From Icons to Symbols: Some Speculations on the Origins of Language*

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ABSTRACT: This paper is divided into three sections. In the first section we offer a retooling of some traditional concepts, namely icons and symbols, which allows us to describe an evolutionary continuum of communication systems. The second section consists of an argument from theoretical biology. In it we explore the advantages and disadvantages of phenotypic plasticity. We argue that a range of the conditions that selectuvely favor phenotypic plasticity also favor a nongenetic transmission system that would allow for the inheritance of acquired characters. The first two sections are independent, the third depends on both of them. In it we offer an argument that human natural languages have just the features required of an ideal transmission mechanism under the conditions described in section 2.

KEY WORDS: Phylogenetic icons, heritability, phenotypic plasticity, phenotypic transmission, symbolic language.

In recent years many workers in cognitive psychology and linguistics have seen their disciplines, quite correctly we think, as subparts of theoretical biology. Despite this, it seems that few have thought it necessary to relate these areas of inquiry to the theoretical core of biology; evolutionary theory. In this paper, we will attempt to say something about the symbolic nature of human natural language from an evolutionary perspective.

We hope to develop a plausible evolutionary scenario from presign behavior to prelinguistic iconic communication systems and from these, in turn, to the symbolic ones characteristic of human natural language. The final destination is an evolutionary explanation of what are generally perceived as some of the most salient features of human natural languages; that they can be used to convey information, that their use is not stimulus bound and that they are recursive in that they make unbounded use of finite means. If successful, such an explanation goes beyond the simple and seemingly obvious assertion that language is adaptive. On route it will be necessary to ground in evolutionary theory the distinction between iconic and symbolic communication. It will also be necessary to carefully distinguish between types of evolution and, in particularly to discuss one type whose importance in human evolution is underappreciated, what we will call evolution with phenotypic transmission.

In bringing evolutionary speculation to bear on linguistic concerns one

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must not try to explain too much. As in other areas of biological research one must recognize that not every organic feature is an evolutionary adaptation. The trick is to pick out the right features. In our opinion, many evolutionary explanations of human behavior fail precisely because they ignore this point. In what follows we will be modest in our aims, keeping prominent both the scope and limits of an evolutionary approach to natural language.

I. THE ICON-SYMBOL CONTINUUM

From the beginning of the theory of signs, researchers have made a rough and ready distinction between two types of signs: iconic and symbolic. According to this view signs are things that stand for¹ other things. For symbolic signs (symbols) the relation of standing-for is supposed to be basically arbitrary, i.e., the relation between the symbol and the thing symbolized is supposed to be arbitrary. Signs are iconic if the standing-for relation is characterized by some similarity between the icon and its referent. This distinction was meant to mark inherent properties of the sign-signified relation, with similarity or lack thereof being the relevant parameter.

This accepted distinction has been attacked by Nelson Goodman (1965) and (1967), who raises a question concerning the notion of inherent similarity and thereby the notion of iconicity. Put briefly, he argues that the notion of similarity between objects cannot be cashed out in terms of the total number of properties the objects have in common. On his view, properties are nothing more than predicates. By simple logical sorcery one can show that for any objects a, b and c, for all the properties a and c have in common. In short, one can prove that all objects are equally similar in the above sense. Furthermore, Goodman sees no other way to elaborate some notion of inherent similarity.

We take Goodman's argument as successfully showing that there is no viable notion of similarity *tout court*. What we clearly need to do is elaborate the relevant respects in which things are similar. Goodman thinks that the relevant respects are largely produced by convention. Although such cases surely exist, we also think that psychological and biological considerations can aid in developing a notion of similarity which can serve some of the traditional purposes for which it was intended — in particular explicating the notion of iconicity. Doing this will require removing the notion of similarity from the province of logic and relocating it in the less rarified domains of psychology and biology.

I.1 Perceptual Iconicity

In psychology the notion of perceived similarity is unproblematic. For a particular organism it is easy enough to show that it perceives object a as more similar to c than b is to c. Moreover, it is possible to isolate the parameters which underlie this perceived similarity. The parameters may be innate or learned. Whatever their origins they can be used to reconstruct a notion of iconicity, perceived iconicity. A sign is perceptually iconic for an organism if the organism takes the sign to stand for what it signifies in virtue of a certain kind of perceived similarity between them. Goodman (1968) discusses a nice example of this. Consider a tailor's swatch. It can be taken to stand for a pair of pants and a suit jacket. It is the fact that the swatch is a bit of the material from which the jacket and pants are made which underlies the sign-signified relation in this case. Goodman calls this exemplification. Exemplification in general is a reference relation between a sign and an object based on the two sharing actual properties. So, the swatch and the suit each share such properties as color, texture, weave, etc. Exemplification is closely related to one type of perceived similarity, namely where one object is perceived as similar to another based on their sharing actual properties. (Perceived similarity need not be based on shared proeprties.) When cases of exemplification involve this type of perceived similarity, they are cases of perceived inconicity.

Exemplification is a dyadic relation between sign and thing signified. Perceived inconicity, on the other hand, is a triadic relation between an organism, a sign and a thing signified; an organism O perceives S as an iconic sign of R just in case S exemplifies R in certain respects and O perceives S as exemplifying R in these respects.

I.2. Ritualization

Perceived inconicity is not the focus of this paper. It does, however, underlie the first step of a process which is of particular importance in the biology of communication, a process called *ritualization*.² According to Wilson (1975, p. 594), ritualization is "the evolutionary modification of a behavior pattern that turns it into a signal [sign] used in communication or at least improves its efficiency as a signal [sign]."³ The end products of this process are signs we will describe as *phylogenetically iconic*. From a synchronic point of view the sign-signified relation may appear to be purely arbitrary, and so purely symbolic. Diachronically, however, one can trace an evolutionary relation between the sign and what it signifies. In those cases where a sign can be described as phylogenetically iconic (and where we can trace the actual phylogeny) the relation between the sign

and the thing it signifies — which synchronically viewed appears arbitrary — can be explained.

I.2a

Ritualization can be characterized as having three stages. At the first stage one organism interprets the action, or some part thereof, of another as a sign of that action. From observing this behavioral sequence the first organism is able to infer (perhaps unconsciously) the behavior of the second. When this happens this part of the action becomes a sign. Typically, the relevant part of the behavioral sequence will be an *initial* part and the inference will be a *predication* of the subsequent behavior. For instance, birds just prior to flight characteristically crouch, raise their tails and slightly spread their wings. Any bird able to recognize that this behavior pattern is generally followed by flight can construe the pattern as a sign of flight. In our terms, the sign is perceptually iconic to the behavior signified in that the sign exemplifies part of the total motor pattern of flight and is perceived as exemplifying it.

The linchpin for this move from behavior to sign is perceived iconicity. At this stage, the change from behavior to sign takes place purely on the receptor side. It involves no change in the original behavior and is solely dependent on the ability of the receiver.

In an evolutionary account of the origins of signs the importance of perceived iconicity cannot be overstated. There are two questions to be answered. The first is why the bird should perceive anything as a sign of flight. The second is why the bird should key on a particular subsequence of the total motor pattern of flight as a sign of flight, i.e., why what functions as the sign should be perceptually iconic.

To the first question, we can give a straight-forward adaptive account. When it is important to know when your colleagues are about to fly, as it is for exemple in some flocking birds, then selection will tend to shape both the perceptual and conceptual apparatus in ways that will enable the birds to take something as a sign of flight.

An answer to the second question comes only when one appreciates the way perceived iconicity functions within an evolutionary explanation of the sort given above. As the case of flocking birds illustrates, there are cases where reliable signs are selected for. What makes a sign reliable? A general feature of causal sequences is that one element is a reliable indicator of the following elements, in fact nothing is more reliable. Some behavior patterns are causal sequences. In such cases parts of a behavioral sequence are reliable indicators of the behavior to follow. Therefore when there is selective pressure for reliable signs, organisms able to treat such subparts of behavior patterns as signs will be at a selective advantage. By definition such signs exemplify the behavior they signify. By natural selection organisms will be adapted to perceive these exemplifications. Therefore selective pressure for reliable signs will be pressure for perceptual iconicity.

I.2b

At the second stage of ritualization the effectiveness of the sign as a communicative device is increased. Typically what happens is that certain features of the behavior which function as the (perceptually iconic) sign are exaggerated, stylized, and articulated. So, for example, in pigeons the preflight behavior pattern which serves as a sign of flight has been exaggerated beyond what is physiologically necessary for flight and beyond what, presumably, was once the preflight pattern, (Lorenz 1977, p. 211). The function of such exaggeration is to make it less likely that the sign will be missed or misunderstood. Changes at the receiver end may also be involved in making the sign more communicatively effective. So, in general, the threshold of perception of the signing behavior will be lowered.

Unlike the first stage which involved only changes at the receiver end, this second stage can, and typically does, involve changes at both ends. Thus selection will mold both sender and receiver in a process which enhances communication.

I.2c

At the end of the second stage signs are still perceptually iconic but ritualization often continues further. By a process we will call *transference* signs evolve which are not perceptually iconic for what they signify. Examples of this process and its results abound. For instance, part of the courtship ceremony performed by the male grey heron involves movements appropriate to fishing behavior (cf. Wilson 1975, p. 226). In general the results of this process will be signs which are *not* perceptually iconic to the things they signify. Perceptual iconicity, then, will not completely explain the sign-signified relation manifest in animal communication.

As in the first stage, transference involves forming a new connection between a sign and what it signifies. In the first stage the sign is newly created and its connection to what it signifies is explained by perceived iconicity. Transference doesn't create a new sign but switches an old sign to a new referent. The new sign-signified relation is not perceptually iconic because transference fully destroys the exemplification relation between a sign and that which it signifies. Presumably, however, perceived similarity is involved in transference and plays the role that perceived iconicity played in the first stage. We should note that without detailed knowledge of the evolutionary history of this process it may well be baffling why some sign is taken as the sign of what it signifies.⁴

I.3 Phylogenetic Iconicity

The results of transference are not perceptual icons. However, there is still an important sense in which they are iconic, they are *phylogenetically iconic*. By this we simply mean that they are the produces of ritualization, and in particular transference. Importantly, even after transference, the particular sign-signified relation is susceptible to an evolutionary explanation. Just as in cases of perceived iconicity where we can explain why some sign has some particular referent, such an account is possible here as well. However, to effect such an explanation one must assume a diacronic perspective.

I.4 The Continuum

Based on our account of ritualization, we can reconstruct the old distinction between icons and symbols by placing them on a continuum on which they mark certain biologically important points. At one end we have the results of the first stage of ritualization; signs which are perceptually iconic. The importance of perceptually iconic signs is that they are the means by which sign behavior originates in organisms.

Ritualization, in particular transference, takes us to a second important point on the continuum; signs which are phylogenetically iconic. Signs of this type have elements of both the purely iconic and the purely symbolic. The iconic elements can be traced diachronically, though when viewed synchronically, they may appear to be purely symbolic. Not only does it appear symbolic to the investigator, but there is a sense in which it must so appear to the organism itself. The reason for this is that after transference the exemplification relation is lost. It is tempting to speculate that the perceptual and conceptual mechanisms used at this point are important preadaptations to purely symbolic communication.

A third important point on this continuum — pure symbols — can be characterized by exclusion. Pure symbols are signs which are neither perceptually nor phylogenetically iconic. Earlier characterizations of symbols depended on notions of arbitrariness. Goodman's critique of similarity carries over to such notions. Just as we must replace similarity *tout court* with similarity-in-certain-respects so too for arbitrariness. Our characterization of symbols tries to pick out the biologically relevant respects.

Up till now we have concentrated on the how and why of the moves to point 1 on our continuum and from 1 to 2. With the exception of human language, the paradigm example of a pure symbol system,⁵ the vast majority of known animal communication systems seem to fall on the continuum somewhere between points 1 and 2. In the remainder of this paper we would like to focus on the move from 2 to 3 (see figure 1). To do this we will have to attend to features of animal communication systems other than the iconicity of their signs.⁶ In particular, we will argue that the move away from the finitude of the systems -30 to 40 different signals on the average (cf. Wilson 1975, p. 183) – and the fact that the messages of the system are tied to the here and now (cf. Lorenz 1977. p. 147) have been selectively important.⁷ Before doing this it will be necessary to discuss the role of phenotypic plasticity in human evolution.



Fig. 1.

II. PHENOTYPIC PLASTICITY AND THE EVOLUTION OF ACQUIRED VARIATION

Phylogenetically iconic communication systems serve many animal species well. Why then did a purely symbolic communication system evolve in *Homo sapiens*? We will argue that this evolution is part and parcel of the evolution of extreme phenotypic plasticity in man. To understand (in an evolutionary sense) certain basic features of natural languages one must understand this selection pressure for plasticity.

II.1 Types of Evolution

Traditionally a distinction has been made between biological and cultural evolution. But this distinction does not suffice for our purposes; to understand human evolution one needs a finer grained view. Abstractly viewed evolution is the process of change in a group of reproducing entities resulting from the satisfaction of the following three conditions:

- (i) Variation: There is some variance among some traits of these entities
- (ii) Heritability: This variation is at least in part heritable.
- (iii) Differential reproduction: Different variants reproduce at different rates.⁸

These three conditions are each necessary and (usually⁹) jointly sufficient for evolution to occur. The traditional distinction between biological and cultural evolution is based on differences in inheritance mechanisms -

genetic vs. cultural. Thus, for example, if a behavior is discovered or invented by an individual in a population and spreads by behavioral means from parent to offspring the resultant change would be described as cultural evolution. in contrast, if a gene predisposing its bearers to engage in that behavior arose, was selected for, and passed to subsequent generations, the resultant change would be described as biological evolution. This distinction however is not very useful. A better way to draw the distinction between biological and cultural evolution is in terms of condition (iii), i.e., in terms of differences in the processes resulting in differential reproduction and in the entities on which they act. Of all the processes resulting in differential reproduction the most interesting are selection processes.¹⁰ Thus biological evolution results from natural selection acting on biological entities and cultural evolution results from cultural selection acting on cultural entities.¹¹ Notice that on this view, to characterize an evolutionary process as biological is to say nothing about the mechanism of inheritance.

In the above hypothetical example the *only* difference was the mechanism by which behavior was transmitted from parent to offspring. The section processes and the entities on which they acted are the same and are purely biological. Thus the evolutionary process as abstractly characterized above is the same. The utility to this way of drawing the distinction between cultural and biological evolution will, we hope, become evident below.

Our focus will be on biological evolution but on a heretofore underappreciated type of biological evolution; what we shall call evolution with phenotypic transmission.

II.2 Heritability

In population genetics heritability (h^2) is a highly technical notion that does not exactly correspond with its everyday counterpart. Some population geneticist *define* h^2 in genetic terms. We will consider this definition shortly but first we need to develop a broader notion, one not committed to any specific mechanism. After defining this broader notion (following Roughgarden 1979), we will be able to appreciate the role of evolution with phenotypic transmission.

A quantitative character is one that shows more or less continuous variation within a population. Examples include height, amount of pigmentation and even such things as disposition to explore one's habitat. Any varying character that can be assigned to some metric can be considered a quantitative trait. This contrasts with characters like wrinkled versus smooth coat in peas.

What is it for a quantitative trait to be heritable in a population? Intuitively, if the trait like height is heritable then taller than average parents tend to have taller than average offspring, and shorter than average parents tend to have shorter than average offspring. This intuition forms the basis of the purely phenotypic definition of h^2 that follows.

Suppose we have some quantitative character (say number of selfgrooming behaviors per day) that varies in a population. Let X_i be the value for any individual *i*, and \overline{X} be the mean value of X in the popultion.

We are concerned with the relation between offspring deviation from the mean and parental deviation from the mean. Let X_o denote the average offspring value (average number of self-grooming behaviors per day) from parents whose midparent value $((X_{\sigma} + X_{\varphi})/2)$ is X_p . The offspring deviation from the mean is $(X_o - \overline{X})$ and the parental deviation is $(X_p - \overline{X})$.

A plot of offspring deviation against parental deviation (a scatter diagram) would yield a regression line whose slope is the heritability, h^2 . The formula is,

(1) $(\mathbf{X}_o - \overline{\mathbf{X}}) = h^2 (\mathbf{X}_p - \overline{\mathbf{X}})$

(Roughgarden 1979, p. 136, formula 9.1). Adding \overline{X} to both sides yields:

(2)
$$X_o = h^2 X_p + (1 - h^2) \overline{X}$$

(Roughgarden 1979, p. 136, formula 9.2). This formula makes clear just what h^2 is. It tells us that the average offspring value in numbers of selfgrooming behaviors per day depends on the mid-parent value to degree h^2 and on the population mean to degree $(1 - h^2)$. The values of h^2 lie between 0 and 1. If h^2 is 1 then the average offspring value is their midparent value, if 0 then the average offspring value is simply the population mean. Thus the higher h^2 the more offspring resemble their parents in deviations from the mean.¹²

Defining h^2 as the offspring-midparent regression makes no assumptions about the mechanisms of inheritance (except that the mechanism works from parent to offspring, a very strong assumption but one not relevant to present concerns). The definition could just as well be applied to the inheritance of height (presumable genetic) as to the inheritance of wealth (presumable nongenetic). But in standard cases of inheritance studies by population biologists the mechanism of inheritance is genetic. Let's turn our attention to a genetic definition of heritability.

The total variance in a phenotypic trait in a population can be divided into two types, *between-genotype-variance* and *within-genotype-variance*. Some phenotypic differences in a population are due to genotypic differences; this variance, *the between-genotype-variance*, is represented by 'V_G'. The remaining variance, obviously, is not due to genotypic differences. The name given this type of variance is *environmental variance*, V_e¹³ Thus we have the following equation (where 'V_T' stands for the total variance):¹⁴

$$(3) \qquad V_{\rm T} = V_{\rm G} + V_e$$

The between genotype variance, V_G , can be broken down into two components; the *additive genetic variance*, V_A and the *dominance variance* V_D . So

$$(4) \qquad V_{\rm G} = V_{\rm A} + V_{\rm D}$$

 V_A is that part of V_G that can be attributed to the separate alleles composing the genotype (independent of their context). Thus V_A is the component which is heritable. V_D is the remaining variance.¹⁵

We are now in a position to give a genetic counterpart to the phenotypic definition of h^2 . From equations (3) and (4) we get the following equality:

(5)
$$V_{\rm T} = V_{\rm A} + V_{\rm D} + V_e$$

The additive component of the phenotype is that which is passed down genetically from parent to offspring, so of the total variance only the additive part is (genetically) heritable. Thus in cases of genetic inheritance we expect the following quantity to be closely related to h^2 :

(6)
$$\begin{pmatrix} \text{fraction of total} \\ \text{phenotypic variance} \\ \text{due to additive effects} \end{pmatrix} = \frac{V_A}{V_A + V_D + V_e}$$

(Roughgarden 1979, p. 154, formula 9.34). In fact using standard onelocus models of population genetics it can be shown that,

(7)
$$h^2 = \frac{V_A}{V_A + V_D + V_e}$$

(See Roughgarden 1979, pp. 155 and 156 for derivation of this formula.)

Some population geneticists take (7) as the *definition* of heritability. We cannot do so since we are concerned with non-genetic modes of heritability. Thus we follow Roughgarden in defining h^2 as the offspring—midparent regression, and taking (7) as a result which holds only under certain conditions. As a rough approximation, one sufficing for present purposes, we will say that when (7) holds inheritance is genetic, and when it doesn't hold the mechanism of inheritance is nongenetic.¹⁶ Thus the purely phenotypic definition of h^2 and equation (7) give us the theoretical background necessary for drawing the distinction between biological genetic evolution and biological evolution with phenotypic transmission.

II.3 Phenotypic Plasticity

As mentioned above, we will argue that the evolution of human linguistic communication is closely connected to the evolution of extreme phenotypic plasticity. Basically phenotypic plasticity is the ability of a genotype to produce various phenotypes. Recall that the total phenotypic variance in a trait can be divided into the between-genotype-variance, V_G and the within-genotype-variance, V_e (equation 3 above). V_e is a measure of the range of phenotypes a given genotype can produce.

Roughgarden (1979, p. 216) suggests that genotypes with large V_e 's be described as phenotypically plastic. We agree, but with this qualification: If V_e is taken as the variance of actual phenotypic distributions of genotypes, then V_e cannot be identified with phenotypic plasticity. Rather it can only be viewed as a measure of phenotypic plasticity, and an imperfect one at that. Phenotypic plasticity is clearly a dispositional notion. A genotype may well be able to produce diverse phenotypes in many diverse environments. But if it happens to find itself in only a small percentage of that range of environments then its actual or manifest V_e may be rather small. Assuming the hypothesis of this example it would be absurd to conclude that this genotype had a low level of phenotypic plasticity. Still, an imperfect measure is better than no measure at all. So recognizing its limitations we will take V_e as a measure of phenotypic plasticity.

II.4 The Advantages of Phenotypic Plasticity

What are the selective advantages of phenotypic plasticity? In a review article on phenotypic plasticity in plants, A. D. Bradshaw (1965) suggests that high phenotypic plasticity is advantageous in environments where fluctuations occur rapidly in time (on the order of a lifetime) or in space.¹⁷ The reasons for this are fairly obvious. The argument becomes even more compelling when one adopts a realistic assumption about plasticity. That is, that plasticity is adaptive. By *adaptive plasticity* we mean that actual phenotypic distributions are affected by environmental demands, so that the likelihood of a given phenotype being produced is greater in environments where it is better adapted and lesser in environments where it is less adapted. For instance, in the water plant arrowhead (*Saggitaria saggittifolia*) submerged leaves have a quite different shape from leaves in air. The ability to produce two shapes of leaves is plasticity. The ability to produce the right setting is adaptive plasticity.

We are primarily concerned with behavioral plasticity. One might think that plastic behavior is "learned behavior", that in contrast to "innate behavior". This old dichotomy is a conceptual muddle. As Mayr (1976, Chapter 47) has pointed out, behavior is better conceived of as governed by programs varying in their degree of openness. So our question is: What are the selective advantages of open programmed behavior? The considerations discussed above seem to apply here as well. In rapidly fluctuating environments where no one behavior is optimal it is advantageous to have the relevant behaviors governed by an open program so that appropriate behavior can be triggered by environmental cues. Here the hypothesis of adaptive plasticity is crucial.

Perhaps the major point to be gleaned from the literature on plasticity is that the more unpredictable the environment the greater the advantage of flexible, open programmed response.¹⁸ We have briefly covered some reasons why this is so. Roughgarden (1979, p. 216) suggests an entirely different reason why this might be so. Before presenting this suggestion we must examine the relations between phenotypic plasticity, heritability, and response to selection.

Recall our abstract characterization of evolution: evolution is the change in a population resulting from the differential reproduction of heritable variation. Why heritable? Intuitively, selection according on nonheritable variation will result in differential reproduction, but the differential reproduction will not affect the next generation, i.e., it will have no evolutionary effect. Agreeing with that intuition the following relation can be demonstrated for cases of directional selection:

(8)
$$\begin{pmatrix} \text{response to} \\ \text{selection} \end{pmatrix} = h^2 \begin{pmatrix} \text{strength of} \\ \text{selection} \end{pmatrix}$$

(Roughgarden 1979, p. 142, formula 9.9). Thus the rate of evolutionary change depends on both the strength of selection and h^2 .

From formula (7) we can see that as V_e tends to infinity, h^2 must tend to 0 (see Roughgarden 1979, pp. 146 ff). The biological reason for this is that as V_e increases the phenotypic distributions of the genotypes increasingly overlap. This has the effect of hiding the genotypic variation from selection Thus the higher V_e , the lower h^2 and so the lower the response to selection.

Roughgarden (1979, p. 216) suggests that in an unpredictable environment the best evolutionary strategy¹⁹ may be to be genetically unresponsive to environmental fluctuations. Why? In an unpredictable environment there is no discernable direction to environmental changes. Environmental states are as likely to reverse as to continue changing in a given direction. Thus the best evolutionary strategy may be to stay put genetically rather than to try to track a capricious environment. If this is so, then there would be selection for high plasticity since as we have just stated high plasticity, high V_e , effectively shuts off genetic response to selection.

Roughgarden's suggestion may partially explain some of the observed plasticity in plant and animal species. We will argue that it has special relevance to the evolution of human linguistic communication. But first we need to ask whether or not high plasticity is an unmixed blessing.

II.5 The Disadvantages of Phenotypic Plasticity

One might think that if the genome could "know" its environment completely and program the correct response for every environmental situation then flexible open-programmed response would be unnecessary. Thus in unpredictable environments high plasticity is advantageous, in predictable environments it is unnecessary but neutral. Such a view ignores the costs of learning (or more generally, obtaining information from the environment). This will receive further discussion later in this paper; for now let us simply note that learning takes time and energy and may often involve considerable danger.²⁰ (Consider for example the problem of learning who your predators are.) Like all other biological traits phenotypic plasticity is not inevitably selected for. Its selective value depends on the ecological setting and may be either positive or negative.²¹

II.6 The Advantages of Evolution with Phenotypic Transmission

To this point we have distinguished biological genetic evolution from biological evolution with phenotypic transmission and have discussed some advantages and disadvantages of phenotypic plasticity. We will now concentrate attention on the evolutionary significance of plasticity in one particular ecological setting — a rapidly, unpredictably fluctuating environment.²² We will argue that the optimal solution to the problems presented by such an environment is evolution with phenotypic transmission (which allows for the inheritance of acquired variation).

Recall the discussion above of the main advantages of phenotypic plasticity. First, open-programmed response is advantageous in that it makes it possible for an organism to respond appropriately to environmental conditions that cannot be predicted by the genome. By hypothesis, such conditions characterize capricious environments. Second, plasticity may well have another advantage in such environments. It effectively shuts off genetic response to environmental change. By hypothesis, genetic tracking will always lag behind the environmental changes. As the changes are not directional, staying genetically put is not less successful than such genetic tracking. Furthermore if one can assume that the capricious environmental fluctuations within environmental space are relatively circumscribed, then staying put at a genotype relatively well adapted to the mean will be better than unsuccessfully tracking the environment. In short, from a genetic point of view phenotypic plasticity is a better solution to the problems posed by rapidly and unpredictably fluctuating environments than the evolution of closed programs of behavior.

However a much better, indeed seemingly optimal, solution exists, namely evolution with phenotypic transmission. We can appreciate its advantages by contrasting it with the above solution.

A feature of the above solution (viz. phenotypic plasticity) is that the information which fills in each organism's open program during its life is lost to the next generation. Unless there is no correlation between successive environmental states, this information will be relevant to the next generation.²³ Genetic evolution cannot gather and transmit this information for the reason already mentioned, viz. genetic change cannot keep pace with the environmental changes. Thus information gathered and transmitted genetically would be consistently out of date. The advantage of the open-programmed-no-evolution strategy is that it is not misleading. It patiently awaits the input of the environment before directing the behavior of the organism. The disadvantage is that the organism has no head start.²⁴ Clearly an optimal solution would be one that was not misleading and yet gave the organism a head start.

The evolution of acquired variation can be just such a solution provided the nongenetic mechanism of inheritance is of the right sort. What is needed is some mechanism capable of reliably transmitting the "wisdom" gathered in an organism's life to its descendants. The reason why this type of evolution succeeds where genetic evolution fails is that it can keep pace with a rapidly changing environment. Unlike the genetic transmission of information which in this ecological situation would inevitably transmit misleading, out of date information, effective phenotypic transmission is capable of transmitting all and only that information which proved useful in the last generation.²⁵ Put another way, the rate of evolutionary change with phenotypic transmission can be much faster than that of genetic evolutionary change.

II.7 Summary

A necessary precondition for evolution with phenotypic transmission is phenotypic plasticity. We have argued that in rapidly fluctuating unpredictable environments phenotypic plasticity has a positive selective value. Furthermore, we have argued that if the capricious environmental changes are not *too* capricious i.e., if the benefit of receiving the still useful information from the last generation exceeds the cost of receiving the out of date information, then the optimal means for adapting to such environmental changes involves the evolution of acquired variation (see Boyd & Richerson 1985).

III. THE EVOLUTION OF LANGUAGE

What features must a mechanism of phenotypic transmission have to solve the environmental problems discussed in II. There are three prominent features that any such mechanism will have. First, it will be adequate for conveying information; in particular, information relevant to survival and reproduction. Second, it will be flexible enough at any time to be able to convey unpredicted messages. What types of information will be biological relevant cannot be predicted by the organism in the context of a rapidly fluctuating environment. Third, it will be able to convey messages which are not stimulus bound. This means that the message can be transmitted and understood in the absence of the referent of the message. To see how this point follows from the earlier discussion will require a bit of a digression.

III.1 Learning

How do organisms acquire non-innate information about their environment? One way is through trial-and-error learning. As Pulliam and Dunford point out, "the obvious problem with trail-and-error learning is error" (1980, p. 435). Indeed, error can be costly if not fatal. For example, an organism that learns that a food source is poisonous by eating it may have acquired this information at considerable cost. A more felicitous way of learning this is to observe your neighbor eating from this source and its consequent effects. Such learning is called *observational learning*. But observational learning is not risk free and in the selection scenario we have been considering, it will be too limited.

We will call a third learning technique *instructional learning*. Such learning essentially involves communication. Thus the learner acquires the requisite information through signs. When the sign is not stimulus bound instructional learning can be even less risky than observational learning. For example, it is better to learn of the dangers of quickly spreading fires by being told, than by observing them in person. This advantage of non-stimulus-bound communication will hold in most environments. However, non-stimulus bound communication is particularly important in unpredictably fluctuating environments. By instruction one can teach or learn the appropriate response to some rare event. Rare events are not necessarily biologically unimportant. Only by non-stimulus-bound communication be reliably transmitted, since by hypothesis one could not depend on the environment supplying the situation necessary for observational or stimulus bound instructional learning.²⁶

III.2 Iconic Systems in Capricious Environments

From this brief discussion, it should be clear that an iconic communication system cannot serve as an adequate mechanism of phenotypic inheritance in a capricious environment. Recall that, as *a matter of fact*, iconic systems are stimulus bound and finite. We have discussed their stimulus bound nature above and have nothing more to add here. The finitude of iconic systems makes them incapable of transmitting the unpredicted (and unpredictable) types of messages which *will* be important in such a scenario. By the nature of ritualization, it is clear that, synchronically, iconic communication systems *must* be finite. Although, there is a sense in

which phylogenetically they are unbounded, the process of ritualization will not be able to introduce new signs fast enough to meet the need at hand. For the purposes of phenotypic inheritance it is the synchronic finitude which eliminates them as a possible mechanism.

In sum, any system which is capable of being an adequate mechanism of phenotypic inheritance, under the selection conditions we have been considering, cannot be iconic. That is not to say that a symbolic language is a necessary condition for phenotypic transmission. Many animals lacking symbolic language do have a rudimentary form of phenotypic transmission (see Bonner 1980). Rather our argument is that insofar as there is selection for evolution with phenotypic transmission there is selection for a purely symbolic communication system. In other words, there is pressure to move from 2 to 3 our icon-symbolic continuum, (Figure 1).

III.3 Three Prominent Features of Natural Language

In the previous section we argued that the iconic communication systems characteristic of animal communication are inadequate as mechanisms of phenotypic inheritance. Now we will point out that three prominent features of human natural languages make human language just the sort of mechanism needed. More interestingly, we will finally argue that these features of natural languages can be explained if we assume that they result from the selection pressure for evolution with phenotypic transmission. Thus, we will be giving an evolutionary explanation of the fact that all human natural languages do have these very features. (We shall not try to extend our argument to an explanation of these features as *linguistic universals.*²⁷ However, we do think our argument would be relevant to such an explanation.)

As has often been noted, human natural languages have the three prominent features that we claim are necessary for any adequate phenotypic inheritance mechanism: the capacity to convey information, the unbounded types of messages that can be conveyed, and the capacity to convey stimulus independent messages. It is obvious that human languages can be used to convey information. The other two features are less obvious and more interesting.

Virtually all investigators of natural languages take as definitive of these systems their unbounded productivity. Two basic features of such systems are responsible for this productivity. First, the basic signs of the system are subpropositional. Second, natural languages are recursive.

Intuitively, a proposition is that which conveys a whole message. Human languages are unique among animal communication systems in that a proposition is itself a sign made up of more basic signs. The message of a whole proposition is a function of the discrete contributions of its parts. This contrasts sharply with all other known animal communication systems, with the possible exception of the waggle-dance communication system of bees.

The discrete subpropositional structure in human natural languages is important here because it allows the recursive production of new *types* of messages.²⁸ In the animal communication systems with no subpropositional structure there is no recursive production of new types of messages and in fact the maximum number of basic messages is between 30 and 40 (Wilson 1975, p. 183). Even in the waggle-dance system new types of messages are not produced. The system is best seen as having one or two basic messages which can be continuously modified along two dimensions (see Wilson 1975, pp. 177–78).

As we have noted previously, the third prominent feature of human natural languages is their stimulus independence. As both Chomsky (1972, chap. 1) and Lorenz (1977 especially pp. 160–61) have emphasized, human languages stand in striking contrast to all other known animal communication systems in that one can use a human language to send or understand messages about things remote from both speaker and hearer in both place and time.^{29,30} Not so for other animals. As Lorenz points out, "an experienced jackdaw can only tell an inexperienced jackdaw that cats are dangerous when a cat is actually there to demonstrate the fact, and a rat can only teach its inexperienced fellows that a particular bait is poisonous when the bait is actually present." (1977, p. 160).

III.4 An Explanation of the Three Features

We have just pointed out that human natural languages have the features required of a phenotypic inheritance mechanism adequate for evolution with phenotypic transmission in a capricious environment. If we assume that our ancestors did in fact live under such conditions, we can explain the fact that human natural languages have these features as due to the shaping effects of natural selection.

Is there any reason to believe that our biological ancestors did live in such an environment? As in all cases of reconstructing the evolutionary past, very direct evidence is hard to come by. But this notwithstanding, the evolutionary coherence of the story we have presented strongly supports this hypothesis. The features of language we have tried to explain are very general and abstract. We have eschewed discussion of the particular mechanisms which underlie this system in humans.³¹ Unless one believes that human language is an evolutionary accident,³² it is *these* very general, basic and distinctive features one would expect an evolutionary account to explain. As everything known about human evolution is compatible with such a view, we consider our account strong evidence in its favor.

IV. CONCLUSION

The primary aim of this paper has been to uncover the origins of human language. To do this it has been necessary to develop replacements for the traditional notions of icon and symbol adequate to evolutionary concerns. These refurbished notions have enabled us to trace an evolutionary relationship between human symbolic languages and iconic communication systems of other animals. On the way to our conclusion we discussed the important selective advantages of the evolution of acquired variation. Our evolutionary perspective led us to search for the adaptive significance of language. In our account, its primary adaptive significance is that language is an adequate vehicle for phenotypic transmission. In other words, our answer to the evolutionary question, "What is language for?", is that its evolutionary purpose is to transmit information across generational time. Interestingly, on this account it is not obvious that language is adaptive. In fact only under certain rather specific conditions would there be selection for language as a mechanism for phenotypic inheritance. However, we want to emphasize that there is nothing in our account that limits the use of language to this one function. For example, to note one important case, it is also the key vehicle for another kind of evolution, namely, cultural evolution. In addition, it is clear that language is also used to tell jokes, order in restaurants, and even to write papers about language itself.

NOTES

¹ In what follows we will say that a sign *stands for* what it *signifies* or its *referent*. Depending on the nature of the sign, the referent is an object, or a state of affairs, or a property, etc. Signs will also be said to express *propositions* or *convey information*. Where relevant the context should disambiguate the type of sign being discussed.

 2 Recently a cultural process analogous to the phylogenetic process of ritualization has been studied in Smith (1977). He terms this process *conventionalization* and uses the term formalization' as a generic term for both processes.

³ The following discussion of ritualization depends heavily on Wilson (1975) and Lorenz (1977).

⁴ For a nice example of this see Wilson's (1975, p. 227) discussion of the evolution of different forms of ceremonial food exchange in certain species of flies belonging to the family Empididae.

⁵ Perhaps there are other examples. See Wilson's discussion of chemical communication in the last part of his discussion of ritualization (1975, p. 231).

⁶ Henceforth the term 'icon' (and its cognates) will refer to signs which we have defined as perceptually or phylogenetically iconic. Our use of the term 'symbol' should similarly be construed as a technical term in accordance with our definition above.

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⁷ In this paper we will not try to explain why systems falling along the continuum between points 1 and 2 are in fact finite and only can produce messages tied to the here and now. Our account of the first stage of ritualization does explain why perceptually iconic signs are tied to the here and now. Transference appears to preserve this link, though it is not clear why. That is not to say that this feature of icons is unexplainable; we just do not have the explanation. Similar remarks apply to the finitude of the systems, although we will have something to say about this below (Sec. III.2).

⁸ Adopted from Lewontin (1978).

⁹ Differential reproduction is a force. Together with conditions (i) and (ii) it will result in evolutionary change provided it is not counterbalanced by other forces (e.g. mutation), see Brandon (forthcoming).

¹⁰ Many biologists equate natural selection with differential reproduction, thus making the distinction between selection and random drift conceptually impossible. That is a serious mistake. For further discussion see Brandon (1978) and (1981b).

¹¹ Cultural evolution has long been thought of as vaguely analogous to biological evolution, but until recently the analogy has not been carefully explored. Now cultural evolution is beginning to receive serious attention from people trained in population biology. For perhaps the seminal work in this field see Cavalli-Sforza and Feldman (1981). They draw the distinction between biological and cultural evolution in a way which agrees with our treatment.

¹² There are important limitations on this purely phenotypic definition of h^2 . For further discussion see Roughgarden (1979, chapter 9).

 13 This is not the happiest choice of terms. The idea is that the variance within a given genotype is due to environmental differences. This may well be, but one should not simply assume it. The possibility that epigenesis is an essentially stochastic process should be left open.

¹⁴ This equation and what follows in the genetic definition of heritability require some strong assumptions. See Roughgarden (1979, chapter 9) for details.

¹⁵ For details see Roughgarden (1979, pp. 148–51).

¹⁶ Strictly speaking this last claim is false. In particular, in multi-loci models of genetic inheritance (7) does not hold exactly. What is true is that when inheritance is nongenetic (7) will not be even approximately correct. To be candid, we should also point out that our claim is hardly operational. Operationally the parent-offspring regression is usually definitive of the additive genetic variance. Nevertheless, in theory, and sometimes in practice, one can distinguish genetic and nongenetic transmission and formula (7) provides the *conceptual* framework for so doing.

¹⁷ Discussed in Roughgarden (1979, p. 216). (See also Levins (1968) and Wimsatt (1980)). ¹⁸ For a fuller discussion see Mayr (1976, chapter 47) or Bonner (1980, especially chapter 7).

¹⁹ Talk of evolutionary strategies is just a convenient way to refer to the results of selection. Of course the selection process involves no foresight or planning.

²⁰ See Mayr (1976, Chapter 47) and Pulliam and Dunford (1980, especially chapter 4) for further discussion.

²¹ See Brandon (1978) for an argument that no trait is invariably selected for.

²² In this context the relevant notion of unpredictability (or capriciousness) is not absolute unpredictability but rather unpredictability-to-the-population. For a nice discussion of related matters see Wimsatt (1980).

 23 For a more detailed discussion of the conditions under which the transmission of information gathered in one generation will be useful to the next see Boyd and Richerson (1985).

 24 Obviously an open program gives some structure to the organism's behavior. By 'no head start' we simply mean that the organism has to wait for environmental input. See discussion in sec. III below.

²⁵ By hypothesis not all information useful to one generation will be useful to the next, but on the supposition that most of the relevant ecological changes will be noncatastrophic some of the information will be useful.

²⁶ For a nice discussion of learning see Pulliam and Dunford (1980).

²⁷ On the notion of linguistic universals see Chomsky (1965, chapter 1) and Hornstein and Lightfoot (1981, introduction).

²⁸ For a semantic analysis of recursivity which sees it essentially as the production of new predicates see Quine (1960, chapters 3 and 4). For a full discussion and alternative view of what recursivity involves see Davidson (1965) and (1967). For our purposes the difference in these views is unimportant.

²⁹ Griffin (1976) has argued that the waggle dance communication system is not stimulus bound. The evidence that bees can refer to nectar sources relatively distant in space is much more convincing than the evidence concerning the temporal dimension.

 30 It is interesting to note that in this case ontogeny recapitulates phylogeny since in developing language young children first talk only about the here and now (see Brown, 1973).

 31 Nor do we believe that an evolutionary account *should* be expected for most of the particular universals linguists discuss, e.g., the structure dependency of transformations or the binding theory. The view that every feature of the genome has an adaptive explanation is not one evolutionary theory is committed to (see Brandon 1981a).

 32 I.e., not a biological adaptation. For a full discussion of the notion of adaptation used here see Brandon (1981a).

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