret. This belief is probably a relic of a pre-linguistic past where names were always used for hortatory and never for descriptive purposes. Similar beliefs about persistent visual symbols, such as idols and holy books, are still found in more advanced cultures, and are used in our own law courts.

We cannot understand the functions of language among ourselves, let alone among primitive peoples, unless we distinguish its emotive and descriptive functions. A great deal of our speech

and writing, particularly on politics and religion, is primarily emotive, and much of our ordinary speech consists of "intimacy signals" such as "Good morning" which have no descriptive function. It would be ridiculous to object to the use of language for this very important purpose. But I suggest that this is a prehuman function, while its descriptive function is specifically human. A child which asks for food or other needs, or calls attention to conspicuous objects, is still a little animal. When it begins to tell its mother where it has gone and what it has seen, it becomes a human being. At this stage, too, it begins to develop an ordered memory of the past, and I doubt whether such an ordered memory, as opposed to memories of striking experiences, existed before the invention of descriptive language.


The capacity for using language is at least partly innate. Most members of all human societies possess it to a considerable extent. Those who lack it are described as idiots, which etymologically means that they lead private lives. Idiocy is often genetically determined. As language developed there must have been heavy natural and social selection against those who were congenitally incapable of using it, and much of what we regard as "human nature" is, in my opinion, the product of this selection.

If descriptive language originated as recently as Pumphrey and I think, perhaps less than 50,000 years ago, almost surely less than 100,000, we can ask many questions. Did it originate only once? If so are all living peoples the descendants of the inventors, or did it spread by imitation? Languages change so rapidly that there is little hope of reconstructing languages more than about 5000 years old unless wholly new techniques are developed. But a historical point of view may help us to use language better. It is possible that our descendants may find it necessary to invent a purely descriptive and non-emotive language, perhaps on the lines of Russell and Whitehead's *Principia Mathematica*. Meanwhile we must use the same words for description and exhortation. We cannot think clearly unless we do our best to keep these functions separate. But I cannot urge you to do this without using language to arouse your emotions. We cannot escape from our history. But a knowledge

of it may help some of us to act rationally.

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