Evolving Brains
2000
John Morgan Allman

1. Brain Basics

"…three themes will emerge: that the essential role of brains is to serve as a buffer against environmental variation; that every evolutionary advance in the nervous system has a cost; and that the development of the brain to the level of complexity that we enjoy – and that makes our lives so rich – depended on the establishment of the human family as a social and reproductive unit." Pg 2

Why Brains? "Brains exist because the distribution of resources necessary for survival and the hazards that threaten survival vary in space and time. There would be little need for a nervous system in an immobile organism or an organism that lived in regular and predictable surroundings. In the chaotic natural world, the distribution and localization of resources and hazards become more difficult to predict for larger spaces and longer spans of time." Pg 2

Brain like functions in Unicellular Organisms. E.coli senses its environment with more than a dozen different protein sensors on it surface. It can sense energy sources, nutrients and toxins, store and evaluate the information and make a final decision keep swimming or roll (to alter direction). Halobacterium salinarium have a visual system similar to human in its light sensitive pigment. Chlamydomonas is another with a vision system. "All brains …… receive a diverse array of inputs that must be combined in such a way as to produce a very much smaller set of behavioral outcomes" pg 6

Genetic Mechanisms. Homologous genes have similar DNA sequences and are derived from a replication of a common ancestral gene. By comparing differences in homologous genes it is possible to make a rough estimate of the time elapsed since the original divergence. The bulk of the DNA sequence are neither genes nor promoters but junk gene – DNA which has been rendered inactive thru mutation – which is a good place to dig for fossils. There is also a DNA sequence in the mitochondria which is inherited exclusively down the maternal line – thus comparing cellular and mitochondria DNA is also very useful in estimating timing.

Controlling the Flow of Information. "The large energy requirements of nervous systems have constrained their development, which is an important factor in the evolution of large brains." Pg11 There are many mitochondria in dendrite branches. Nervous systems utilize both analogue and digital signaling. Jellyfish are the simplest organisms to possess nervous systems. Early fish began to wrap neurons in fatty myelin which greatly facilitates axonal transmission and evolution of larger brains. Changes in the brain and parental care were a crucial part to enabling animals to maintain a constant body temperature.

2. Comparing Brains

"Some brain structures are remarkably constant in all vertebrates and presumably perform a very basic functions common to all vertebrates. " pg 16.

Weighing the Brain. "The glia serve to guide the migration of neurons in development, regulate the chemical balance of extracellular fluids in the brain, and manufacture myelin…" pg 16.

Harry Jerison noted that when the body weights of different animals are plotted against brain weights, the animals of particular groups fall within well defined polygons. Brain evolution appears to be linked to predatory behavior. Three conclusions can be drawn 1) body weight and brain weight are correlated 2) larger brain weights of mammals and birds are associated with much larger energy requirements 3) expansion of brain size occurred in different classes of vertebrates independently.

The serotonergic stabilizer serotonin often modulates the response elicited by other

neurotransmitters (except for examples like the pyramidal neurons in the cerebral cortex). Serotonin is made from the amino acid tryptophan which the human body must obtain from dietary sources (abundant in meat and fowl). The serotonergic system was essentially in place 500 million years ago, has been amazingly conserved thru evolution and participates vitally in the most complex aspects of our thinking and emotions. Fourteen types of serotonin receptor are known. The activity of serotonergic neurons are closely related to arousal in cats. The relation between activation of the serotonergic system and repetitive muscular activity may account for the sense of well-being that many experience following exercise. In mice a decrease in serotonin increases exploratory, eating, sexual behavior, and fear induced aggression. Serotonin is intimately linked to social status in monkeys. Low serotonin levels are related to stronger motivational drive and greater sensitivity to rewards and risks.

The Neocortex. Is a thin sheet of neural tissue covering most of the mammalian brain. It is the most variable in size of all the brain structures.

Mapping the Neocortex. Different muscles are represented in exquisite detail in a fine grained mosaic. The size of each area depends on experience and on the level of control/sensitivity required. Cortical fissures are in part formed by the expansion of sensitive areas.

Mapping the Visual Cortex. More cortex is devoted to the central retinal image than the periphery.

Why are there Maps in the Neocortex? Wiring economy to minimize distance between areas processing information which must be compared/combined.

Building on the Past. Each new component of the brain is necessarily built on the pre-existing components. A major mechanism in evolution has been the replication of body parts due to genetic mutation.

3. Duplicated Genes and Developing Brains

Repeating Structures and Archetypes. There have been various proponents over the years, now backed by genetics, who have supported the idea that the variation in organisms is based on basic repetition of basic elements with change.

Variations, Transformations, and Evolution. Bateson created the term homeosis to express of making two things similar. “The discontinuity of species results from the discontinuity of variation. Discontinuity results from the fact that bodies of living things are made from repeated parts …. Variations in number of parts is often integral, and thus discontinuous .. [A Structure] may suddenly appear in the likeness of some other member of the series, assuming at one step the condition to which the member copied attained presumably by a long course of evolution.” Vertebrae are prime examples where the transformation to ribs can occur in either direction.

Gene Duplication and Homeotic Genes. The first homeotic gene was discovered in the fruit fly. A duplicated gene escapes the pressures of natural selection operating on the original gene and thereby can accumulate mutations that enable the new gene to perform previously non-existent functions, while the old gene continues to perform its original and presumably vital role. Lewis discovered that the fruit fly genes controlling the development of the thoracic and abdominal segments are located in the same order in the chromosome as the topographic order of the body parts whose development they controlled.

Homeobox. Making the Nervous System from the Neural Tube. The central nervous system forms from a long tube in vertebrate embryos. The major components of the brain begin as bulges in this tube.

Making the segments of the Hindbrain. The role of homeotic genes in the formation of brain structures and their connections is best established in the hind brain. He vertebrate

hindbrain is organized in a series of repeating elements, the rhombomeres.

Making a Head. Genes that control head and brain formation in fruit-flies are very closely related to the genes that control the formation of the more anterior parts of the brain in mammals.

Brains and Guts. In most animals the brain is located near to the entrance to the gut which suggests that the brain arose as the gut's way of controlling its intake by accepting nutritious foods and rejecting toxins. There are several families of genes that govern both brain and gut development. There is strong evidence that the brain and the gut compete for metabolic energy in the organism and that gut size limits brain size.

Bad Copies.

The Regulation of Development in Space and Time. The spacial ordering of the main set of homeotic genes has been conserved for more than half a billion years. The collinearity of the gene location in chromosomes and the gene expression during development are related and driven by increasing concentration of retinoic acid. Both replicated structures and replicated genes have the capacity to undergo evolutionary change.

Ancient Assassins. There are examples, such as the retina, where many cells are initially produced only to be pruned later during development by an ancient family of enzymes known as caspases.

4. Eyes, Noses and Brains

The evolution of the axon and action potential enable neurons to communicate over long distances which in turn enabled larger and more complex animals. Many of these early animals may have been predatory. It is unclear why the Cambrian explosion of diversity in living things occurred at this time (540-520 million years ago). There were 10 oscillations of rapid proliferations followed by mass extinctions which exceeded the mass extinction at the end of the Cretaceous when 75% of species became extinct. Following the Cambrian, highly developed sensory systems and large brains have developed independently in two major groups: vertebrates and cephalopods.

The Early Evolution of Eyes. Cambrian animals lived in water and as a result developed eyes sensitive to those frequencies with little attenuation through water. One gene produced the antecedent to the rod-type photoreceptors (low light) and another for the antecedent to the cone-type photo-receptors (developed further into color vision).

Eyes and Brain and Chordate. "This remarkable constancy in the location of serotonergic neurons in amphioxus and vertebrates points to the fundamental nature of the serotonergic system and its stability in evolution." Pg 71

Include diagram on page 72

The Rise of Vertebrates. The earliest vertebrates (jawless fish) appeared about 470 million years ago (shortly after the close of the Cambrian period). "Thus the earliest vertebrates, like the earliest amphibia, the earliest mammals, and the earliest primates, were small predators." Pg 73 The homobox genes in amphioxus make up a single co-linear set that contains all the individual genes homologous to those found in the quadrupal sets of homobox genes in vertebrates. In each replicated set of vertebrate homobox genes, some of the genes are missing." pg 73. About the same time the control of homobox genes changed, the neural crest developed (respiration, olfaction and vision), and primitive hemoglobin.

Gene Duplications Create a Keen Sense of Smell. There was a massive multiple-duplication of the genes for olfactory receptors. The "smell-brain" hypotheses holds that the early evolution of the telencephalon as dominated by olfactory input and function. This may be the basis for the richly evocative capacity of odors to elicit memories, particularly with respect to appetite and procreation.

An Ancient Map. There is a tight mapping between the retina and the optic tectum.

The Origin of the Cerebellum. Successful predation requires rapid movement and hence a stable retinal image which is achieved with the vestibular system which senses head movement and signals the hindbrain which drives compensating eye movements.

Myelin: A Crucial Vertebrate Innovation. Myelin is a material that insulates axons and is fundamental to the functioning of the brain in higher vertebrates (its failure causes MS).

Cephalopods: The Second Great Pinnacle of Brain Evolution. The cephalopods (nautilus, squid, octopus and cuttlefish) developed brains independently with basic visual systems etc. However, their evolution was fundamentally limited by their failure to develop an equivalent to myelin. Another limitation is their blood (green) which only carries 25% of the oxygen that hemoglobin does.

5. Warm Blooded Brains

"The brains of warm-blooded vertebrates, the mammals and birds, tend to be larger than the brains of cold-blooded vertebrates of the same body weight. The larger brain in mammals and birds are a crucial part of a large set of mechanisms for maintaining a constant body temperature. Since all chemical reactions are temperature dependent, a constant temperature brings about stability in chemical reactions and a capacity for precise regulation and coordination of complex chemical systems. However, maintaining a constant body temperature requires a tenfold increase in energy expenditure." Pg 86

The Invasion of the Land: Predators Lead the Way.

Include picture on pg 87

Staying Warm and Keeping Cool. The evolutionary changes required to maintain a constant temperature have included changes in the quantity of food consumed and the way it is chewed, in breathing, in locomotion, in parenting behavior, in the senses, in memory, and in the expansion of the forebrain. "….it is less energetically expensive to heat the body than it is to cool it ……. Today mammals maintain their body temperature at about 37-39 degrees Celsius, which is near the high end of the range of the daytime temperatures to which it is exposed, because it is easier to heat the body than to cool it." Pg 93.

The Cynodonts Become More Active. Predators that ranged in size from that of modern ferrets to wolves. "Thus the differentiation of the teeth for specialized functions in preparing food for rapid digestion and the formation of the forebrain are under the control of the same gene, and this implies a close linkage in the evolution of the teeth and the forebrain in the mammalian line." Pg 94. Another important change was in the formation of a bony barrier between the oral and nasal cavities to allow the cynodonts to swallow and breathe at the same time. There was also a better olfactory system, reduction of ribs in the lumbar region and energy efficient sleeping position. "The evidence for a higher metabolic rate suggests that the cynodonts had begun to develop parenting behavior; which is inextricably linked to temperature homeostasis." Pg 96. "Milk is a complex food …. The functional maturation of the brain probably depends on this precise mix of nutrients, since there is evidence that human infants raised on natural human milk have significantly higher IQ's than infants raised on formula milk when both are administered through bottles." pg 96 The tactile and visual spacial maps overlap in the midbrain of a mouse and the aural and visual spacial maps overlap in the midbrain of the owl. "In small mammals, lactation triples the amount of food that must be eaten by a female." Pg 97

The First Mammals. Appeared at the end of the Triassic (220 million years ago). There were major innovations in the brain, the hearing mechanism and in tooth development but an initial setback in vision. Two bones that were part of the jaw joint in the Cynodonts became incorporated into the hearing apparatus in the earlies mammals and that

appears to be related to the capacity of mammals to discriminate much higher frequencies than reptiles and birds (ie from 10-100kHz). In addition, mammals have three rows of outer hair cells in the cochlea which can change their shape extremely rapidly in response to sound and enhances discrimination of higher frequencies. This effectively gave mammals a private communication channel for distress signals and the like. The onset of permanent teeth (rather than continual replacement) allowed better fit and grinding capability. Senescence (increased risk of dying with age) potentially reduces the competition between generations. Evolutionary adaptations are interdependent and incremental.

The First Birds. The thecodonts survived the great extinction at the end of the Permian period and gave rise to the birds and the dinosaurs.

Uniquely Mammalian: The Neocortex. Is a sheet like, six-layered structure in the roof of the forebrain that is found in all mammals and in all mammals; it is possible that it may actually have evolved earlier, at some point after the separation of the line leading to the mammals from the lines leading to reptiles and birds. "…. The neocortex probably evolved as a set of adaptations related to temperature homeostasis." Pg 108. "… topographical maps are an ancient feature of neocortical organization. " pg 110. The role of genetics verses inputs in determining the architecture of the neocortical maps is as yet unclear but there is considerable similarity within and between mammalian species.

The Mouth Leads the Way to Cortical Development. In embryos, the first part of the neocortex to develop is the part which will represent the mouth and tongue and then in concentric rings extending out from this core region. The may be the result of the need by young to nurse as soon as they are born. Thumb sucking in the womb may stimulate formation of the cortical map and may result in hand preference in later life.

Diverging Patterns in the Telencephalon of Mammals, Reptiles, and Birds. The organization of the telencephalon took an entirely different course in birds and reptiles than it did for mammals. The visual cortex in reptiles contains only a very crude topographical map of the retina. In birds there is a considerable expansion of this part of the telencephalon, especially in the wulst. This single map is more economical in terms of wiring than the mammalian equivalent which integrates multiple maps. "The volume of neocortical white matter, which contains the "wire", the axon fibers that connect the different parts of th neocortex. The volume of neocortical white matter increases at the 1.318 power of the volume of neocortical gray matter. This is very close to a 4/3 power law relationship, which suggests that there may be a simple geometrical factors that govern the increasing size of the white matter." Pg 116.

Forebrain Expansion and Memory. Young reptiles function as miniature adults but baby mammals and birds are dependent because of their poor capacity to thermo-regulate – a problem often solved by parenting. "Although synapse formation and modification in the forebrain occur throughout life, these processes are most active during the period in which the infant is dependent on its parents for sustenance." Pg 118 A molecular participant termed telencephalin is located in the membranes of dendrites and cell bodies but not axons and thus corresponds to the sites where neurons receive synaptic contacts. An analogous system in fruit–flies suggest that memory may depend on the physical tightening or loosening of the synaptic connections between neurons.

Warm Blooded Paradoxes.

6. Primate Brains

A 6 mile wide meteorite struck Yucatan 65 million years ago, but the mammals survived the cold/dark period while the dust settled. Once the dust settled, that environment became much warmer than today's world, and

tropical rain forests covered a much larger portion of the planet than they do now.

Eyes, Heads and Brains. The prosimians (before the monkeys) developed a greatly expanded representation of the central retina separated into two distinct processing streams: one sensitive to motion and small differences in contrast and the other responsive to shape and form. The visual cortex was expanded and new areas developed including a specialized area for visual guidance of muscle movement. Then about 40 million years ago a gene duplication resulted in the development of trichromatic vision and an expansion of the system for emotional communication via facial expression (and reduction of olfactory communication)

Advantages and Costs of Front-Facing Eyes. The "visual predator" hypothesis holds that keen vision and superb eye-hand coordination were required to feed of insects from the trees with maximal quality retinal image, improved binocular vision, stereoscopic depth perception, and the ability to break camouflage. The "fine-branch niche" hypothesis similarly holds that high quality vision is required immediately in front of the animal. Front facing eyes do however limit the detection of predators approaching from behind - countered by keen hearing and group alerts.

The Optic Tectum: An Ancient Visual System Transformed. In non-primate vertebrates the map from the retina to the Optic Tectum is almost completely crossed to the opposite side. In primates there is a large mapping to the same side and only the opposite half of the visual field is represented in each tectum. The role of the tectum in primates is to cause the eyes to fixate on interesting objects (with eye movements rather than head movements)

Seeing Motion and Form. In Primates the major output from the retina travels in the optic nerve to the lateral geniculate nucleus in the thalamus which in turn connects with the visual cortex. The LG nucleus consists of several layers: the magnocellular layers are sensitive to rapid movement and minimal contrast in light intensity ; the parvocellular layers detect finer detail but are less sensitive to motion and contrast. The magnocellular layer projects to the middle temporal area in the visual cortex which in turn projects to higher cortical areas in the posterior parietal lobe for planning movements of the eyes and hands. Another projection from both magnocellular and parvocellular layers projects to V2 and on to V4 where neurons are sensitive to size and shape.

Include diagram on pg 131

Seeing Spots, Lines and Curves. Most neurons in the primary visual cortex are arranged in columns and are exquisitely sensitive to the orientation of straight lines and edges and others to ends and intersections and still others to tiny spots and long rectangles.

Area MT and the Perception of Motion. Is devoted to the analysis of movement. MT neurons respond maximally to a preferred direction and are often inhibited by movement in the opposite direction. Adjoining columns along one axis contain cells with the opposite directional preference and along the other axis the preferences change gradually.

Seeing the Visual Context. The perception of qualities of objects depends heavily on the surrounding visual context. MT neurons are sensitive not only to the direction of motion of objects but on the movement of the background.

Seeing Size and Distance. The motor act of fixing on an object is sufficient for accurate size judgment for near objects, but the visual context (binocular stereoscopsis, perspective and shading) is required for judging the sized of more distant objects. With visual context adults can judge size accurately beyond 30m but children to only 3m. Without the visual context humans underestimate the true size. Possibly explains why the world seemed bigger as a child. There are neurons in V1 and V4 that respond to the nearness or farness of objects suggesting that the 2D maps in the

visual areas are supplemented by the 3rd dimension by these embedded cells.

Evolution of Color Vision. The retinas of ancient animals contained a single photoreceptive pigment that in the course of evolution differentiated into first two (about the time of vertebrates) and ultimately into three pigments (about 40 mill years ago in Old World monkeys) that were sensitive to different parts of the spectrum. In some nocturnal primates mutations have rendered one of the pigment genes inoperable - a current example of a fossil in junk DNA. Spectral opponency is a characteristic feature of neurons in the parvocellular layers of the lateral geniculate nucleus, and in parts of the V1, the primary visual area.

Making and Seeing Faces. Primates rely on facial expressions to communicate their emotions. Olfactory systems are much reduced. Large cortical representation of facial muscles suggests that expressions are not merely automatic behavioral responses. The amygdala has an important role in interpreting emotional (particularly fear) content in both faces and voices.

Establishing Priorities. In primates the frontal lobe has an important role in establishing priorities and planning (see Damasio)

Unique to Primates: A Center for Visuo-Motor Coordination. The ventral motor area contains neurons that respond when the subject observes another performing an action. (mirror cells). Broca's area (involved in the production of speech sounds) is located in approximately the same position in the human brain as the ventral motor area in other primates. Across primates, the size of the projecting cortical area is a constant fraction of the cortex implying that refinement of motor control is proportional to processing power of the cortex.

Saving Wire: The Formation of Cortical Maps and Fissures. The visual field is represented as a first order transform in the optic tectum, V1 and area MT, and as second order transforms in V2 and other visual areas. These second order mappings allow the different maps to fit together in the cortical sheet in such a way that there are no major discontinuities in the visual field. The folding in the cortical sheet also appear to reduce wiring length between areas and there is a theory that it is actually the mechanical tension of the interconnecting neurons that causes the folds during development.

The Evolution of Multiple Cortical Areas. Many areas appear to share common features suggesting that they resulted from the duplication of preexisting areas: V1 and V2 are an example. The origin of many of the areas beyond V2 probably occurred over the span of only a few million years. “The idea that each cortical area has a distinctive function is an attractive notion, which is well supported by ..... However, evolution through gene duplication suggests alternate ways of thinking about the functional roles of the different areas.” pg 157. It is the differences between the photo-receptor pigments that enable the color vision that no one of them can support in isolation. The inner and outer hair cells cooperate to improve hearing in mammals. Hemoglobin is a four chain molecule that has superior oxygen transport capabilities and it is the result of a fourfold replication of the gene.

7. The Evolution of Big Brains

If large brains are so great why are they so rare? Large brains are costly in terms of time, energy and anatomical complexity. Lengthy maturity requires energy expensive parenting. The brain competes with other organs/activities for energy.

Bodies, Brains and Energy. For non primates log brain weight = 0.74 log body weight – 1.3 and for primates log brain weight = 0.75 log body weight – 0.94 (ie nearly parallel but and 2.3 times larger). The rate of energy use by animals at rest also scales at the ¾ power of body weight and is related to the branching geometry of blood vessels. However, there is considerable variation at any one body weight so residual variations from the regression line

must be used for a valid comparison between animals. Primates that eat fruit tend to have larger brains than leaf eat eaters. Fruit has higher energy and is easier to digest but is more widely dispersed in space and time and subject to greater competition. The main energy using organs are the heart, liver, kidney, stomach and brain so there is a forced trade off between brain and digestive organs.

Brains and Time. Relative longevity and brain weight are strongly related in monkeys apes and humans and becomes more strongly correlates in higher apes and humans (who are exactly on the regression line)

The Social Brain Hypothesis. There is no significant relationship and group sizing and the weight of the brain or the amygdala in particular (has a role in social communication). However, there is a significant relationship between group size and the ratio of neocortex volume to the volume of the rest of the brain. In primates, social group size predicts about 47% of the variation in neocortex ratio and and life span predicts about 45% of the variation (and the two measures are only 3% dependent).

Big Brains and Parenting. “In a newborn human the brain absorbs nearly two thirds of all the metabolic energy used by the entire body. .....and ..... Nurturing a large-brained baby imposes enormous energy costs on the mother because of the burden of lactation, which is far more costly than digestion.” pg 175. Human brains only reach their full size about the time of puberty with myelination continuing until around age 17. Synaptogenesis is much slower in the frontal cortex than the primary visual cortex. Time is also required for the experience dependent development. The author hypothesized that in large brained species that have single births the sex that bears the greater burden in the nurturing of the offspring will tend to survive longer. High status in primate groups for males is much more dependent of social skills and coalition building than on aggression. There is strong evidence to suggest that high status does confer reproductive success in female chimpanzees, and it is clear that social competence plays an important role in determining the female dominance hierarchy. “The mechanisms responsible for the survival differences between caretakers and non-caretakers may ultimately be related to neuro-chemical differences that favor risk-adverse behavior in caretakers and risk-seeking behavior in non-caretakers, as well as greater vulnerability to the damaging effects of stress in non-caretakers.

Brain evolution in Hominids. “Humans development with respect to non-brain structures appears to be a truncated version of ape development, with humans becoming reproductive at an immature stage relative to apes.” pg 197 The invention of the extended family enabled humans to evolve much larger brains and avoid the constraints imposed by the extremely slow maturation and low fecundity associated with such large brain size.” pg 198. “Primitive language may have developed in early humans as a means to facilitate family bonding and coordinate food acquisition.” pg 200. “Two areas of the human brain are responsible for speech, both located in the left hemisphere in most people. ..... Rizzolatti ... proposed that Broca's area is involved in matching observed vocal and manual gestures with the production of these same gestures . ..... Wernicke's area is more concerned with the comprehension of language. .... In the bottom of the adjacent superior temporal fissure , there is a region that is responsive to both auditory and visual input ..... Desimone proposed that these parts of the temporal lobe, which are concerned with multi-modal communication in monkeys, may be related to Wernicke's area in humans.” pg 200 “The human evolutionary success story depends on two great buffers against misfortune, large brains and extended families, with each supporting and enhancing the adaptive ability of the other.” pg203 “Because we participate in so many different social networks, it is impossible to specify a social group size for humans. Participation in each of these social networks requires a different set of behavior depending on the context. The adaptive significance of self awareness in humans in the ability to navigate these different

networks with the appropriate behavior for the particular context." pg 203

Dances with Wolves. Wolves and humans shared much in common – highly mobile cooperative predators across prey large, small and scavenged – highly vocal extended families with shared parenting. Humans domesticated wolves with considerable complementary survival advantages for both. The relative brain sizes of both dogs and humans have decreased over the last 35000 years – possibly as a result of domestication reducing the very environmental variability for which brains were developed.