The Evolution, Structure and Function of the Nervous System: From Fish to Philosopher

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This essay is dedicated to György Buzsaki MD, PhD.
His book, Brain from Inside Out is foundational to much of the content of this essay.

Summary

This essay addresses one of humanity's longest-standing questions. Where does human understanding come from?

We address this question by first noting that understanding is a function of the nervous system. Thus, to understand understanding, we need to understand the evolutionary origin of the nervous system and its structure and function. Human understanding, while grounded in the mechanisms by which other animals are sentient, is something beyond that understanding. Thus, we examine what is distinctive about the neural outputs of the human nervous system to address the question of where human understanding originates.

Questions about human understanding have long been the domain of philosophy. We now tell the story through the remarkable advances in neuroscience, which may answer these questions. The answers that neuroscience provides are unexpected and awe-inspiring, reminiscent of how the discovery of DNA and its code resolved longstanding problems of inheritance and the gene. We believe that the answers provided in this essay will serve as a foundation for future discussions on humanity's role in the world.

The essay is organized into three parts. The first part examines how the nervous system evolved into a distinct organ system in animals. The second part describes the expansion of the vertebrate forebrain that led to the higher brain functions of so many animal species. The third part examines what is unique about human brain output, which ultimately underpins the remarkable understanding humans now have of the natural world.

Our essay tells the story through an evolutionary lens, explaining how neural mechanisms generate behavior, cognition, and consciousness. It traces the origin of the neuron as a specialized eukaryotic cell whose molecular components, particularly voltage-gated ion channels and synaptic proteins, predate neurons themselves. Nervous systems and muscle tissues co-evolved to enable the rapid, directed information transfer required for adaptive movement in animals. Comparative studies across animal clades show that synaptic, electrochemical, and centralized nervous systems conferred a decisive evolutionary advantage, culminating in the vertebrate brain.

While brains initially evolved to enable action, subsequent evolution enabled predictive mechanisms that supported more informed action through the development of sense organs. As a result, the brain has become a predictive mechanism in which action is followed by sensory evaluation to enable better action. This is the inside-out model of brain function, which has undergone explosive evolutionary exploration across vertebrates.

The expansion of the vertebrate forebrain, especially the cerebral cortex, underlies advances in planning, memory, cognition, and consciousness. Neural function is explained by interconnected networks of excitatory and inhibitory neurons. These networks encode information about the external world as memory engrams shaped by experience-dependent plasticity. Continuous electrochemical activity within and between networks generates brain oscillations that coordinate information flow across cell assemblies, ultimately determining brain outputs.

Brain outputs generate behaviors that ultimately determine individual and evolutionary success. For humans, brain outputs are more complex. In addition to motor behavior, brain externalization includes language, mathematics, and creative arts. Because humans live in cooperative groups of increasing size, these outputs represent the externalization of thought into the collective mind. Ideas circulating within the collective mind can be conceived of as memes. Allowing internal brain models to be externalized allowed for ideas to be shared, shaped, and refined across generations. These culturally mediated outputs dramatically accelerated the acquisition of understanding and enabled translation into technology, amplifying the adaptive impact of the nervous stem far beyond its original biological constraints.

These are remarkable developments that neuroscience has brought to the table. They should inform discussions of humanity’s place in the universe and much else. They address the question of where human understanding originates.

Introduction

I am a physician scientist. What has amazed me most about science is not the result of any particular experiment but rather how much we can understand the world simply by studying it. Channeling the spirit of Einstein "The most incomprehensible thing about the universe is that it is comprehensible." How is it possible that humans have come to understand the cosmos in such detail at its most fundamental levels? The grand theories of science such as quantum mechanics, general relativity and evolution by natural selection are astounding achievements of human creativity, accuracy and truthfulness. How does such understanding come about?

Understanding is the product of the nervous system. Thus to understand the source of understanding we must understand the nervous system. This essay outlines the evolution, structure and function of the nervous system as has been revealed by over a century of neuroscience research.

Interest in the human mind has been longstanding and until the rise of neuroscience, philosophy was the only important source of ideas about the mind. Rene Descartes is the most influential philosopher of the human mind. His famous "cognito, ergo sum" (I think, therefore I am) set the agenda for much of modern philosophy. Descartes asserted that there exist two forms of substance, material and immaterial. The brain was material and thought was immaterial. He viewed the mind as containing a central observer of incoming sensorial information within a Cartesian theatre who makes executive functions. This observer he called the human soul. Others have called it "the ghost in the machine". Descartes was a dualist, a philosophical viewpoint which still exists. The fatal flaw of Descartes and dualism in general was the absence of a mechanism by which material and immaterial substance interact. He said that the interaction occurred within the pineal gland but experiment soon showed that was not true. In fact, with the rise of neuroscience, almost all of Descartes ideas about the nervous system have been found incorrect. Based on experimental evidence and evolutionary reasoning neuroscience has concluded that both the brain and mind are due to material processes which occur in the brain. We will explain that evidence and reasoning.

While Descartes' theories on the mind were found wanting, the suggestions of the empirical philosophers David Hume, Immanuel Kant, Ludwig Wittgenstein and Daniel Dennett proved more constructive and helped shape how modern neuroscience thinks about the mind. In essence philosophy provided ideas about the brain and mind which neuroscience experimentally investigated and at times validated. Thus this essay will elucidate both the scientific and philosophical contributions to human understanding about the nervous system.

The essay contains both facts and ideas beginning with evolution, proceeding to a structure function analysis together with an outline of the philosophical unity of ideas beginning with

Hume and ending with Dennett. Like mathematics in physics, philosophy in neuroscience has improved understanding of the mind through critical analysis of ideas via logic and use of precise language.

Structural Evolution of the Nervous System

The defining structure of life is the cell. Over 3.8 billion years ago life arose on Earth from the geochemistry of warm deep sea alkaline hydrothermal vents. At the origin of cellular life two different Prokaryotic lineages emerged from the hydrothermal vents as Archaea and Bacteria. Cells were the entity through which evolution diversified living forms by the mechanism of natural selection. Over the subsequent 2 billion years these lifeforms explored many ecological niches and evolved the rich genetic diversity that characterizes the biochemistry of all life today. At a single point some 2 billion years ago in life's history, two separate species from the lineages of Archaea and Bacteria symbiotically merged to create the third major cellular type of life, the Eukaryote. Eukaryotes gave rise to all visible macroscopic life on Earth. Everything you see around you today is composed of Eukaryotic cells.

The neuron is an Eukaryotic cell and is the defining cell type of the nervous system. It is a markedly asymmetric cell with extended structures called axons and dendrites. Neurons originated from epithelial cells over 600 million years ago during the Ediacaran era of life on Earth. Thus the nervous system with its defining neuronal cell type comes late in the evolution of life on Earth.

The characteristic molecules of the neuron are voltage gated ion channel proteins which are over 2 to 3 billion years of age having originated among the Prokaryotes. Voltage gated ion channels enabled the development of action potentials and the electrical transfer of information. Electrical transfer of information is much faster and more directed than chemical diffusion and in turn, their use by neurons within the nervous system enabled the development of large complex organisms which required rapid transfer of information. In addition to voltage gated ion channel proteins, other neuron specific proteins include synaptic proteins which regulate the operation of the electrochemical synapse. These proteins had their origin in early unicellular Eukaryotes, over a billion years ago. Overall the molecular components which define the neuron have a much older origin in evolutionary time than the neuron itself.

Together with other cell types such as glia cells, astrocytes and oligodendrocytes, blood vessels and blood derived cells, neurons form the tissue of the nervous system. The nervous system co-evolved with muscle cells in the body to enable controlled movement in search of food, avoidance of predators and the finding of reproductive mates. Thus, at its origin the nervous system evolved to enable adaptive action.

Animals are metabolically defined as heterotrophs that use other organisms as their food source. This metabolic classification is in contrast to plants which are phototrophic using solar energy to generate food sources or autotrophic Prokaryotes who use inorganic chemicals as sources of energy and electrons for metabolism. Animals require movement because they feed on plants or other animals. Hence the need for a system to initiate and control movement. That system was the nervous system.

Animals diversified over evolutionary time as carnivores and herbivores and created the complex ecological systems seen on Earth today. Of all living forms, only animals have nervous systems.

Five major clades characterize the origin of animal life. These are Porifera, Placozoa, Ctenophores, Cnidaria and Bilateria. All but Porifera (sponges) have nervous systems which may have had a nervous system but subsequently lost it. Evolution experimented with three different methods for how neurons communicated with each other. In Placozoa, neurons secrete neurotransmitter molecules which diffuse to their target cells (the chemical model of neuronal transmission). In Ctenophores neurons fuse their membranes with each other to generate a large single neuronal syncytium through which action potentials propagate (the electric model). In Cnidaria and Bilateria, neurons communicate with each other via synapses (the electrochemical model). The electrochemical model of neuronal transmission ultimately won out in the evolutionary struggle and diversified during animal evolution likely due to the fact that the synapse provided an extra level of control and plasticity enabling learning, memory and other cognitive activity which the chemical and electric modes lacked.

Evolution experimented with two forms of neuronal organization. The first involved distributing neurons throughout the body as a nerve net to control muscular body contraction for food acquisition as seen in jellyfish. The second experiment in neuronal organization was to centralize nervous tissues to varying degrees. There were three ways centralization was evolutionarily explored. These are the partially centralized nervous systems as seen in Cephalopods where a single central brain operates in tandem with brains placed at the base of each arm. Each brain unit can function semi autonomously giving each arm independent action. In Arthropods the nervous system is organized as head region containing a centralized brain and two ventral tubes of nervous tissue running in tandem along the ventral surface of the body. Each anatomical segment contains nervous tissues which regulates muscles of that segment. Lastly in Vertebrates the brain is centralized in the head region together with a single spinal cord that runs along the dorsal region of the animal. The head region brain has a tripartite arrangement with hindbrain, midbrain and forebrain and controls the movement of the body.

Centralized nervous systems came to dominate animal evolution at different periods of evolutionary time. Arthropods were the first apex predators during the Cambrian era from 540 million to 480 million years ago. This was followed by Cephalopods who were apex predators from 480 to 420 million years ago. Vertebrates became apex predators about 420 million years ago when jaws first appeared in the fossil record. Vertebrates have remained in this ecological position of dominance since that time.

The Vertebrate tripartite centralized brain emerged to become evolution's masterpiece. The central brain located in the head is connected to the spinal cord and has three segments. The hindbrain contains vital neural centres that regulate patterns of motor response in the body, in addition to centres that regulate breathing and cardiovascular function. The cerebellum is attached to the hind brain and provides feedback control of movement. Next comes the midbrain which contains reflex centres to process visual and auditory sensory information in an instinctive response as a motor action. There are also other centres in the midbrain which coordinate muscular movement. The forebrain is the last but most interesting component of the vertebrate tripartite brain. Among the three segments, the forebrain has displayed the largest diversification in structure over Vertebrate evolutionary time.

In fish the forebrain is primarily composed of the plate-like pallium which processes olfactory information to assist in feeding. In all later Vertebrates the pallium expanded tremendously and in humans, forms the bulbous cerebral cortex, the limbic system and the basal ganglia. The basal ganglia coordinate muscular movement, the limbic system houses neural components for emotions, memory, spatial and temporal navigation, control of the body's endocrine system and regulation of the stress response among other activities that set the conditions for whole body homeostasis. The limbic system also contains the thalamus which in part, is the gateway by which electrochemical information enters the cortex from other portions of the brain and body and through which motor commands exit the cortex.

The cerebral cortex is the crown jewel of evolutionary innovation. It is the seat of consciousness, cognition, creativity, memory, planning, executive action and free will. These are the functions of the brain that create the mind which characterizes human life (and probably the inner life of all other cortex bearing animals especially mammals). These functions have been the subject of much study by philosophers and other humanists. The rise of modern neuroscience now sheds light on how the miracle of thought based on the cortical forebrain has come about.

An evolutionary perspective offers an explanation as to why the forebrain underwent such dramatic expansion after fish left water and entered the terrestrial environment some 375 million years ago. The selection forces have to do with the transparency of water versus air thereby allowing the animal to better plan action. Relative to air, water is much less transparent allowing the animal less time to plan action and selecting for instinctive rapid responses. On land the senses especially vision allow the collection of information from far greater distance permitting more detailed planning before undertaking action. This opportunity opened an evolutionary space that enabled the dramatic expansion of the forebrain as animals transitioned from fish to amphibians to reptiles including dinosaurs, birds and ultimately mammals. The cognitive planning that is undertaken by terrestrial Vertebrates takes place in the evolved cortical structures in the forebrain.

Evolution of Neural Function

How function is carried out in the nervous system is deeply tied to the organization of connections among its neurons. Most importantly, neurons are organized into networks. In fact neurons require contact with other neurons in the brain in order to survive. Without a synaptic connection a neuron dies through programmed cell death. Nearly all neurons in the nervous system are connected directly or indirectly with all other neurons via synapses through which electrical impulses stimulate release of neurotransmitter molecules. Neurotransmitters interact with a protein receptor on the receiving side of the synapse to trigger or inhibit the development of another action potential in the adjacent neuron. Neurons receive information through multiple dendrites and transmit information via a single axon. All dendrites are short structures while axons range in size from less than a millimetre to over a metre. Thus the vast numbers of neurons in the centralized brain are organized into a near single network of neurons with a specific architecture.

The architecture of a neural network is classified as a small world network with most axons in the millimetre range and rare axons in the centimetre to metre range. This allows localized neural structures to develop, but ones which are also connected to distant regions elsewhere in the brain.

Organized local neural networks acquire specific functions within the cortex and elsewhere in the brain. Most famous are the somatosensory and somatomotor maps of the body initially discovered by the great Canadian neurosurgeon, Wilder Penfield. These maps or homunculi reflect a remarkably distorted body image. They are created in response to natal and post natal life experiences as vividly seen during the spontaneous random movements of the newborn which mature into the controlled purposeful movements of the child. These homunculi are somewhat flexible or plastic as they change in response to environmental factors such as loss of a body part or training requiring specific movement such as piano playing.

Other locally organized neural networks found in the cortex include the motor speech area found in most people in the left frontal cortex and labeled Broca's area after the nineteenth century French neurologist, Paul Broca. Similarly the receptive speech area in most people is located in the left temporal lobe and labelled Wernicke's area after the nineteenth century German neurologist, Carl Wernicke. Again as these centres form, it is remarkable to see how the babble of babies matures over a five year period into the fluent speech of the child. Several functionally similar localized centres exist in the cortex dedicated to vision, face recognition and letter recognition in addition to several others functions localized to other regions of the cortex. These local small world networks create the modular organization of brain function which modern neuroscience has uncovered.

However, much of the cortex is not constrained by assigned functions and is available for other mental processes such as memory, cognition, creativity, planning, executive decision making among other psychological functions. John Locke famously visualized the brain at birth as a blank slate which is inscribed by the unique experiences of an organism as it pursues it way through life. Neuroscience has shown how this comes about. For example, long term memory is exported to cortical neural networks from the hippocampus with multiple neurons in a given network supporting a specific memory and with the overlapping neurons found in multiple networks of memory. Memories are not localized to single neurons and the overlapping of use of neurons in multiple networks allows for linked memory and for recall. Interestingly, a major function of the hippocampus is to navigate the organism through space perhaps explaining why memories are best retrieved through spatial and temporal associations.

As mentioned neural networks have both short range and long range axonal connections. Each neuron receives on average input from 1000 axons whereas each neuron generates output via a single axon. The neuron functions as a binary or all or none computing unit. Each neuron's output is triggered by the summed weighted average of multiple inputs before generating an output much like a computer chip. Thus computation is the basic function of a neuron.

Neurons have either excitatory or inhibitory synaptic activity. About 80% of neurons are excitatory and 20% are inhibitory. Excitatory and inhibitory neuronal activity is determined by the neurotransmitter secreted at the synapse with the amino acid glutamate being excitatory and glycine or gamma amino butyric acid being inhibitory. Many other neurotransmitter modify the excitatory or inhibitory response at the synapse and such neurotransmitters include dopamine, serotonin, norepinephrine and epinephrine. Other transmitters serve specialized functions in the nervous system such as acetylcholine for attention, endorphins for pain relief and oxytocin for pair bonding. The precise amount of excitatory, inhibitory and modulatory influences at the synapse determine the ways that information flows through a network.

Layered on top of the network architecture and types of neurotransmitters, the structure of the neuronal synapse can be molecularly modified by lived experience to facilitate transmission and thereby underpin learning and memory. Thus multiple steps are built into the neural network to regulate the flow of electrochemical information.

The size of a network that encodes a given memory is estimated to be between dozens to thousands of neurons in number. As applied to memories, the neural networks are called engrams. The specific architectural arrangement of specific neurons encodes specific memories and thus a given electrochemical neural arrangement encodes a specific feature of the external world.

Neuronal networks are evolution's way of encoding facts about the external world. If these facts are useful they are reinforced through recall and shape the behaviour of organisms over the life course. It is amazing to realize that the external world is encoded in the brain through the architecture of specific neural networks. What a feat of evolutionary ingenuity!

Given the centrality of neurons to nervous system function, animals in different ecological niches have markedly different numbers of neurons. For instance jellyfish have around 10,000 neurons, ants around 250,000 neurons, fish around 10 million neurons, octopus around 500 million and humans an astounding 86 billion neurons. Neurons are unevenly distributed in the human brain with about 15 billion in the cortex, 70 billion surprisingly in the cerebellum and 1 billion elsewhere in the nervous system. Human's closest evolutionary relative, the chimpanzee has about 6 to 7 billion neurons in the cortex less than half the number observed in humans.

Neuronal networks are the functional units of brain. Because of the influence of excitatory and inhibitory neural transmitters, these networks are always electrically active generating brain waves or oscillations over a wide range of frequencies from 1 to 4 hertz as delta waves, 4 to 8 hertz as theta waves, 8 to 12 hertz as alpha waves, 13 to 30 hertz as beta waves and 30 to 150 hertz as gamma waves. As a metaphor brain waves continuously sweep across the brain like the murmuration of a flock of starlings whose coordinated motion serves to avoid predation by an avian predator. Thus brain waves are the product of evolutionary forces that enable brain function that results in behaviour that is evolutionarily beneficial.

Brain oscillations are involved in the final transfer of information through neural networks prior to brain output as part of specific functions. They provide temporal windows that determine which neurons can communicate, when and with whom. Brain waves in general are an emergent property resulting from the oscillatory activity of excitatory and inhibitory neurons. They are evolutionarily conserved and homologous rhythms are seen across vertebrates and even invertebrates. Brain waves affect neural network transmission dynamics by regulating the receptivity of the post synaptic membrane to stimulation by an incoming electrochemical impulse. Post synaptic membranes are resistant to further depolarization for highly variable periods of time. Thus the continuous oscillatory spread of brain waves allows for new neuronal assemblages to form on top of memory engrams in order to guide the flow of information through neural networks. For instance alpha waves support wakefulness, gamma waves occur during active cognition and linked theta-gamma waves are part of hippocampal memory activity. Interestingly pacemaker cells also determine the oscillatory rhythms in the hippocampal neuronal system which appears to determine the temporal organization of cell assemblies. Certain central pattern generators also exist in the hindbrain to generate rhythmic breathing, walking and swimming.

Electroencephalograms (EEG) record brain waves predominantly from the cerebral cortex although oscillatory waves occur throughout the brain. In medicine the absence of cortical brain wave activity represents brain death and is clinically used in deciding when to withdraw life support systems that artificially maintain life. Thus cerebral cortex brain wave activity is essential to consciousness and consciousness related brain functions such as speech, cognition and voluntary action among others. These activities give meaning to life and without these activities, society has concluded that the value of life has been lost.

The constant and dynamic brain wave activity is extraordinarily energy demanding. Despite consisting of only 2% of body weight, brains consume 20% of energy needs of an organism. Much of the energy requirement of the brain is related to recharging membrane potentials and opening and closing voltage gated ion transport channels. Such a large energy demand relative to that among multicellular organisms without brains is a measure of the evolutionary selective value of nervous systems to animals. Since most selected traits that evolution favourably acts on are around the 1% benefit level, the 20% advantage as inferred from excess energy demands of brains means that the selective advantage of nervous systems is extraordinarily large. The only other trait in biology which is known to have a larger selective advantage is sexual reproduction where the two fold cost of reproduction is offset by protection against epidemic infectious disease which results from the increased genetic diversity that sexual reproduction provides. Thus the evolution of the nervous system like sexual reproduction ranks among the greatest of evolution's inventions.

Currently neuroscience sees the selective advantage of the nervous system as a prediction mechanism that coordinates an organism's behaviour to favourably align with positive evolutionary outcomes like finding food, avoiding predation and mating. To many the notion that the brain's function is primarily a system for prediction and not an organ of perception comes as a surprise.

Neuroscience demonstrates that within the skull there is no sound, light or colour, only active neural networks that are creating electrochemical models of the world which are updated based on sensory feedback. Hence sensations are collected in response to action and are used to refine subsequent neural network electrochemical models to enable action. Evolution's mechanism of natural selection is a harsh task master and only those networks structures that enable increased alignment with the external world allow their hosts to survive and propagate. Through eons of times the capacity for generating abstract electrochemical network maps of the external world that become ever closer to coding for reality are selected for. In this way the brain's mechanism for mapping reality increasingly approaches truth. However the rate of progress in this capacity is based on evolutionary timescales measured in millennia.

This view of nervous system function is called "the inside out model" of neural activity by Gyorgy Buzsaki, a Hungarian American neuroscientist. In this model, muscular action is first generated by the nervous system and then secondarily assessed by the sensory system. This view is the exact opposite of most philosophers and some scientists who posit that the mind is a primarily a perception mechanism in which sits an observer within the Cartesian theatre making decisions after due consideration. Neuroscience shows how far we have come from what now seems like a naive egocentric model of what the brain and mind actually do.

To humanists and scientists alike, most of the interesting activity of the nervous system occurs in the cerebral cortex. Among those activities are cognitive problem solving, creativity and consciousness. Neuroscience has increasingly defined the basis of these cortical activities. For instance cognition involves electrochemical mobilization of models and memories of the world from the back half of the bilateral cortex to send to the frontal lobes to try out solutions in imaginary space to solve a problem. The selected behavioural solution is then sent over to the motor cortex for execution. The enacted behaviour is then assessed by the sensory system to determine the effectiveness of the action. If the action fails then a new plan based on analysis of the failure is then computed by the frontal brain and executed by the motor system. This manner of cognition is called the global workspace theory and is how many neuroscientists now propose that the brain decides on the type of behaviour that is beneficial to an organism. Failure to compute accurately under Darwinian logic can result in death and hence the stringent selection for electrochemical systems that do the computation most accurately.

Consciousness in this way is an added cognitive mechanism to ensure that the chosen plan is not subject to error or deception. After all deception is everywhere in the biological world. Hence in a metaphorical sense our own brains become self aware of the cognitive processes in order to select among competing models for the one that is most likely to map on to reality. Interestingly, consciousness has also given rise to the belief that there exists another entity in our minds which oversees our actions, a soul in the Cartesian theatre. Thanks to neuroscience we now have other ways of the thinking of consciousness, ways which are based on evolutionary and biological reasoning.

It is remarkable that consciousness is not needed for intelligent cognition. Much intelligent thinking is done subconsciously as observed with instinctive behaviour or even during sleep when solutions to difficult problems arise. The fact that intelligence can occur without consciousness is relevant to computer based artificial intelligence. The fact that consciousness improves the accuracy of brain based planning, suggests that it is widespread among animals, certainly among those animal groups with a cerebral cortex and maybe even more extensively in the animal kingdom.

Vertebrates belong to the animal Bilateria clade which means that the body plan is bilaterally symmetrical including the brain. The brain while bilaterally symmetrical does not mean that each half replicates what the other half does. We have already seen specialization of cerebral hemispheres in functions like speech and handedness. More widely in animals, neuroscientists have concluded that the left hemisphere is more specialized in detecting predators and the right in detecting food. In general this has been interpreted to mean that the left hemisphere is more specialized for detecting objects and the right for determining relationships. While this line of thought has neuroscientific support, it has been extended into more speculative thinking about lateralization of brain functions without a great deal of evidence.

In all animals, including humans the nervous system regulates the musculoskeletal system to execute behaviour. In humans other forms of nervous system output are exploited within the social context of culture. The rise of society and culture is based on the human ability to cooperate with both kin and strangers and this in turn has given rise to the unique cultural advantage that humans enjoy in our living world. Cooperation has been key to human's ecological success.

In effect, among humans models of thinking within the nervous system are externalized into a cultural milieu to take advantage of the social collective mind to construct ever more useful models of world. Richard Dawkins has called the ideas which circulate within the collective mind, memes. Ways of externalizing thinking include language, mathematics and artistic creation. Through cultural forces, models are reformulated and can be re-internalized as more accurate and increasingly truthful models of reality. The more aligned any given mental model is to external reality the more successful becomes any individually chosen behaviour.

The use of the collective mind has enabled society to generate increasingly useful understanding of the world. This understanding can be exploited by technology that becomes available to all members of society. Thus individuals can benefit with increased understanding of the world through technology but without themselves having to acquire that understanding. This cultural breakthrough is unique to humans.

Examples include the understanding of evolution through natural selection which led to the discovery of the gene and the technologies of molecular biology with the benefits in medicine such monoclonal antibodies, CAR T-cells and recombinant proteins. Or understanding of gravity that led to Newtonian mechanics and General Relativity which allowed sending rovers to the Mars and the development of global positioning sensing. Or the understanding of the structure of atoms which lead to quantum mechanics which created the entire electronic industry which built the computer on which I am typing.

Importantly cultural influences through the collective mind act on a much more rapid timescale (days, weeks, months or years) than does the evolutionary timescale (measured in millennia). The collective mind has acted as an unprecedented accelerant to the acquisition of human knowledge and understanding. These culturally mediated outputs amplified the adaptive impact of the nervous system far beyond its original biological constraints.

Philosophy and Neuroscience

We next consider how philosophy has guided our journey towards a comprehensive understanding of the nervous system and thus of human understanding. Until modern neuroscience, only philosophers kept alive questions on the remarkable features of human thought, behaviour and achievements. The transition of these questions to neuroscience was abrupt. After 2500 years of philosophical thinking about the mind, the era of neuroscience was ushered in with the foundational textbook, The Principles of Psychology by the great American philosopher and neuroscientist William James in 1890. His textbook ignited over a century of ongoing experimental approaches to understand the brain and mind.

With the neuroscience advancements that we have today it is possible to see the path from the philosophical founders of today's neuroscience which began during the age of Enlightenment. A unitary line of thinking links David Hume, Immanuel Kant, Ludwig Wittgenstein and Daniel Dennett. We now describe that unifying framework and its links with today's neuroscience.

At its deepest level, the link among these thinkers is their rejection of the immaterial account of Descartes and their search for a naturalized account of cognition. Each, grounds knowledge in human practices—whether sensory experience, conceptual synthesis, linguistic use, or cognitive evolution. Their philosophies trace a movement from the world of impressions (Hume), through the structuring capacities of reason (Kant), to the linguistic articulation of meaning (Wittgenstein), and finally to the computational and evolutionary models of mind (Dennett). Together, they form a coherent narrative of how philosophy becomes progressively more rigorous about the mechanisms by which understanding itself arises.

David Hume stands as the great empiricist skeptic, the philosopher who dismantled traditional metaphysics by reducing all knowledge to impressions and ideas derived from experience. For Hume, the mind is not a repository of immaterial concepts but a repository of perceptions and memories. Every idea is a faint copy of a preceding impression, and all reasoning, including causal and moral reasoning, ultimately rests on the habits of the human imagination.

Hume's framework was revolutionary in two respects. First, it denied that reason alone can discover necessary connections in nature. What we call cause and effect is merely the mind's projection of expectation after repeated conjunctions. Experimentation is required to discover new information about the world and to test old theories. Second, it treats the self not as an immaterial substance but as a "bundle of perceptions," an ever-changing flux of sensations and memories.

Thus, Hume grounded human understanding in psychological regularity rather than immaterial truth. Knowledge is a product of natural belief-formation, not divine illumination or pure logic. This move of understanding thought as a phenomenon within nature—set the stage for all later philosophy of mind. But it also left a problem: if all we have are impressions, how do we account for the universal features of human thought—mathematics, morality, and the spatial temporal structure of experience itself?

This problem became Kant's starting point. Immanuel Kant famously wrote that Hume "awoke me from my dogmatic slumber." Kant accepted Hume's insight that knowledge begins with experience, but not that it is caused only by experience. Instead, Kant proposed a new synthesis: while all knowledge begins with the senses, it is structured by the innate capacities of the brain, that is, necessary structures of human cognition. The mind, in Kant's framework, is not a passive mirror but an active organizer of phenomena. Concepts such as causality, substance, and necessity are imposed upon experience by the mind's own mechanisms of thought.

This was a profound transformation. Kant preserved Hume's naturalistic humility by restoring rational necessity to the human standpoint and by showing that the regularities we find in nature reflect in part, the mind's own constitution. In Kant's hands, philosophy becomes an investigation into the structure of representation: how sense data become experience, how judgments are possible, and how reason regulates itself through principles such as causality and morality.

This move from psychology (Hume) to epistemology (Kant) would later inspire Wittgenstein's move to linguistics—the next level of the same inquiry. Ludwig Wittgenstein carried Kant's mind project into the realm of language. He proposed that the world and language share a logical form: "The limits of my language mean the limits of my world." Where Kant had sought the innate forms of intuition and thought, Wittgenstein sought the logic of how language allows representation and investigation about the facts of the world. Wittgenstein relocates in syntax the logical grammar that allows the world to be described. Wittgenstein also realized that language is not a single logical system but a collection of language games, embedded in social activities of life. Meaning, he concluded derives from shared uses of words and language based on their practical uses. Wittgenstein proposed that language works to uncover reality because language has a logical structure that can encode the logical structure of the external world. The alignment between language and reality is honed by its public, social and contextual use.

The continuity of Wittgenstein with Hume and Kant is profound. Like Hume, Wittgenstein sees meaning as arising from human practice; like Kant, he sees those practices as governed by logical rules that make understanding possible. These rules are conventions sustained by a community of speakers.

Thus, the philosophical framework shifts once again—from the psychological (Hume) to the innate (Kant) to the linguistic (Wittgenstein). Each stage seeks the conditions of intelligibility at a different level, culminating in the insight that understanding is neither in the world alone nor in the mind alone, but in shared linguistic and social practices.

Daniel Dennett extends this lineage of analysis by grounding the same questions in neuroscience and evolutionary theory. Where Hume sought the psychological origins of thought, Kant its innate forms, and Wittgenstein its linguistic forms, Dennett seeks its computational and evolutionary mechanisms.

Dennett's philosophy of mind is a naturalized continuation of the same project: explaining how representation and understanding can arise within nature. Dennett argues that consciousness, intentionality, and meaning are emergent products of evolutionary processes—complex informational systems shaped by adaptive pressures.

Dennett's central innovation is the intentional stance: the idea that we can explain the behaviour of complex systems by attributing beliefs and desires to them. This stance predictively compresses information about their anticipated behaviour and is successful from an evolutionary point of view by uncovering the logical structure of the external social world. The intentional stance insight explains many features of human cognition including our ability to anthropomorphize.

Dennett's framework unites the naturalism of Hume, the structuralism of Kant, and the uses of language of Wittgenstein into a scientifically coherent philosophy of mind. Like Hume, he is skeptical of immaterialism about the self; like Kant, he sees cognition as structured by internal (evolutionary) mechanisms; and like Wittgenstein, he emphasizes the public, functional character of meaning and thought.

Dennett further proposed that real patterns emerge from complex biological systems which evolution identifies as points for natural selection to act upon. Brain waves are an example of an emergent property of complex neural networks that have both excitatory and inhibitory activity. Evolution has seized upon brain oscillations as a control mechanism for the flow of information through neural networks in order to regulate cell communication prior to brain output.

For Dennett, the mind is not a Cartesian theater but a distributed computational architecture, a set of interacting “drafts” or processes that collectively produce the illusion of a unified self. This “multiple drafts” model of consciousness is articulated as the global workplace theory of modern neuroscience. The structure of thought is no longer imposed by pure reason but by adaptive design—a biological analogue of the innate conditions that Kant described.

The philosophical lineage from Hume to Dennett charts the evolution of epistemology into neuroscience. Hume’s psychology anticipated the associative models of learning; Kant’s innate structures prefigured modern cognitive architectures especially the function of the hippocampus in defining space and time; Wittgenstein’s language games anticipated the social uses of language in the collective mind; and Dennett’s naturalism integrates all of these within a Darwinian explanatory framework. Their unity lies not in shared doctrines but in a shared methodological attitude: to make sense of human understanding from within the world, using the resources of human reason and observation. Their collective achievement is to show that mind and meaning are not alien to nature but are inherent in it.

Summing Up: What is the origin of human understanding?

We began this essay by asking how is it possible to gain understanding of reality. Part of the answer lies in Einstein’s profound insight that the universe is comprehensible. The long term existence of the universe (>14 billion years) means that there are mechanisms within the universe that maintain its existence. It is these mechanisms that all of science is seeking to discover and understand.

Understanding also means deciphering the informational content and mechanisms for the flow of information in the system. Logic is what defines information and lies behind the mechanisms of its flow. Given that a logical structure exists within the universe, it is not so extraordinary that biology has uncovered ways to tap into those logical structures for biological benefit.

Biology does this by finding ways of encoding useful facts about the world that ultimately inform models of the mechanisms in Nature, the so called Laws of Nature. The Laws are less about telling Nature what to do than describing how Nature operates. Useful facts here has multiple meanings, including proximately useful to survival of an individual animal to ultimately useful in explaining how a system operates.

So what are the ways of biologically encoding informational facts of world? As an analogy to what we see with the nervous system, consider the central logic of the gene. In this model

DNA makes RNA, RNA makes protein and protein makes the cell. Information flows from sequences in DNA to RNA to protein and ultimately to the evolution of the cell. It is to the great credit that the code was deciphered by molecular biologists in the 1960s. A run of three nucleotides in DNA and RNA defines which specific amino acid is incorporated into a protein sequence. Thus the hitherto confusing bases for heredity and the gene were resolved. When finally uncovered it seemed so simple!

In a metaphorically analogous situation the brain has evolved electrochemically active neural networks whose specific architecture is a trace of a useful fact about the world. If it is repeatedly used that pathway network architecture is reinforced to create a memory engram. Such engrams can be assembled to create models that determines the behaviour of an organism by the dynamic oscillatory behaviour of the neural network. To the extent that a model reflects reality and enhances an organism's ability to reproduce, that biological mechanism to create neuronal network architecture will be maintained and improved by evolutionary feedback. As such, better and better systems come into being. Such systems are incrementally able to better approach truth about reality.

Among humans a new process builds on top of that created by biological evolution. That process depends on the cooperative instincts of human and increases the effective of cooperation among human groups in a self re-enforcing manner. The process involves externalizing thinking by sharing language, mathematics and works of art. These externalities represent models of reality that could be used to guide the choice of human behaviour. Language in particular uses a coding function that links information in sound (in the case of speech) or vision (in the case of written words) with ideas that relate to useful facts about reality. Externalization uses logic based rules of language to communicate ideas. The ideas align with meaning after consensus arises from the public use of words or sounds. As ideas circulate in the collective mind as memes in human societies they are accepted, improved or discarded before they are re-internalized in an individual and used to shape their behaviour. A similar process guides the use of mathematics in uncovering facts about the external world in an even more rigorous way.

When externalized models are especially useful they can move from being beneficial to an individual to being useful to entire population through the creation of technology. Individuals who use technology no longer even need to understood the model logic behind it.

Thus are created the grand theories of science, great works of art and amazing forms of technology. These culturally mediated outputs of the brain amplify the adaptive impact of the nervous system far beyond its original biological constraints. Through understanding reality we increasingly come to enjoy the beneficence of life.