# Notes on the Evolution of Behavioral Systems:
# Part 1•: Information Processing, Signaling, and Biochemical Computers

**Eth. & Behav. Ecol.**
**Biology 287**
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## I. Introduction

A. You are familiar with matter and energy as the bases of the physical world. Likewise, they form much of the basis for the biological world. You are used to thinking about the structures and processes of an organism being designed to build or destroy structure and store or release energy.

B. We define the term "**<u>state</u>**" to refer to a particular pattern of matter and energy. A state contains information to the extent that it can be precisely defined (i.e., to the extent that the positions, movements and magnitudes of matter energy is known).

1. Behavioral systems are those that initiate actions (or block them) in response to the presence of certain internal/external states.

2. <u>At a fundamental level, behavioral systems are shaped more the rules of information handling than by the types of information they must handle and the actions they must initiate</u>.

3. Therefore, the rules of information processing act as one of the fundamental constraints on how behavioral systems evolve. To understand the reason why behavioral systems function as they do, we must gain some understanding of information theory.

4 Thus, behavioral systems are foremost, **information processing systems**.

## II. ABOUT INFORMATION AND STATES

### A. What is information?

**1. <u>Entropy and Information</u>:** Generally information is defined in terms of entropy.

(a) A totally <u>"disordered" or entropic state</u> is one that contains no information (moreover, it is one that also contains no potential energy and can do no work). **<u>On a macro level, matter and energy are everywhere the same</u>**.

(b) On a <u>micro level</u> there <u>may be differences over time and space</u> but they <u>balance each other out</u> so that the macro state appears featureless over both time and space.

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(c) To the extent that the above are not true, the system is said to contain information.

2. Let's try to look at this a bit differently. Given what we have just said, then the presence of information is the presence of some defined state, that is, a particular ***pattern or distribution of matter or energy*** that is different from entropy -- for example, a particular arrangement of matter or concentration of energy in one place or time as compared to other areas.

(a) At no level is information independent (as far as science is concerned -- remember that we are interested in materialistic explanations) of matter and energy.

(b) The **information content** of a particular area of the universe is related to knowledge of its state at the moment.

(i) Systems are said to be more disordered when we know less and less of the actual positions, values and motions of matter and energy. This tends to correspond with more possible positions.

(ii) Here are two examples -- a randomly shuffled deck of cards is highly disordered because there are an extremely large number of orders for the cards and, since the deck has been shuffled, we have no idea which of these combinations correctly describes the order of cards at the moment. We have very little information (essentially none) as to what card will be found in what place. On the other hand, a highly ordered state (where for example the deck is any arbitrary but defined order) contains a great deal of information because we know what card we will find in each position. Likewise, imagine the same gas molecules in large volume and a small volume. In the small volume there are relatively fewer positions available for each molecule and therefore we know more about their location and therefore possess more information. Got it!?!

What is the meaning of information?

**B. Information and "Meaning".**

1. You may now be bewildered. One thing you are almost certainly thinking is "I thought information had something to do with utility or usefulness?" As we have just seen, in a theoretical sense it does not. The implication above is that there is an incredible amount of "information" out there. It should also be obvious that the vast majority of it is unimportant to a particular organism. By unimportant, I mean that it cannot affect its fitness.

2. **In a very real sense, meaning is determined by the organism!**

(a) It must possess some sort of mechanism that can recognize particular information (a certain pattern from all others) and then initiate action.

(b) Thus, the same pattern of matter or energy (information state) may have very different meanings and produce very different actions depending on the organism.

(c) It is inescapable that "meaning" is conferred either directly or indirectly by evolution!

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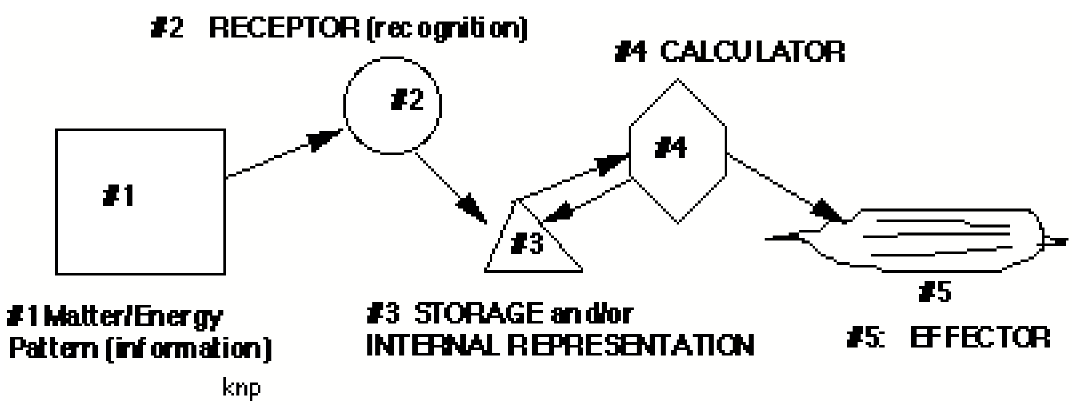
| Please think carefully about the last few statements. Do they preclude learning as a means to attach meaning? Are they too narrow and do they, for instance, ignore much of human experience? Or could natural selection be indirectly involved in all of human experience? |

3. **Symbolic representation of information states**:

(a) The actual information (whatever is in the environment) obviously does not enter the individual. However:

(b) **A particular pattern (information) can be represented by ANY other pattern provided there is some mechanism capable of making that recognition.**

(c) We will see that information processing involves changes in the symbolic representation of the information. Moreover, as the information moves through the system it is either altered and/or triggers additional informational flows. The schematic below shows a particular environmental state, it is sensed and a coded message is transmitted and perhaps stored. Another computational center acts on the information and generates a response:




**C. Symbolic representations of Information:**

1. The simplest representational system is where one object or a collection of energy can exist in **two possible defined (non-random) states or patterns.**

(a) This simple pattern, represented as **yes vs. no** (or 0 vs. 1, or + vs. - , hi vs. low, etc.) is referred to as a **binary** system.

(b) Notice that without modification, this system can only contain two pieces of information.

(c) However, if we add the additional concept of **combinational rules** where the method by which bits are combined has a certain meaning, then, in theory it is possible to represent any information with just two alternative entities (e.g., 0 and 1) so long as they repeated according to some sort of rule. The most **common combinational rules** are simply ones of:

(i) **Relative spatial position** or

(ii) **Temporal order**

(d) Lets assume that we need to represent 4 pieces of information using a binary system. How could we do it?

(i) Let's assume that position in left to right sequence has meaning (left to right is relative spatial position).

(ii) Note that as before, information is made up of unique states or patterns. Therefore, to represent 4 different things, we need four different patterns.

(iii) Using just 1 and 0 as symbols, we can generate 4 different patterns:

00, 01, 10, 11

Each of these is an information state itself and therefore each can be used to represent information. The number of unique states that this particular system can represent is:

1a. # of states = $2^n$

where **n** refers to the number of positions or places. Thus, in our example there are two positions (spatial or temporal) being used and two possibilities for each of those positions. The total number of unique defined states is $2^2 = 4$, exactly as shown at the top of the page.

Suppose that there were 2 possible states used in "words" that were exactly 16 positions long. We would call these 16-bit words.

How many unique 16-bit words (unique states) could be generated?

ANS: $2^{16} = 65,536$

**!** Again, the meaning of these 16 place representations is up to whatever decodes them. For instance 0000000000000001 could just as well represent 1, 61113, or strawberry shortcake. Don't get hung up on the meaning of these symbols according to our usual rules of numbers, counting and order. All that matters is that there are some rules -- not which ones!

2. **"Information density"** is related to the amount of space or energy needed to write a piece of information. So far we have worked on the assumption that unique pieces of information are only built up with various combinations of one symbol (or two but where one of the symbols may simply be

the lack of a symbol in a certain place). However, patterns can be based on any number of unique informational representations that are organized spatially and/or temporally. You are reading this page by using one such system that consists of well over 50 unique states (letters, punctuation marks and spaces, and numbers). Where more states occupying a certain extent of space or time can be produced, then potentially more informational states can be generated in a given amount of space. The representation of the information is more "dense".

a. Note however, that in all cases each piece of information still has **one unique representation**, e.g., eight, 1111, and 8 (we have decided that these stand for the same things; in each system the concept eight has one unique physical state).

b. Note also that any information system, regardless of its "density", can in theory represent any piece of information. In other words, density does not define the ability of a system to represent information.

A more generalized form of the equation that predicts the number of possible states (see eq. #1 above) is:

2. # of unique states = $S^n$

where S is the number of states at any time or location and n is the number of positions in the larger representation ("word"). Thus, using 2 positions, each with 10 possible shapes, gives 100 possible unique states

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| Note the relationship between structure and information in DNA, a molecule you are familiar with!<br>**?** How many unique shapes are possible for a single position in DNA? What is the role of the sugar phosphate backbone in the storage of information in nucleic acids. Does the backbone contribute directly (in terms of its shape) to the information content? How about the nitrogenous bases?<br>Assume that amino acids and nucleic acids are about the same size (in fact n.a. are a bit bigger). On a positional basis only, which chemical could represent more information in a given amount of space? |

**D. <u>Information Operations</u>:**

1. Information operations involve combining and sorting symbolic representations of some physical reality (or idea).

2. The symbolic representations of physical reality are arbitrary tokens – unique structures of matter or energy states.

3. Thus, any chemical reaction involving the change of one or more substances into a new structure or new energy state can be used to instantiate an information operation. Here are some examples:

The **reaction of A to give B or X and Y to give Z (or vice versa)** as:

3a. A <----> B

3b. X + Y <----> Z

we can show the energy transformation equivalent as:

4a. Energy State A <-------> Energy state B + $\Delta$entropy

4a. Energy State X + Energy State Y <-------> Energy State Z + $\Delta$entropy

The important thing to realize is that **any process involving matter and/or energy certainly involves a change in state and therefore information and/or a representation of some information state.**

**E. Computers -- Analog and Digital Computations**:

1. This section will seem to be a bit of a digression but it will present a number of important ideas and give you some experience with understanding how **any computer** must work. Please bear with me.

2. One very artificial but nevertheless very important distinction between different types of computers depends on how the information is represented.

a. So called **analog or continuous representations** involve conditions where there are no discrete steps between each value. In other words, between any two numbers are an infinite number of numbers. In many ways this is analogous to the point concept in geometry -- points occupy no space and an infinite number of points can be found between any two. The same can be said of real numbers.

b. Analog computers operate with variables and rules that are expressed in an analog fashion -- as the level of one variable varies smoothly, so does the output variable.

3. By contrast **digital computers** work with **discrete information** that is, information that is expressed exactly. Well, not really. The fact is that many variables from the environment are essentially continuous. To express them discretely, the procedure is to define all values within a certain range as having the same average value. So, the representations are not necessarily exact in the sense that they actually reflect the variable in the environment.

> **!** Most modern computers are digital computers; this choice has had mainly to do with the ease with which such computers are programmed and the fact that electronic components can be made that can deal very rapidly with operations of exact numbers. Moreover, electronic components can easily be made to distinguish between widely separated values of voltage. Thus, an electronic digital computer has circuits that decide whether a voltage is above or below a

certain threshold value. Voltages near zero are taken as one state and near 5V are taken as another. All voltages are placed into one of these two classes.

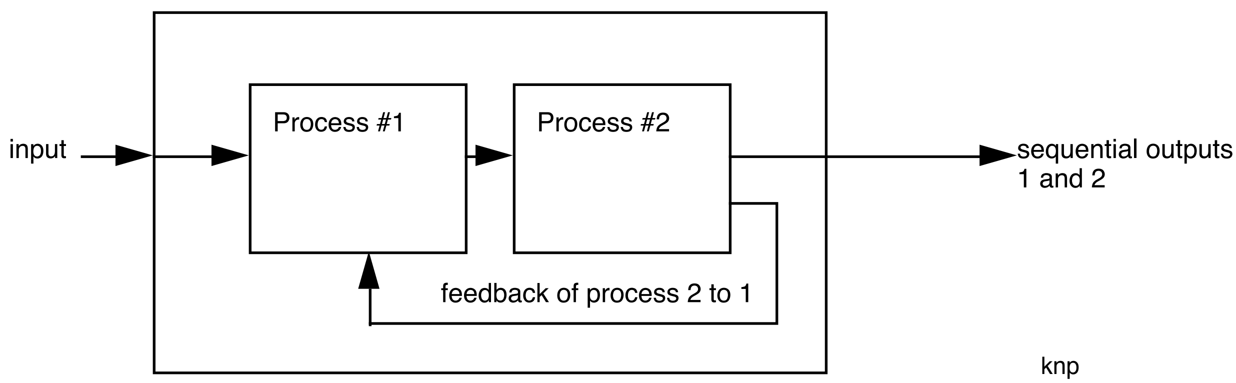
Before your eyes totally glaze over, we will soon see that proteins behave in a similar manner. Thus, we will see that chemical computers (us) and electronic computers solve many problems in similar ways although the exact entities doing the solutions (transistors and capacitors vs. proteins) are very different.

**F. Another Important Computational Digression: Series and Parallel Computation:**

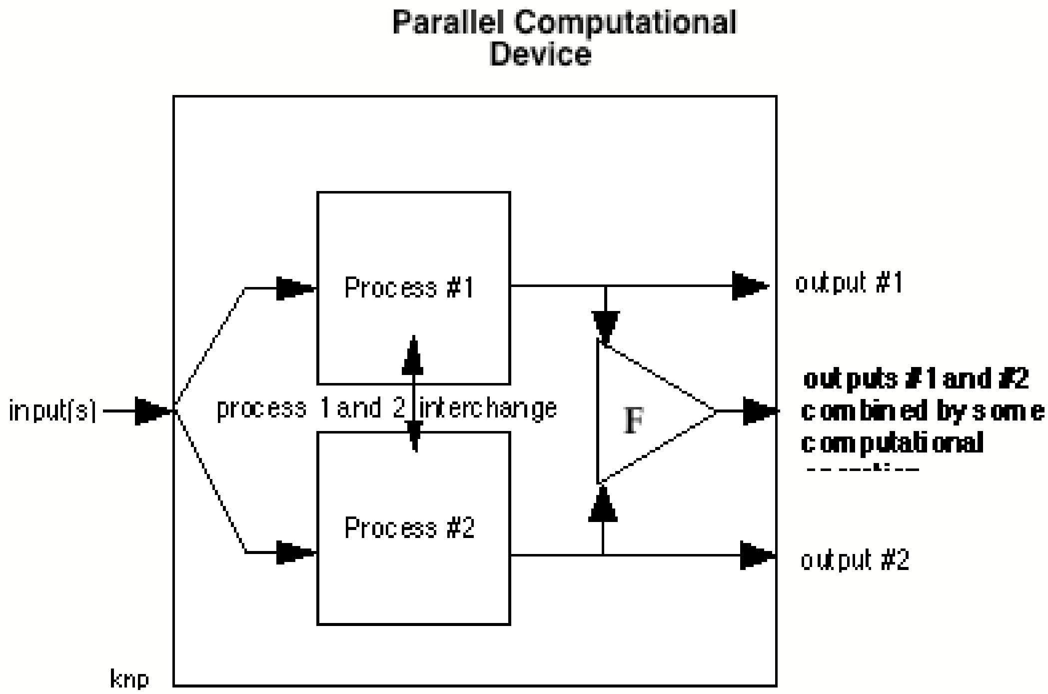
1. There are two possible general arrangements of flow processes (and information processing is a flow process): series and parallel. They are very easily distinguished from each other.

2. In **series operation** computations (transformations whatever), the operations are performed in **temporal sequence** -- one after the other. These may be distinct computational units or it might be the same unit used over and over (as is largely the case in most present digital computers):

**Series Computational Device**




3. By contrast in **parallel computation**, different operations are performed at the **same time** in distinct computational units:




> **?** What are the advantages of serial or parallel computations over each other?
> Which is faster?
> Which takes up more space? Does space matter?

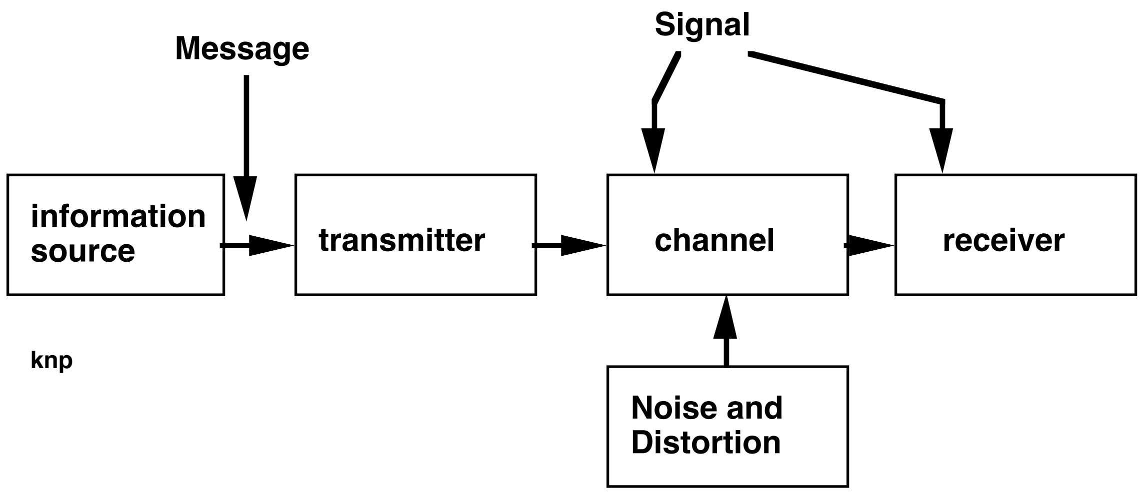
**III. About Communication**:

A. Introduction: A concept that is vital to understanding information processing is **communication**. Since information gathering, storage, computational and effector elements of a behavioral system are always to at least some extent physically separate from each other (even when they all occur in a single cell), there must be some way for these systems to communicate with each other.

> **!** Communication is a very important aspect of biology, philosophy, and psychology. Entire lives are devoted to its study. Language studies, rhetoric, etc. are all vitally important endeavors. What follows is in no way meant to simplify the richness of communication anymore than the previous section was meant to do so with information. But be aware that it is in some ways a very simple treatment. For instance, it supposes that all communications are "honest " -- they are meant to correctly convey information. This ignores the fact that some communications are "meant" to be deceitful.
>
> The reason that we will ignore the possibility of dishonesty (which, let's face it is one of the most important parts of communication) is that we are only concerned in this course with communication of one part of an organism with

another. No advantage is to be gained by dishonesty -- if one part gains some other part loses or worse yet, the entire individual loses. It is an entirely different story when whole organisms are considered.

A. Here's how an engineer might look at communication:




**Note:** the elements in this system do not necessarily correspond to distinct cells, proteins or pathways. We will see a number of examples where the same physical entity, at least some level, appears to take on two or more functions.

**B. Let's look at the individual elements of the system:**

1. In some ways the most important element of the system is the **RECEIVER** since it's capabilities are what allow information to be identified as such. Receivers filter through the vast amount of potential information and focus on relatively specific manifestations.

2. The I**NFORMATION SOURCE** and **TRANSMITTER (XMITTER)** are often the same or are certainly closely connected entities. If they are the same, they are simply something that produces at least two discernibly different (to a receiver) states. More formally,:

a. the **SOURCE** creates the information as something we refer to as a **MESSAGE** (information that can potentially be received and acted upon) and passes it on (internally) to the xmitter.

b. The **TRANSMITTER** takes the message and **TRANSDUCES** (changes) it to a different form and then "broadcasts" the information into some portion of the surrounding environment.

3. At this point, the message is now refereed to as a **SIGNAL**, with the difference being that the message can be thought of as information located in some place while the signal is a representation of that information that moves.

4. The particular physical or chemical means by which the message propagates is referred to as its **CHANNEL**. For instance, messages that are converted into vibrations of air molecules are signals utilizing the **ACOUSTIC**

channel; broadcasted pheromones are said to be signals that use the **CHEMICAL** or **CONVECTIVE-DIFFUSIVE CHANNEL**, displays that consist of moving of various body parts (ex: waving arms or wings, etc.) are examples of signals using the **VISUAL CHANNEL** as are bioluminescent and chromatophore signals.

5. Notice that the signal may be **DEGRADED** -- that is, the information contained in it can be lessened or even changed. There are two general ways this can happen:

a. **NOISE** -- random, unpredictable signals that mask the signal of interest to sender or receiver.

b. **DISTORTION**: specific operations that in a potentially knowable manner alter the signal.

c. the process of removing or minimizing noise and distortion by the receiver is termed **FILTERING** This is a very important process and one that generally needs to be minimized within an organism if possible -- it is far better (i.e., more **reliable**) to generate signals for internal use that are reliably passed than to try to reconstruct them at the receiver.

**Example of Noise and Distortion:** Using the chemical channel, a noise would be other chemicals that would potentially interfere with the signals detection by a receiver; an example of distortion would be a situation where a signal consisted of a mix of two chemicals but one traveled better than the other -- over distance one would be predictably lost.

C. Given these elements, let us now reconsider and refine what we know about information:

1. The presence of a suitable receiver is required for information to have any real meaning -- without it, we can talk about potential information at best.

2. In order for information to be transmitted:

a. There must be at least two different states produced in the channel.

b. **Difference is, in part, a property of the receiver.**

? Can you think of any less complex system capable of storing and transmitting information?
? Does the transmitter need to be "purposeful" to send information -- in other words, does the signal (and message) need to be designed by the transmitter in some sense (even if the sense is simply that of a system designed by natural selection).
? Why does the receiver seem to have such a central role?
? Can receivers create information or merely exploit what is already present?
? What is the difference between random and regular? Irregular?

**IV. Chemical Computational Systems**:

**A. Introduction:**

1. We will start with chemical communication systems since they are central to understanding the operation of nervous systems. They are also the **oldest form of communication and computational system used in living systems** and t**hey can be seen to be most directly linked with genes**.

| **?** Why do you suppose that chemical communication is considered the most primitive form of communication and computation? |
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2. Any chemical system above absolute zero is constantly in flux (in fact, such systems are even in flux at absolute zero due to quantum effects, but the flux is minimal).

a. Each second, myriad interactions (operations in our informational terminology) occur.

b. Many of these interactions are totally random and tend to reverse immediately. They represent the noise of such a system and are not our focus. These are the **entropy component** of the system. They can be thought of as noise.

c. However, other interactions are in some sense more thermodynamically directed and are used for computational purposes.

d. Thus, we can speak of **any chemical *system* as being a potentially very complex, real time, massively parallel (and serial) computer.** It is our challenge to see how given all of the potential information that could be handled by such a system, certain factors are ignored and others are amplified and operated on.

**B. A Review of the Relevant Features of Proteins**

1. Recall that **protein structure determines function** and it is a result of the interplay between the interactions of amino acids making up the protein and the environment.

a. The **structural gene** that codes for the linear sequence or amino acids making up a particular protein blindly "expects" a certain environment in order to produce a protein with a certain three dimensional shape.

b. The function of the protein is determined by its exact shape -- produced by this interaction of the primary amino acid sequence and the environment.

| ☞ **Note:** for the discussion below, imagine that we are considering a type of protein whose role it is to respond to a signal when it reaches a certain level. |
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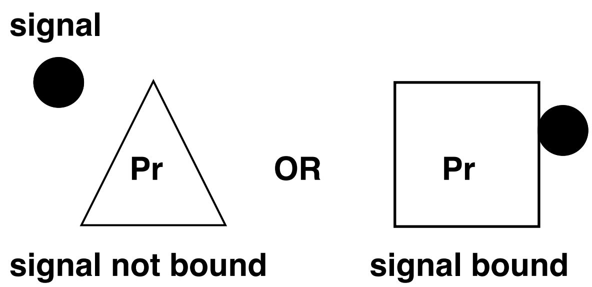
2. **Functions of individual members of a protein species vs. function of the population of that protein species.**

a. A **protein species** can be defined as all molecules with the **same primary protein structure** (same amino acid sequence). Put another way, they are all derived from the same allele (or multiple copies of that allele).

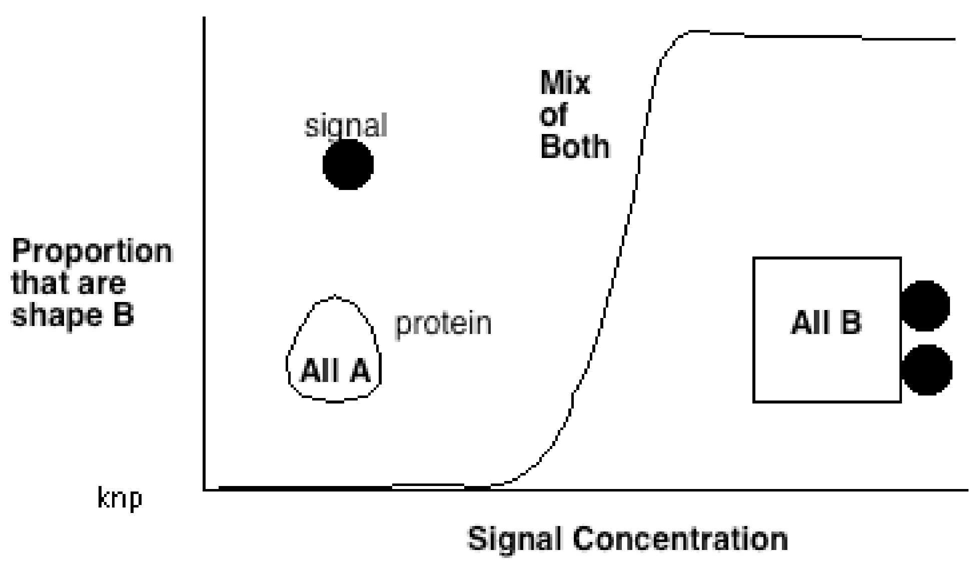
b. We need to be familiar both with how individual molecules work and how a protein species functions as a whole or population in processing information.

(i) **<u>Individual function</u>**: each molecule of a particular type of protein can exist in several conformational states. To make this simple, we will assume that the protein we are interested in has two possible shapes (functional levels) that correspond to whether or not the signal molecule is bound:

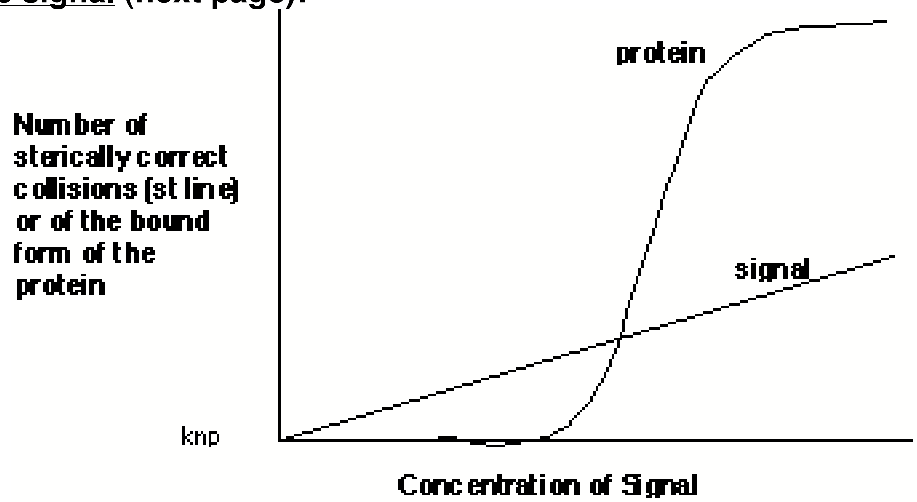



Thus, the protein exists in one of two shapes and these shapes register the presence of a signal.

(ii) **<u>Population function</u>**: Normally there are multiple copies of the same type of protein present in a cell. Thus, the protein responds as a population to the signal and since not every protein will bind with the signal and change shape at exactly the same time(local concentrations differ as do local conditions that affect the ability of the proteins to bind), the behavior of the population is a curve:



**!** Notice however, that <u>the smooth continuous (analog-like)</u> **<u>increase of the signal</u>** <u>(x-axis) has been</u> **<u>converted</u>** <u>by the protein population</u> **<u>into a much more discrete signal</u>** **(next page):**



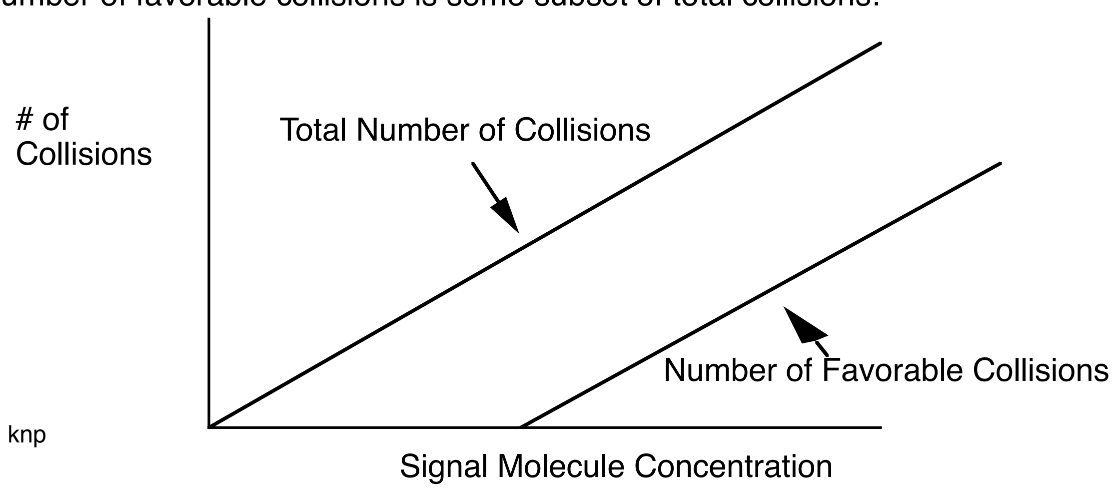

The shape of the curve is related to two important characteristics of proteins and protein populations: affinity and number.

**3. Proteins and affinity:**

a. In order to have an interaction between a protein and some other substance, they must come into contact. Furthermore, the contact must last for some period of time.

i. As concentration increases, favorable collisions always become more common. This would be true in any system.

ii. If this was all that mattered, then a simplistic (but illustrative) way to view this would be to envision a linear relationship between concentration and the probability of binding signal molecule to protein where the number of favorable collisions is some subset of total collisions:



b. However, it is not this simple because when a favorable collision occurs there is a certain probability that the protein will hold on to the signal long enough for a shape change to occur.

**!** Keep in mind that the binding between ligand (signal) and protein is usually (but not always) weak (H and vander Waals) -- it is generally not covalent. As a result, ligands are relatively easily displaced from the binding site.

i. This probability function is synonymous with a property we call **affinity**.

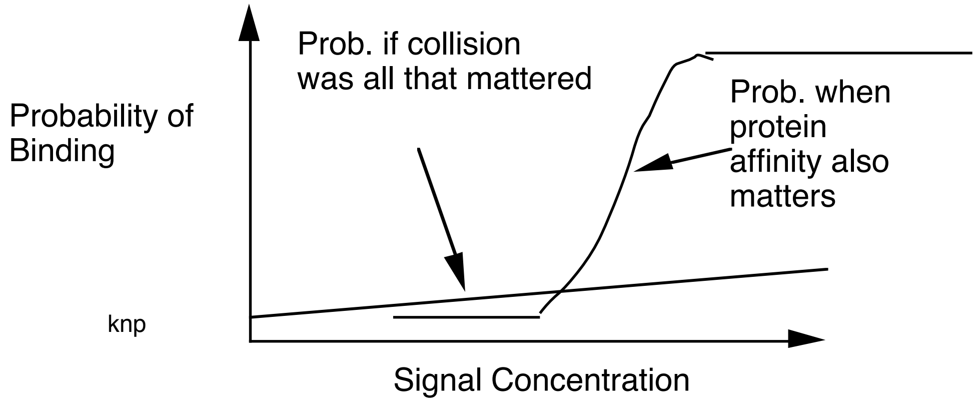
ii. Affinity itself is simply a measure of the strength of binding between the protein and the ligand (signal).

(a) Thus, for a given favorable collision rate, a high affinity protein is **more likely** to possess a bound ligand at any moment in time than is a low affinity protein.

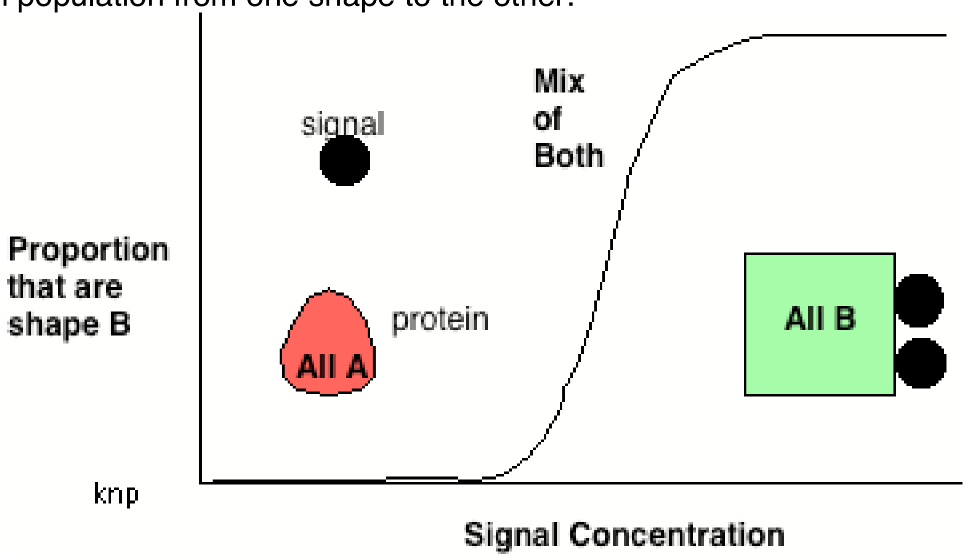
(b) Viewed as a population, in a high affinity population a greater proportion of the protein molecules will possess bound ligand for a given concentration (favorable collision rate) than will a low affinity protein population.

**!** Note that the preceding discussion only applies to concentrations that are low enough that not all of the binding sites would be occupied (saturation, see below).

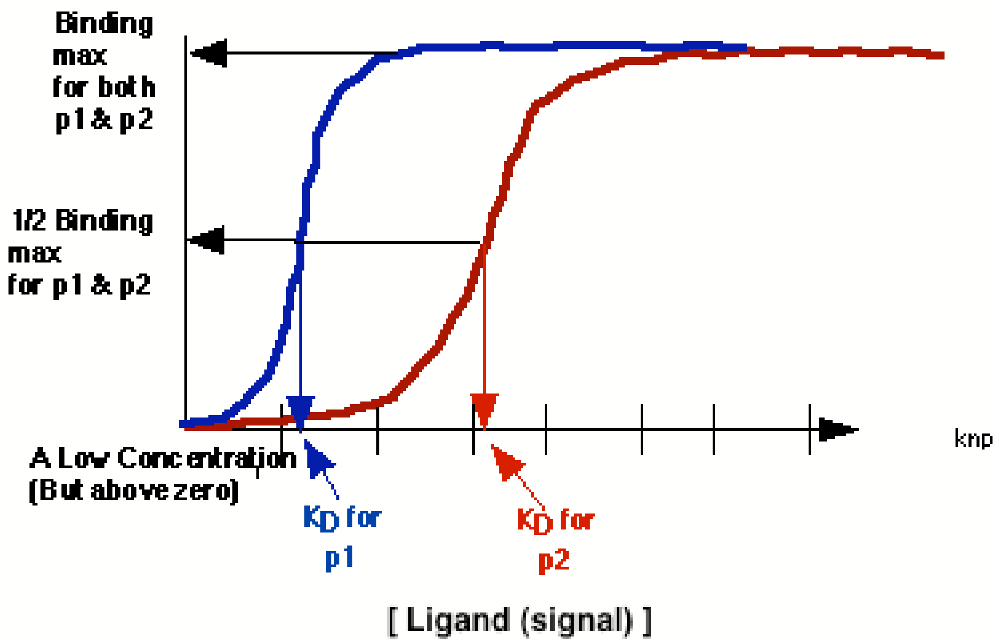
iii. Thus, at relatively low concentrations, not only is there a low chance that the signal will attach to the protein correctly but also since the signal does not bind covalently to the protein there is a chance that it will be broken lose before any shape change occurs. The more strongly it binds the signal when it does touch the protein, the greater the chance that it will remain long enough for a shape change to occur. The strength of this binding therefore determines the affinity and the affinity therefore helps to determine the likelihood that a protein will be in one shape or another at a given concentration of substrate:




Taking these factors into account we see that a population of proteins will behave such that at low concentrations very little ligand will bind long enough to induce and continue a shape change; at high concentrations, ligand is nearly always bound and therefore nearly all of the protein is in the shape associated with binding and at intermediate concentrations there is a rapid transformation of the protein population from one shape to the other:




**Saturation** is the point where, even though more collisions are still occurring, we see no further increase because none of them involve the binding site. The graph below shows the binding curves for two different proteins that both bind the same signal. Notice that at concentrations below saturation that the higher affinity protein always has a greater proportion of its population flipped into the shape consistent with binding:



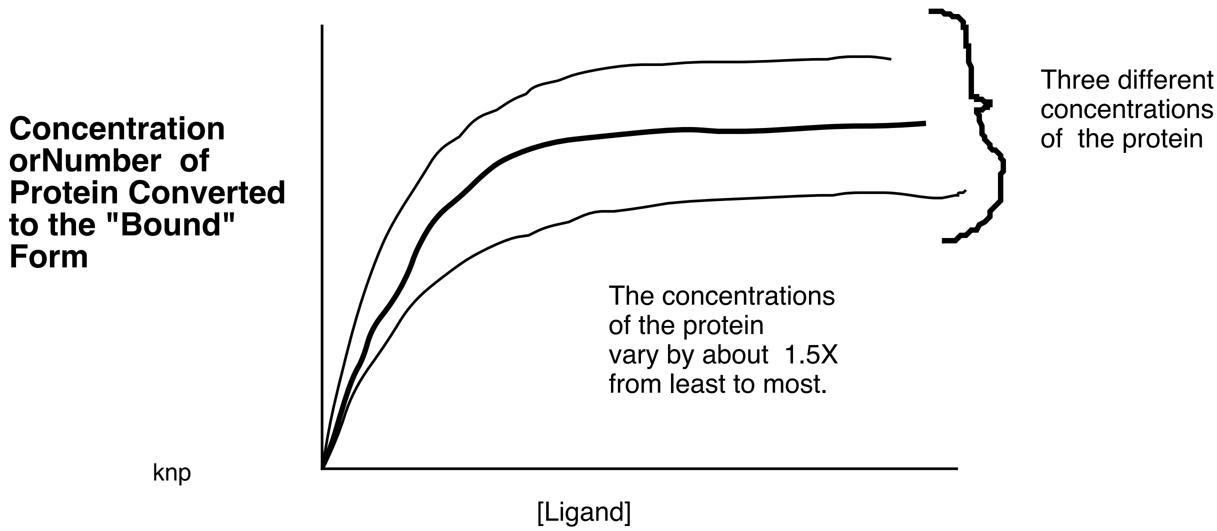

Note the parallels between this curve and the typical curve for enzyme kinetics. Notice that the dissociation constant, $K_D$, is an analog of the $K_M$ and numbers of proteins that have changed shape is the analog of $V_{max}$. In "chemical" biological computation both enzymes and binding proteins will be important.

**?** What is the role of affinity in biological information processing and communication?
From what you know about proteins, how can the response properties (at the protein level of organization) of a biological computer be modified on both the short and long terms?
In what sense does a protein act to "digitize" a continuous signal into a binary?

**4. Signal Size:**

a. We have just seen that if a protein is being used to register the existence of some state in a cell, the decision on when to register an event is largely tied to the affinity of the protein for the signal.

b. Given that a protein has registered a change, an important factor is the **magnitude of the registration signal**. This is primarily determined by the concentration of the protein since the greater the concentration, the greater the potential number of signal molecules registering a change:




c. This is another **populational aspect**. The maximum potential size of the signal is controlled:

i. At the **<u>level of protein synthesis</u>** where the control of transcription and translation results in a certain number of proteins being produced

ii. At **<u>regulatory levels associated with the protein molecules themselves whereby certain cellular conditions, essentially signals, change the functionality of the proteins.</u>**

**C. Chemicals and information and communication: A binary model.**

1. For the simplest model we will assume that <u>**each element** in a computer or communication system can exist in **one of two STRUCTURALLY DISCRETE STATES**</u>

a. One state corresponds to the **ABSENCE** of the signal.

b. The other corresponds to when a **SIGNAL EXISTS AT SOME CRITICAL LEVEL**.

**NOTE:** These states are different shapes (proteins) or numbers of certain shapes (any elements). In the case of proteins the shapes can be associated three different important actions:

(i) Changed catalytic properties

(ii) Changed abilities to bind to other molecules such as proteins, in a non-catalytic way.

(iii) Changes in shape that alter the ability of other substances, such as ions, to move from one place to another via the protein. In this case the protein is a special type of ion channel called a gate. (This feature will be important when we consider what we will arbitrarily designate "bioelectrical systems")

2. The elements toggle between these states as a result of recognizing something as a signal.

a. Thus, with chemical signals, a protein must BIND or be **INFLUENCED**[1] by some signal.

b. **Recognition is registered by a shape change. <u>Shape changes are synonymous with function changes</u>**.

**! Note** the first feature here -- **<u>selectivity</u>**. Of all possible information, given elements of an informational system only pay attention to certain environmental events. As a result they ignore non-essential information and further, they can be optimized to deal with certain types of information. Think about how many things you ignore -- most of which you do without ever even knowing that they exist! Another name for this is **<u>stimulus filtering</u>**. This is a fundamental feature of all systems -- in living ones it is attributable to protein structure.

**?** What about the role of selection in the evolution of receivers and signaling? How does a signal become established as a signal? How is it "decided" evolutionarily that something is information?

c. Clearly not only selectivity but also affinity and signal size are important at this step.

3. The result of the **<u>toggling of structure</u>** can be to:

a. Produce a signal that <u>symbolizes that a certain state has been reached</u> (see earlier discussion of proteins responding to ligand signals); this signal could be used in <u>further computations</u> or stored (next item).

b. <u>Store information</u> (arbitrary signals) -- e.g., the presence of a particular structure might be used to mark that something has happened.

c. Directly <u>trigger a process that responds to the signal</u>, for instance by activating some biochemical pathway(s).

**? What is memory**? -- what do you need for a memory system?
Devise a chemical system that remembers.
Devise a system that records recent events but eventually forgets.

### D. A bit about the evolution of signaling and computational systems

1. In the simplest situation, for a signal to evolve, all that is needed is for some protein to be able to bind it. If that happens, then, in one sense there has been a form of chemical communication since the protein recognized the signal.

2. However, it is hard to see how selection would increase the frequency of the allele for a protein that recognized some chemical unless it

[1] An example of influenced would be something like pH or temperature that that could affect protein function without actual binding.

somehow altered the organism's function in a way that increased its fitness. Thus, the affected protein, the receiver, will need to fit into or affect some larger physiological system. If and when this happens selection can evaluate and perhaps improve the receiver.

3. In general, if a communication system based on some protein receiver becomes established we will expect the following to happen:

a. There may well be an increase in receptor **AFFINITY** AND **SELECTIVITY**. Both of these would be achieved by a modification of the amino acid sequence -- therefore they both depend on mutations to structural genes.

? How long would affinity continue to increase? What would determine whether or not selectivity increased?
Try to frame your answer in terms of optimality -- are greater and greater affinities and selectivities always better? Is there a point where it becomes counter-productive?

b. **Improvement in the degree of response by the individual receivers -- how unambiguous is its response?** (Conformational change eventually leading to other effects). If the original conformational change is small and results in a relatively small affect that does not necessarily always trigger other changes with which it is paired, it is reasonable to assume that there will be selection:

i. On the receiver to improve the "distinctiveness" of its response to the signal

ii. On the component(s) cell system(s) directly affected by the receiver to make them better able to recognize the change. (Notice that this is exactly analogous to the process occurring between the receiver and the environmental signal. Only here, since it is internal communication we are talking about, it is not only the receiver (the affected process) that is acted on by selection, but also the signal (the receiver aimed at the environment).

iii. Both of these would be achieved by modification of the structure of the two types of receivers. This could be achieved either by different amino acid sequences or different internal environments.

c. **Improvement in the overall magnitude of the response to a signal. If the receiver protein was originally rare, there may well be selection to increase its numbers and thereby generate a greater receiver response for a given size of signal.** This is largely a question of gene expression -- rate of transcription and translation vs. rate of removal.

**?** How does this relate to signal to noise ratio?
Can you think of times when it would not be important to increase the total number of receivers even if they were relatively rare?

We will apply these principles to the analysis of real systems in the next set of readings.