Lloyd D. Partridge, Ph.D.

Neurophysiologist

Curriculum Vitae

Education

1948 B.S. in Chemistry
University of Michigan
1949 M.S. in Physiology
University of Michigan
1953 Ph.D. in Physiology
University of Michigan

Academic Employment

1953 – 1956 Instructor, Department of Physiology
University of Michigan
1956 – 1962 Assistant Professor, Department of Physiology
Research Associate, Department of Neurology
Yale University
1962 – 1970 Associate Professor, Department of Physiology
University of Tennessee
1970 – 1994 Professor of Physiology, Department of Physiology
University of Tennessee
1965 – 1973 Deputy Chairman, Department of Physiology
University of Tennessee
1994 – 2005 Professor Emeritus, Department of Physiology
University of Tennessee
1994 – 2005 Adjunct Professor, Department of Biomedical Engineering
University of Memphis

Society Memberships

American Academy of Neurology
American Physiological Society
Association of American Medical Colleges
Behavioral and Brain Sciences
Biomedical Engineering Society (*founding member)*
Biophysical Society (*charter member)*
Engineering in Medicine and Biology Society
International Brain Research Organization
Institute of Electronic and Electrical Engineers *(life senior member)*
Society for Neuroscience *(senior member)*

Consultant

1957 – 1962 Neurophysiology and Bioengineering
Connecticut State Hospital
1957 – 1963 Biomedical Engineering
University of Southern California
1982 – 1987 Boelter Bioengineering Center
University of California, Los Angeles

Visiting Professorships

1965 – 1966 Department of Physiology
University of Vermont

1981 Academy of Sciences
Sofia, Bulgaria

1981- 1982 University of Western Ontario

1985 Medical College of Ohio

1985 Department of Biomedical Engineering
Memphis State University

1987 Academy of Sciences USSR
Moscow, USSR

1989 Pavlov Physiology Society
Moscow, USSR

Editorial Boards

1973 – 1981 *Transactions in Biomedical* Engineering

1981 – 2000 *Behavioral and Brain Research*

1985 – 1994 *Annals of Biomedical Engineering*

Professional Boards

1976 – 1981 American Physiological Society

1977 – 1979 Engineering in Biology and Medicine IEEE Professional Group

1985 – 1898 Biomedical Engineering Society

Lloyd's Research Career: a Son's Perspective

The nervous system takes in information about the world through the various sensory receptors, and it produces an internal representation of this sensed world, which is the basis for our perceptions. One of the principal uses of these perceptions is to allow us to control the movement of our body — unconsciously, in balance and posture, and consciously, in voluntary movements.

The strategies by which the nervous system controls muscles — that is, motor control — was the primary focus of Lloyd's research career. His 40-year quest to understand the basis for balance, posture, and voluntary movement took three approaches: first, to investigate how the nervous system carries out its role as a controller of muscles; second, to study how muscles respond to this control; and third, to comprehend how the nervous system and muscles function together in the moving animal.

Large portions of the central nervous system, including areas of the cerebral cortex, the cerebellum, the basal ganglia, and the spinal cord, are dedicated to the initiation and control of movement. The simplest neuronal circuit involved in the control of muscles, the spinal stretch reflex, consists of just two neurons: a sensory neuron, which brings information about muscle length into the spinal cord; and a motor neuron, which controls muscle contraction. This reflex, which is tested with a reflex hammer during each medical exam we have, has intrigued neurophysiologists since the beginning of the 20th century.

In his early research at Yale, Lloyd sought to understand how such a simple reflex could act out its crucial role in posture and movement. He began with an investigation of the distorted information about muscle length that is provided to the stretch reflex by receptors in the muscle — distorted because it includes components other than muscle length. Significantly, he observed that such distortion is necessary for the nervous system to control the positions of limbs accurately. He then went on to demonstrate the important role of the cerebellum in preventing oscillations that the stretch reflex would otherwise cause during voluntary movement. In one novel series of studies, he used himself as a subject, even including a photo of his own hand in the publication of his results — quite an uncommon type of picture for a research journal! From these experiments, he deduced characteristics of the motor commands from the brain that modify the spinal stretch reflex during voluntary movements (*Am. J. Phys. Med.* 40:96).

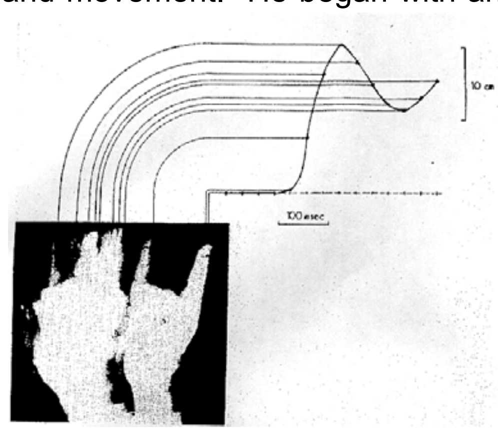
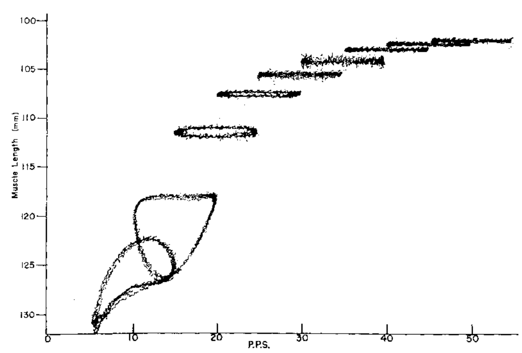


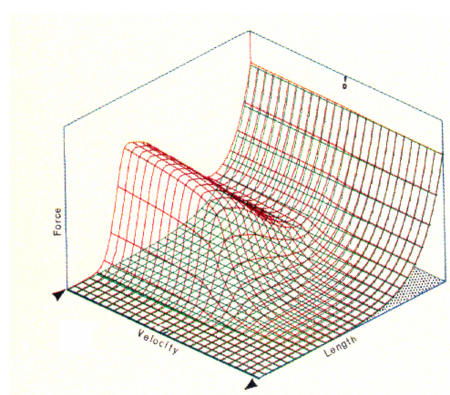
FIG. 1. Stroboscopically superimposed pictures of successive positions of finger,

An important component of posture is balance. Anyone who has ever been dizzy knows that the vestibular system of the middle ear provides essential information for balance. One of Lloyd's most complex studies of nervous system control of muscles was a series of experiments he undertook at the University of Tennessee, in which he measured the response of muscles that control posture to stimuli of the vestibular nerve. This work provided sufficient insight into the function of the vestibular system in motor control that he was able, by stimulating the vestibular nerve appropriately, to produce the coordinated limb movements necessary for good balance.

Lloyd's second approach in his research concerned muscle response to nervous system control. Movement requires a motor, and the motors in animals are muscles. Just as a motor in a car responds differently to pressure on the accelerator depending on speed and weight of the vehicle and steepness of the terrain, so do our muscles respond in a very complex way, depending on many factors, to commands from the nervous system. Lloyd's first studies of muscle were recordings of the electrical properties of muscle cells made using the microelectrode technique. (Paradoxically, he jokingly criticized me 15 years later for using this technique, for, as he said, it provides data only about single cells rather than about the whole organ.) After moving to the University of Tennessee, he continued to study neural control of muscle, but, in an effort to understand this complicated organ that is so effectively controlled by the nervous system, he became increasingly interested in the intrinsic properties of the muscle itself. He began by using computer-generated signals to stimulate muscles, thereby eliminating nervous system input altogether. The resulting data showed clearly that muscle does not simply respond passively to whatever the nervous system tells it, but that it actively modifies its input. Here is one graph of these data (*Am. J. Physiol.* 210: 1178), which has a certain aesthetic appeal, an appeal that I think Lloyd appreciated and aimed for in his published figures.

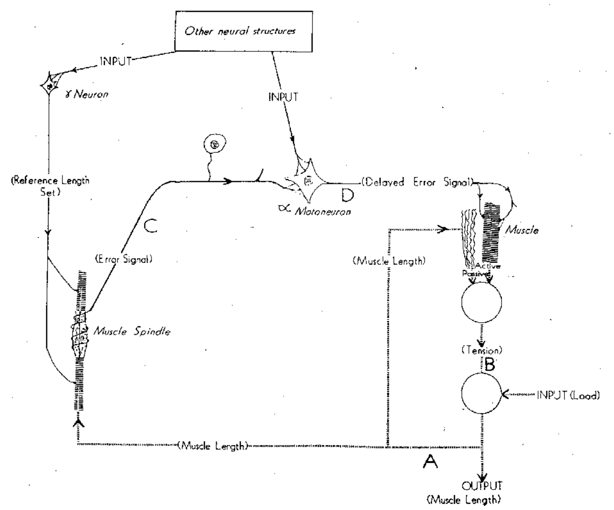


Lloyd summarized much of his and others' work on how muscle works as a motor in his comprehensive chapter in the *Handbook of Physiology*. In the epilogue of that chapter, he made a fascinating and insightful statement: the evolution of muscle, with all its complex characteristics, predates the evolution of the nervous system; thus, it contains the design specifications upon which much of the nervous system has developed. So the master came after, and is modeled on, the servant! Here is one figure from that chapter, reproduced here because I think it is the most classic representation from all of Lloyd's publications. This figure neatly summarizes all



of the mechanical properties of muscles and shows the complexity of the motor that the nervous system must control. I use this figure every time I lecture on muscle.

The third approach in Lloyd's research dealt with how muscles and the nervous system function together. He was particularly taken with the biological applicability of control system analysis, a powerful tool used in engineering to study regulated systems. Early in his career, he started thinking about motor control in these terms, and in the late 1950s he pioneered the use of this technique in investigating the function of spinal reflexes in posture. He published this first control system diagram as an interesting blend of anatomical and engineering elements (*J. Neurophysiol.* 23:257). In the 1960s he extended this approach, considering the isolated muscle itself as a self-compensating system. Lloyd posited that muscle is mechanically self-controlled and subsequently showed that input from the nervous system must instruct it to move to a new length, but that maintaining the new length requires a much less precise neural signal. Lloyd's confident use of control system analysis is readily apparent in this statement from 1969: "Without the control system approach these effects could have been recognized by a good biomathematician. With a control system approach the theoretical manipulations were simple enough so I could understand them. If you want to study these systems the hard way, Good Luck! For myself I will continue to misuse and distort techniques stolen from control engineering—and dream about someday understanding the principles of movement control in the intact animal" (*Fed. Proc.* 28:65). This willingness — eagerness! — to "steal" techniques from other disciplines informs the chapter he wrote in *Engineering Principles in Physiology* "Integration in the Central Nervous System," in which he treated the entire nervous system as a control system. Lloyd's engineering approach was perhaps too successful, since control system analysis, which he was so instrumental in instituting, he later believed was overused in the study of motor control. That is, organisms operate within their own physiological dimensions, and we may be led to misunderstand these operations by trying to contain them within the physical dimensions implied by the boxes and arrows of a control system diagram.

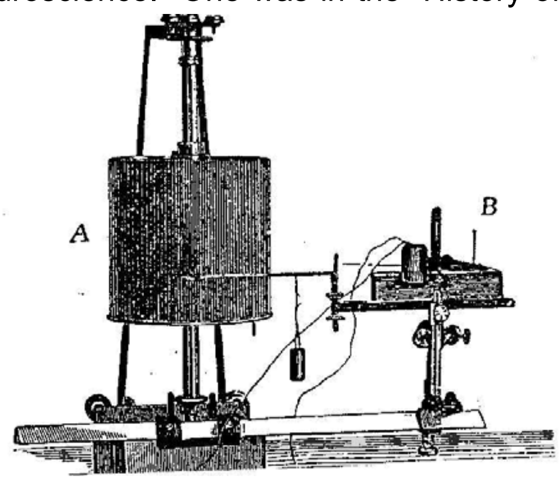


After the *tour de force* of his chapter in the *Handbook of Physiology*, Lloyd very much took on the role of a senior scientist-philosopher, a role that fit him well. This is apparent in his publications after 1980 in the unique journal called *Behavioral and Brain Sciences*, whose goal is to "contribute to the communication, criticism, stimulation, and particularly the unification of research."

Each issue contains several controversial articles along with a series of invited commentaries on them. In all, Lloyd was asked to provide commentary on six articles in this periodical.

Lloyd's publication list seems unusual to a 21st-century neurophysiologist, as his papers show only a small number of co-authors. The average number of authors on his papers is 1.7, and a full 60% of these papers are his alone. In contrast, the April 2005 issue of the *Journal of Neurophysiology* has an average of 3.1 authors per article and only 8% single-author articles. To some extent, this reflects the changing times in the field, since research has become more team-centered, but I think it also represents Lloyd's research personality. On the one hand, he was very extroverted and gregarious, voluble at discussing his and others' ideas. I never had any trouble locating him among 25,000 professional meeting attendees, because his stentorian voice always pinpointed the group of which he was the center! On the other hand, in the lab he did most of his experiments and thinking on his own.

In addition to the two textbooks we co-authored, Dad and I presented two papers at annual meetings of the Society for Neuroscience. One was in the "History of Science" session, proposing the hypothesis that technology affects the way neurophysiologists view the world (Technological bias in neurophysiological thinking, *Soc. for Neurosci. Abs.* 110.6, 1997). The other paper was in the "Neural Basis of Behavior" session, proposing a hypothesis for the biological basis of consciousness (A theory of percept processing, *Soc. for Neurosci. Abs.* 820.10, 1995). We spent a lot of time discussing the ideas for the latter paper, and it formed the basis for the last chapter of our second book. Looking back, I remember it as the last topic we argued about and worked hard on together. It was Lloyd's last publication. I like to believe that this short chapter, reproduced below, can be grasped independently and fairly easily.



Mind: A Transition Function

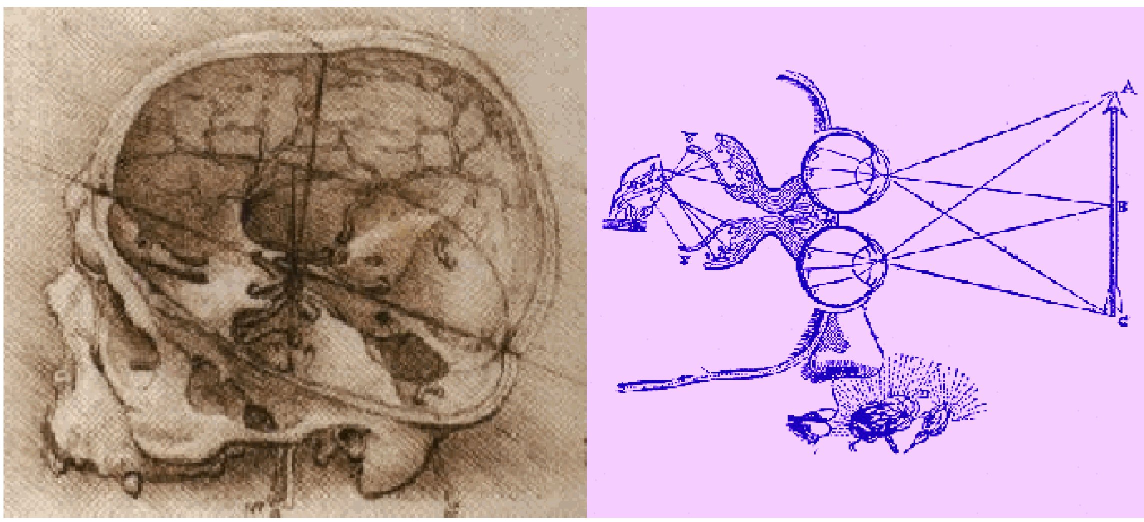


Figure 1 Left: Drawing by Leonardo da Vinci from 1489 of a human skull with intersecting lines indicating the site of the *senso comune*. Right: Convergence of visual sensory information (ABC) with olfactory sensory information (D) at the pineal (H). From René Descartes, 1664.

Figure 1 shows a drawing in which Leonardo da Vinci indicates, with intersecting lines, the *senso comune* in the third cerebral ventricle, where he thought there was a confluence of the senses. Figure 1 also includes the equally famous drawing of René Descartes showing the convergence of sensory inputs in the pineal body. The process of producing and assembling percepts into a perception is clearly not the only higher function of the nervous system, but it is certainly one that is frequently considered. An important goal throughout the rich history of neuroscience has been to identify the one place where receptions are converted into perceptions. It is now apparent that there is not a single locus (a Cartesian theater) where this occurs, but rather it is a distributed function of much of the brain. It is appropriate that we conclude this book on nervous system interactions with a brief consideration of the higher functions that might be called the mind.

It is useful to begin with a hierarchical description of the processing of sensory information. While sensory processing is a multifaceted continuum, we will define four distinct processes that reflect successively more complex integration of sensory information. These are fixed action patterns, reflexes, simple perceptions, and an integrated perceptual space.

A fixed action pattern is the response that is based on an input in a single dimension of one sensory modality. There is no plasticity in the response, so the sensory information is invariably interpreted in the same manner. Fixed action patterns are based on genetically-determined parameters, so the interpretation of the sensory information and the subsequent response were selected because of a long history of experience with the environment by previous individuals. An example of a fixed action pattern is the swimming response of the mollusk *Tritonia*. Whenever this marine animal comes in contact with a predatory starfish, it initiates a very stereotypic escape response. Repeated contacts always lead to the same response, and there is little or no opportunity for the individual to modify its interpretation of the information contained in this particular sensory stimulus.

A reflex is a more complex response to a stimulus that usually encompasses several dimensions of a single modality. Reflexes exhibit some plasticity, and there is some room for the past experience of an individual to influence the future interpretation of the sensory information. We have on several occasions considered the stretch reflex in which tapping the patellar tendon causes a contraction of the quadriceps muscle. This reflex is one means by which the nervous system controls muscle length. Many factors can modulate the output of this reflex to a given input. Some examples are contraction of the muscles of the arms, voluntary contraction of an antagonistic muscle, or conscious concentration on the movement of the knee joint. Thus the same sensory information can be interpreted differently under different circumstances to produce efferent responses that could better fit the demands of the environment.

A simple perception is a response, without an efferent component, to a multidimensional stimulus in a single modality. We all have extensive experiences with perceptions, although most of them are more complex than the simple case that is defined here. A fairly pure example of a simple perception is the “bug detector” found in the retina of frogs. These third-order visual neurons accomplish a considerable amount of sensory processing and respond only to a small dark moving object on a stationary background. It seems reasonable to interpret this as a perception of “bugness.” At this level of processing, the categorization of sensory objects is based on previous experience with similar objects. As a result of this categorization, there is generally an increase in the speed of perceptual interpretation, although there also arises the possibility of false interpretations.

Finally, an integrated sensory space is the event that Leonardo da Vinci depicts as occurring in the *senso comune* and Descartes in the pineal. Here, sensory inputs from several modalities (percepts) are bound together to produce a perception of all aspects of some object in the environment. Our consciousness of the environment is the result of this level of sensory integration. One well-defined example of an integrated sensory space is the cells in the brain of an owl that respond to both visual and auditory stimuli coming from a specific location in the environment.

The nervous system has a special controlling or modifying action over most bodily functions, although neurons depend on the same metabolic processes as do all other cells. The brains of mammals function in an extremely protected environment. Not only are they isolated from most physical insults, but they reside in an environment in which pH, temperature, and O_2 supply are regulated better than in any other organ of the body. In addition, the blood-brain barrier isolates the fluid bathing the cells of the brain from many chemical and infectious agents that can find their way to other regions of the body. This highly evolved homeostatically-regulated environment exists at a considerable expense of metabolic energy. Such a privileged environment must have been selected in spite of its cost to the individual.

Some of the benefits to neurons that are derived from operating in this privileged environment are sophisticated intercellular communication, intercellular interconnections that persist for the lifetime of the individual, and a stable environment of chemical substances that, in other regions of the animal, are subject to considerable fluctuation. These conditions make possible the formation of the complex neuronal networks of the brain. We have seen previous examples of properties that exist in networks of neurons that are unique to the network and that cannot be observed in the individual component neurons. These emergent properties are essential for the generation of the complex functions of the brain. Gerald Edelman has speculated that it takes the stable biochemical *milieu* found in homeothermic animals in order to have a nervous system capable of making the linkages of perceptual information that are necessary for consciousness.

We will define primary consciousness as the function of the nervous system that permits an animal to interact responsively with its current environment. Higher-order consciousness, on the other hand, is a function of the nervous system that permits an animal to form scenarios about past and future environments. Primary consciousness arises primarily as an extension of an integrated perceptual space, but both primary and higher-order consciousness require the formation of perceptions from sensory input information.

We have previously discussed the terminology of attractors and basins as a way to describe perceptions. One simple form of a sensory attractor is a receptive field with a basin consisting of those dimensions of the appropriate modality that cause a specific neuron to respond. A sensory attractor, however, does not necessarily have such a distinct spatial geography as is common in the somatotopic or retinotopic representation of the somatosensory or visual system or even in the tonotopic representation of the auditory system. Receptive fields in the olfactory system, for instance, are probably better represented as a temporal pattern than as a spatial one, but still, these can be described as attractors with their corresponding basins. Attractors and their associated basins can also exist in an integrated perceptual space, and, in this instance, the basin will have dimensions from several modalities so that the attractor defines a perceived object rather than a simple percept.

Adjacent basins are separated by a sepatrix that forms an unstable equilibrium region between the inputs to two different attractors. A sepatrix field defines the pattern of sepatrixes that divide all of the basins of a given class. The integrated perceptual space includes attractors for different perceptions, and each attractor is fed by all of the percepts that define that perception. A sepatrix field determines the shape of these basins and defines the distinctions between the basins. A unique sepatrix field in the integrated perceptual space arises because of an individual's experience with the environment, and it changes as those interactions change and when there are encounters with different environments. Every perceiving individual has a distinctive sepatrix field that defines that individual's perception of the environment, so this sepatrix field defines the primary consciousness of that individual.

Since effective interaction with the environment will certainly enhance the fitness of an individual, there must be a selection for the development of those perceptual basins that distinguish among the important elements of the environment. Thus there is an adaptive pressure to separate similar attractors with their own discrete basins in the integrated perceptual space and to have a well-defined sepatrix field to separate these basins. It is not clear, however, that there is any strong adaptive pressure for primary consciousness, but rather it may arise simply as a byproduct of this sepatrix field.

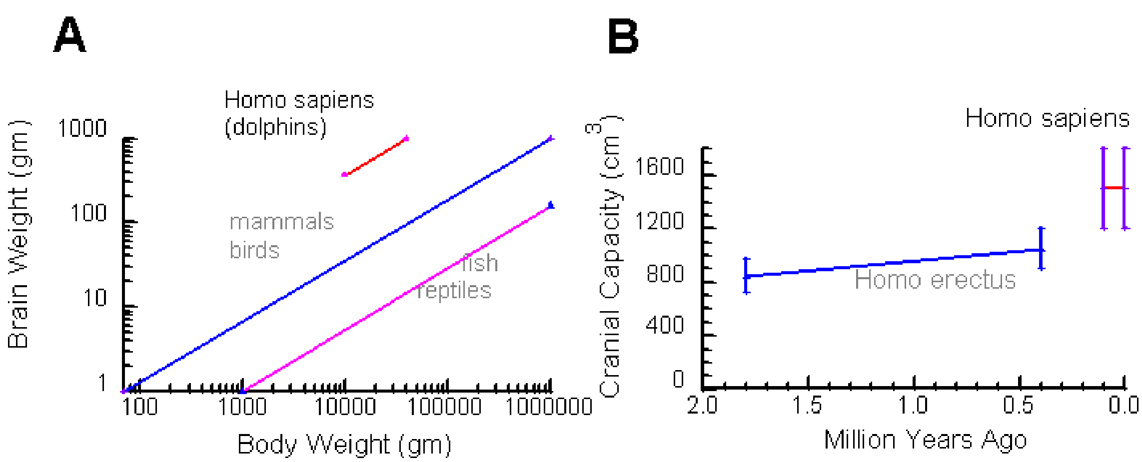


Figure 2 **A.** Approximate relationship of brain weight to body weight. Brain weight (gm) increases with about the 0.7 power of body weight. In many fish and reptiles this holds for body weight in kilograms, for many mammals for body weight in hectograms, and for humans and a few other species for body weight in dekagrams. **B.** Approximate cranial capacity and its range for *Homo erectus* and *Homo sapiens*.

Many complex brain functions distinctive to humans seem to have developed very rapidly in evolutionary time. There is a well-defined relationship between brain size and body size among vertebrates since bigger bodies require bigger brains. Some primates, including *Homo sapiens* (and dolphins), however, have bigger brains when compared with other mammals than would be expected for their body size (figure 2A). There has been a remarkable increase in cranial capacity over the two million years of human evolution. The cranial capacity of *Homo habilis* increased gradually over time from around 800 to about 1000 cm^3, and then around a half million years ago, with the emergence of *Homo sapiens,* cranial capacity rapidly increased to about 1500 cm^3 (figure 2B) This increase in cranial capacity was accompanied by sustained bipedalism and a change in the jaw insertion that would permit functional organs of speech. There are no brains from pre-human ancestors for comparison, but some inferences can be made from chimpanzee brains. When compared with chimpanzee brains (with a cranial capacity of about 700 cm^3), human brains have a large increase in the size of the visual and somatosensory areas of the cortex, but have the greatest increase in dendritic branching and synapses in the associative cortices. Humans and chimpanzees, however, are identical in 99% of their genes. Interestingly, while gene expression is essentially identical between the two species in housekeeping locations such as the liver and blood, there is a three-to-four-times difference in gene expression between the two species in the brain. It appears that the big difference is in the genes that regulate when specific proteins are expressed. Certainly none of this evidence proves that there was a sudden development of complex brain function associated with the mind in *Homo sapiens*, but it does provide suggestive evidence that there may have been a rapid development in the means by which information was processed and in the outcome of that processing.

In addition to the complex functions of the neocortex, a more primitive region of the brain called the limbic system is involved in several of the higher functions of the brain that are usually associated with the mind. These include certain memory functions, a vast range of functions that are categorized as emotions, a strong input of olfactory sensory information, and, interestingly, regulation of many of the homeostatic functions of the body. There is a strong autonomic response to emotional situations including increased blood pressure, pupillary dilation, salivation, inhibition of GI action, and generalized arousal. The same system of the brain that regulates these autonomic responses is responsible for our conscious interpretation of emotions, some of which may be simply a sensory awareness of the autonomic responses.

We introduced, at the beginning of this chapter, a hierarchy of processing of sensory information leading from fixed action patterns to an integrated perceptual space. Furthermore, we proposed that primary consciousness was a byproduct of the perceptual basins that define the integrated sensory space of any individual. This hierarchy is a progression that allows more and more integrated interpretations of the environment. The progression, as Daniel Dennett describes it, gradually makes a trade-off of "speed and economy" for "truth and accuracy." (An analogy would be the difference in analyzing each pixel in a digital image as opposed to analyzing the nature of the image generated by the pixels.) Ultimately this progression leads to animals that gather information for its sake. They become what have been called informavores.

The further extension of this hierarchy of sensory processing almost certainly involves language. Human consciousness is too recent to be hard-wired into the brain, and so it is essentially dependent on plasticity of already existing circuits. The neuronal circuit that produces a fixed action pattern or a reflex can be accurately described, and the plasticity in the circuit can even be ascribed to specific modulatory effects acting on specific neurotransmitter systems. The brain areas involved in language have been known since the work of Paul Broca in the middle of the 19th century, and the neurons in these areas form connections that are similar to those used in the circuits for fixed action patterns or reflexes. The similarity begins to fall apart here. We do not expect to be able to construct a wiring diagram for a word or sentence like the wiring diagram that can be drawn for the *Aplysia* gill withdrawal reflex. The role of plasticity moves from a shaper of a pre-designed action to the basis of the action itself. Our success as a species in using language depends not only on our ability to use neural circuits to learn, but on our ability to use these circuits to learn how to learn. Language not only provides an opportunity to exercise the limits of the plasticity of our brains, but it becomes the basis for our movement fully to higher-order consciousness. As Gerald Edelman describes it, language breaks us away from the "tyranny of the remembered present." With language we have become exquisitely capable of forming scenarios about the past and future and passing those scenarios on to other individuals.

René Descartes and Leonardo da Vinci were just two of the many philosophers who sought to describe a specific locus where all sensory information comes together. Daniel Dennett has called such a locus a "Cartesian theater" to give the analogy of the external world being projected onto a screen where the inner self can watch and interpret the action. Descartes was a dualist who saw the body as a machine and the inner self as a ghost that inhabits the machine. It is easy to discount this as an unscientific thought from a less informed age, but the Cartesian theater can come up in many guises, and it is an easy trap to fall into. Whatever properties one would like to attach to the inner self, it is unlikely to exist at any specific locus in the brain and it is most likely to arise from the functioning of the brain itself.

To take one further step out of the realm of the Cartesian theater, it is also unlikely that there is a single executive center that coordinates the perceptual processes at multiple localities throughout the brain. Some areas are certainly more important than are other areas for this particular function, but it is much more likely to be a distributed function of many brain areas. A useful analogy is to consider that neuronal processing occurs in a loose confederation of interacting processors and that mind is an emergent property of this confederation.

The literature of neurology contains descriptions of the abilities of unfortunate individuals with lesions in specific parts of their brains. The preserved abilities of these patients give some insight into how certain complex brain functions are accomplished. The extensively studied amnesiac H.M. (see Milner, *et al*., 1998) has almost no ability to form new memories. For example, he knows how to solve a problem called the Tower of Hanoi puzzle, but does not know that he has this ability. If given the puzzle, he claims never to have seen the puzzle, but his ability has improved over the years to that of a fairly proficient player. The Russian neuropsychologist Aleksandr Luria in *The Man with the Shattered World* tells of a soldier who received a head injury in the battle of Smolensk in 1943 and lost much of his ability for language and his ability to recall his past history. However, there was clear evidence that much of the information about his past was still there, and the problem was in retrieving this information. Eventually he was able to write out an autobiographical diary and through reading the diary was able to recognize certain things about his past. There are many examples of other neurological cases that fascinate us because they seem so bizarre when compared to our consolidated experience with our own minds.

It is well known by psychologists that people are generally not very good at explaining or even describing the way in which they perceive or think. Witnesses in court are notoriously inaccurate in recounting the most straightforward sensory data, and we all have experiences with vivid childhood memories that turn out not to be grounded in fact. These examples are primarily instances where the sensory information stored is different from that retrieved at a later time. Even our perceptions may not be a good representation of the receptions made by our sensory receptors. Our lack of awareness of the visual blind spot (see figure 3) indicates how we perceive our visual world to be different than the information provided by our visual sensory receptors.

Figure 3 The blind spot is the region of the retina where the axons of the ganglion cells exit to form the optic nerve. Since there are no photoreceptors here, no visual information can be transduced from this location. The blind spot is located nasal to the fovea in the retina, so it occurs temporal to the fixation point in the visual field. To locate the blind spot in your right eye, shut your left eye, and look straight ahead and fixate on the + with the • to the right. Hold the book at about 30 cm and move it nearer and further until the • disappears.

The preceding examples suggest a poor ability accurately to recount sensory information either immediately or after some time. It is also difficult for individuals to provide accurate information about other complex brain functions of the mind. Most of us are quite unaware of how we carry out skilled motor functions and generally become immediately less skilled at the motor function when we try to analyze the underlying succession of muscle actions. One important skill of a good athletic coach is the ability to analyze and describe the process of carrying out a skilled motor action. Another example where we have difficulty describing a complex brain function is the decision-making process. Imagine picking up two objects and deciding which is heavier. You are very aware of the acquired sensory information, but typically rather unaware of the actual decision-making process.

Clinical and experimental studies of complex brain function require either that the subject reports directly on the function or that the clinician or investigator makes observations about the response of the subject. In the first instance, the function is distorted by the inherent inaccuracy of the reporting individual and, in the second instance, there is the added inaccuracy of the sensory perception of the observer. Purely objective information about the operation of the mind is difficult to achieve.

Important advances have been made in functional brain imaging. Initially EEG and PET studies and more recently fMRI and MEG studies have been able to pinpoint region of the brain where there is increased activity in response to specified mental activities. The spatial and temporal resolution of this information is gradually being improved, so that very useful clinical and experimental information is becoming available. Ultimately, this will produce anatomical information about where neural activity occurs in response to a specific action, but it does not tell much about how mind occurs.

We have been concentrating largely on the process of formation of perceptions from the receptions of sensory receptors. At the level of an integrated perceptual space, inputs from multiple sensory modalities are combined to produce the integrated perception that we know as an object. When we use somatosensory information as the input for the perception of a solid object, motor outputs become an integral part of the information about the object. Information about the object's texture, shape, and temperature are certainly important in constructing a perception of the object. In addition, however, we have information about the location of the finger that touches the object, how much force we are applying with that finger, and the compensatory response of the muscles of the rest of the body to that force. This is not only proprioceptive information, but efference copy about the motor commands that are being sent to the muscles. Muscles are controlled in synergies rather than as individual units and an important component of the complex function of the nervous system is that related to controlling its complex output to effectors.

Just as the mind is a function of the particular set of input basins that parse the sensory world into a unique set of attractors, so there are individually unique output basins that determine how an individual interacts with the physical environment. Most sensory-motor interactions are highly dependent upon the ongoing learning of control of synergies of groups of muscles. Activities that we take as much for granted as walking are only possible because we have learned a good-enough, and perhaps unique, sequence of motor acts that can link a series of unstable postures for a particular distribution of masses in a specific gravitational field. As much as the operations on the input information, the translation of the brain's output into effective motor synergies determines what produces our unique conscious experience of the world.

In this chapter, we have made the claim that the complex functions of the human brain, such as intelligence and consciousness, arise as an emergent property of brain structures and their interactions. This claim sounds very much like a description of a computer, albeit perhaps an incomprehensibly complex one. Philosophers who study the mind have grappled with the ramifications of the parallel between information processing in computers and brains. Their theories concerning artificial intelligence (AI) fall into two categories. Weak AI claims that computers can be made to act as if they were intelligent, while strong AI claims that computers that act intelligently have consciousness. Weak AI generally does not present a problem, since it simply says that a computer can be made to mimic human intelligence without actually being consciously intelligent. The strong claim is much more the subject of debate, since it attributes a cognitive state to computers. Whether or not computers will ever have consciousness is not so much the issue with which we would like to conclude this discussion; but rather, if they did achieve consciousness, would this be a model for how these complex functions are produced in the human brain? Several lines of evidence appear to argue against computers ever providing a good model for human intelligence. First, human intelligence does not appear to result from a massive computational ability of the brain. This implies serial processing of symbolic representations of the world, and such a description is a poor fit to what we know about the function of neuronal circuits. A better fit to human intelligence comes from models that involve the action of neural networks. Computers utilizing this type of model have had impressive success in simulating learning and pattern recognition. The human brain, however, is so much more adept at learning – especially in rule-based problems such as language – that one has to question whether it even operates by the same principles.

Problem: Imagine yourself as a non-Chinese speaker locked in a room with a small slot through which cards can be passed, but you are otherwise unable to communicate with the outside world. You have a set of Chinese characters on cards and a very extensive set of rules that tells you to assemble a specific string of characters for each string of characters that you receive through the slot. A Chinese-speaking person on the outside inserts questions as sequences of character cards through the slot and receives sequences of character cards as answers. Because the rules that you have are so good, the sequences of characters cards that you return through the slot are absolutely indistinguishable from the answers that would be given by a native Chinese speaker. The Chinese speaker on the outside would attribute the ability to understand Chinese to the person in the room, but would you consider yourself to be speaking Chinese? Can you extrapolate from this scenario to the claims of strong AI? Can you draw any conclusions regarding the question of using the operation of a computer as a model for how the brain functions?

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Lloyd D. Partridge

He was a member of the American Physiological Society for more than 50 years and attended all of the APS annual meetings during those years. He was also a member of the Society for Neuroscience, American Academy of Neurology, Biomedical Engineering Society, and the IEEE. He served these societies in various capacities including section editor for the *Annals of Biomedical Engineering* and associate editor for the *Proceedings of the IEEE*.

Dr. Partridge's 50 year research career was dedicated to understanding mechanisms of motor control. From his initial work on the stretch reflex and cerebellar function, he went on to be one of the first to bring control systems analyses to understanding the control of muscle function. His chapter "Muscle, the Motor" in the *Handbook of Physiology* (1981) was a bold attempt to explore the ways in which the geometric and functional complexity of muscles represents a solution to problems that are inadequately handled by the computational algorithms of the nervous system. In addition to his contributions to the understanding of motor systems, his scientific interests spanned a broad range from sensory transduction and filtering, to measurement and analysis of scientific communication and literature, to the history of physiological instrumentation.

He will be especially missed by the generations of medical and graduate students who benefited from his insightful and challenging teaching style. He never felt that learning stopped at the end of a lecture or laboratory exercise, but that it continued in hallways, coffee shops, or mountain tops with no limitations on the scope of the acceptable input information.

Notes from former students.

Date: Thu, 07 Apr 2005
From: Gary Bledsoe < bledsoeg@slu.edu
Subject: RE: Lloyd Partridge

Don,
It is with great respect and admiration that I write to you to express my sympathies and condolences on your father's passing. He was one of the most supportive faculty members that I encountered as a graduate student in BME at Memphis, and though I have had little contact in the last couple of years, I will always remember him with fondness.

One of the best things he taught me is that sometimes it is better go get away from the office to do the hard work, particularly the writing. I recall stories he told of completing manuscripts while camped on top of a mountain somewhere, of conversations with gurus in Nepal, or simply of walking the hills at Shelby Forest. Following his advice, I completed my dissertation in front of a cabin fire in BC following days of skiing. His contribution to my personal growth was excessive, and my gratitude everlasting.

Sincerely,
Gary

J. Gary Bledsoe, PhD
Assistant Professor of Biomedical Engineering
Saint Louis University

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Date: Thu, 07 Apr 2005 10:17:26 -0500
From: Sarma <ramalinga.danturthi@mu.edu
Subject: RE: Lloyd Partridge

Greetings
You may think that this is an unsolicited mail, but this is the Eulogy for Dr. Lloyd Partridge, whom I know for more than 3 years - from what I know. If you had worked with him, you would know what I mean. This is a bit long but well this is the final ode to Dr. Partridge. I feel sad he is no more.

Dr. Lloyd Partridge who was with me in my graduating years, was not like all other graduate school teachers. He was a genius; the sort of guy you dream to meet in your childhood. Physically even he was an outstanding personality. Standing over six feet seven inches and sporting a silver hair and beard and a turtle neck shirt, I always felt intimidating to stand opposite to him in the school corridors while chatting. But he was very simple; in fact as simple as a layman and never gave the slightest hint that he was a Ph.D. in neurological studies. Rather, he was a mine of knowledge but covered with lots of shrubs and bushes - like his beard - externally. One had to go and dig the mine to get all those valuable stones. The deeper you dug, the more valuable stones you always found. Here are some examples.

When I bought my first camera - with the money I eked out from my monthly stipend at graduate school, I went to see him with the pictures I took, for he always showed interest to see pictures of other cultures and other people. He had a huge collection of pictures on his computer which he would edit from time to time and also had a camera with a gigantic zooming lens with which he would take his pictures. He had a very good eye of a photographer. I was buying my first camera and had no great knowledge of photography (and even now). All I could afford was the standard auto focus camera available for fifty bucks at the wholesale price club. The reason I actually went to him was to get more data on how to connect my equipment in the laboratory to get good images of the flow equipment I was setting up at that time. While discussing I mentioned about the auto focus camera and why it would not take a picture from less than 2 feet. His answer made me laugh heartily for several days. Even now a smile escapes when I remember his wit. He said "Oh, the auto focus camera is out of focus." Then proceeded to explain the intricacies of what is f number, what is focus etc. Yeah, simple things we studied in physics labs years ago but this professor is one who could remember them in his 70s and show them practically what they are about. He edited his pictures on the computer and was an expert in that too. Occasionally when I was in his office he would show me a picture, he took 2 or 3 decades ago, of some equipment which looked like the telephone Thomas Edison first invented. You would understand nothing of it. He would explain every line in the picture and tell how to get this or that photographic effect. At one time in the lab my equipment broke and refused to work. I asked him if he could come and tell me what was causing the problem. He had no office times, and it was like an open door policy. You could go anytime and chat with him - about anything. He came to the lab and while checking, pulled his car keys and the small plastic magnifying glass attached to the key chain to see what was wrong in the shutter mechanism. He asked me to see too. The gate inside the shutter broke. I had a big magnifying glass in the lab but never had the idea to make use of it. I had the opportunity to travel with him a few times in his own vehicle. He used to keep a small rough notes right on the dashboard with a pen ready to scribble something. When he spotted an out of the state car immediately he would write the plate number and name of the state. He explained to me that he was collecting data of the out of state cars that were spotted in the city each month. While I wondered what good it would do to collect such data, he explained to me. This data can reveal which month there are more visitors to the city and can tell the city officials to provide better resources to the visitors. This is not a thing you could expect from a neurology expert, you would think. But his expertise of life spawned that way. He also had a small temperature reading unit installed in his vehicle. It was connected to some sensor outside of the vehicle and could show him temperature inside the vehicle and outside the vehicle. Lots of stuff like that he had in his office as well. All you had to do was to get to know more of him and you will be left wondering what a mine of knowledge he was. When I met him first he was about 73 and had no health problems to the best of my knowledge. If I asked him some information, he would usually pull a couple of books and articles and give reading material to me that would keep me busy for next several weeks, leaving me wondering how he collected all those books etc.

Aside from work, I invited him to my apartment when my wife joined me in the USA. He came and ate without any restrictions what all we prepared. I was worried that the spicy food would effect his health and thus prepared not so spicy stuff. But he came and asked why the Indian food was not spicy in my home and wanted to know if my health was alright! I had to laugh and laugh till he asked me the reason. While at my apartment he mentioned the Taj Mahal he saw years ago in India and Nepal. He could even recall the food names in the local dialect. Next day I went to him to see if he was OK and felt guilty to ask him if he had any stomach upset because visitors to my apartment usually had stomach upset due to the spicy food I offered. He shot back and said - I am just fine how about you? At an age of 70 plus he used to walk all the steps of 3 floors to reach our department office whereas I *used to take the elevator to go up. After seeing him walking I decided to walk too and even now I walk the steps instead of taking elevator in my office. There was so much to learn from him in day to day life. He mentioned a lot of times about his forefathers and how they lived up to one hundred years and more. One of the greatest secrets of eating I can recall from him was that he would eat an orange along with the peel. I tried to do it several times and it tasted awful to me. But I have practically seen him eating the orange along with the rind. Absolutely no kidding. There was another young professor in his late 30s who sat in the room next to Dr Partridge. This guy had no research projects and used to scratch a dog there and here to get by. When the department asked him to write a proposal to the local company, he wrote project using simple mechanics to get about $15,000. When Dr. Partridge wrote a project he wanted to use brand new Sun workstation and the state of the art voice technology to capture voice data. I was stunned, because the late 30's guy was supposed to go with new technology and the 70's professor usually might depend on low technology. But it was just exactly the opposite. Seeing such instances of knowledge you usually can guess why he was a professor and a knowledge mine. Even when he joined our department at an age of 70 plus, he used to go and sit in the class of another professor listening to the already known subject of physiology. And when I tried to thank him for the help he gave me, he would just wave his hand and say, "ah, no problem at all."*

Frankly I can tell you one thing. There are professors and there are teachers. Dr. Partridge was a real professor. I only wish I met him when he was in his 30s and 40s. This was one man who never showed any signs of ego. He would not mind to come to your office for a meeting if you are late and supposed to meet him at his office. Age had no bars for him. He was learning and teaching even when he was in 70s and 80s. I wonder how many of us are going to keep in shape like him or at least stand tall and erect when we reach our 70s, if at all we do. This is all I know while touching the tip of the iceberg. May his soul rest in peace.

Sarma Danturthi
Milwaukee, WI

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Date: Fri, 08 Apr 2005 18:28:33 -0400
From: "Demir, Semahat S." <sdemir@nsf.gov
Subject: RE: Lloyd Partridge

I am sorry to hear that Lloyd passed away. I have always enjoyed running into him at different places (at Starbuck Poplar Plaza, in the UM ET hallways and in the UT Nash hallways and in conferences) during 1996-2004. He was always very cheerful and informative. I learned something new from each conversation I had with him.

I had the greatest honor since he attended all of my lectures of Physiological Control Systems course that I developed and taught in the Spring 1997. It was the first course for me to develop and teach as a new assistant professor. He even attended my lectures for the same course during Spring 1998. He was dedicated to life-long learning and teaching. He used to drive from UM to UT to attend my lectures. I was and am very very honored. He always praised me and my lectures; I enjoyed receiving feedback and encouragement from him. He was an excellent mentor.

I will miss him.

Semahat S. Demir, Ph.D.
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