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The Deep History of Ourselves: The Four-Billion-Year Story of How We Got Conscious Brains

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ABSTRACT

The essence of who we are depends on our brains. They enable us to think, to feel joy and sorrow, communicate through speech, reflect on the moments of our lives, and to anticipate, plan for, and worry about our imagined futures. Although some of our abilities are comparatively new, key features of our behavior have deep roots that can be traced to the beginning of life. By following the story of behavior, step-by-step, over its roughly four-billion-year trajectory, we come to understand both how similar we are to all organisms that have ever lived, and how different we are from even our closest animal relatives. We care about our differences because they are ours. But differences do not make us superior; they simply make us different.

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Introduction

A couple of years ago, I came across a quote supposedly attributable to the American poet, Ralph Waldo Emerson: “as soon as there is life, there is danger.” I think the author was referring to the fact that the moment that human life begins in the womb, the baby is at risk, and remains in such a condition until the eventuality of death. But for me, it had a different meaning. What I took from the Emerson quote is that danger began when the first cell managed to survive long enough to divide and start the long history of continuous life on earth. Danger is only meaningful in the context of life. Non-living things passively change in response to the environment over time—water evaporates and rocks degenerate—but living things, organisms, must continuously keep themselves alive. When they no longer can, they become non-living matter and passively degenerate.

The Deep History of Ourselves: The Four Billion Years Story of How We Got Conscious Brains, was motivated by my long-standing interest in how organisms detect and respond to danger, but it was more about the more

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general topic of what organisms must do to survive, and how this changed, but also remained the same, over the long history of life.

Deep History (which is how I will refer to the book here) consists of a Prologue and Epilogue, and sixty-six short (1500-2000 word) chapters divided into fifteen parts. My thinking was that this snippet format would allow readers to absorb one basic idea per chapter, rather than try to wade through single, long chapters with many ideas and no obvious break points. I was not an expert on evolutionary history, and this format made it easier for me to write the book, and I also think for non-expert readers to consume it. Admittedly, I ended with more chapters than I expected, and certainly more than my publisher wanted, but that's how it had to be to complete the story. After all, I did cover four-billion years (actually more, since the story really starts with the Big Bang, which occurred 13 billion or so years ago).

One way to think about *Deep History* is that I wrote the first third as a science journalist, summarizing facts about evolutionary history, much of which I learned doing research for the book. By contrast, I wrote the remainder as a working scientist discussing topics I know about from decades of research. Some reviewers said I could have skipped the first part, but I disagree. Researching these chapters gave me insights into how we and our brains came to be, and ignoring this, given the story I wanted to tell, would have been like writing a biography of a person starting at age 60 or 70.

Prologue

I am a neuroscientist, not an evolutionary biologist. There are evolutionary neuroscientists, but I am not one. I've spent most of my career working on how the brain detects and responds to danger, working out neural circuits. In 2009, I spent some time at Cambridge on sabbatical and re-connected with Seth Grant, who I knew when he was a post-doc in Eric Kandel's lab in New York. Seth is a neurobiologist who researches the evolution of genes involved in synaptic plasticity to understand better the biological mechanisms of learning and memory. In his studies, he found parallels in plasticity-related genes between rodents and sea slugs, suggesting that they may each have inherited the ability to learn from a common ancestor that lived many hundreds of millions of years ago. But even more interesting, some of the same genes exist in single-cell protozoa. That's relevant, since animals and current-day protozoa share a common ancestor that lived over a billion years ago. Some of the learning-related genes in our nervous system may therefore come to us via microbial ancestors that didn't have a nervous system, but were able to learn about danger and avoid it. And since bacteria go back to the early days of life, and approach nutrients and avoid danger, behavior may be as old as life itself. If so, behavior is not fundamentally a psychological process, but is simply part of an organism's biological

survival kit. From there I climbed back up the tree of life, examining how behavior changed as different organisms evolved, and how at some point mind and consciousness entered the picture. The bottom line is that the roots of behavior are deep, but consciousness has a shallower history.

The Biology of Life

An important theme in the book is how Darwin's idea of a life as a branching tree was preceded by ladder metaphors in which organisms are linearly stacked on top of one another. Key to the evolutionary tree metaphor is the idea of common ancestry. We have monkeys and apes in our past, but not present-day monkeys and apes. Instead, we share a common ancestor with present day apes, and they share a common ancestor with present day monkeys, and so on, all the way back to the earliest cell billions of years ago. That's the amazing thing. Modern science, especially genetics, shows that Darwin's basic idea was correct. All of life can be traced to a common ancestor, a cell living billions of years ago.

So how did that early cell that gave rise to the rest of life come to exist? I got really sucked into the fascinating views called "beginning of life theories." There are many such ideas, including the primordial pond struck by lightning, sugars from space, chemical evolution resulting in replicating molecules, black smokestacks in the oceans, and hydrothermal vents that catalyzed life in rock pores where replicating molecules were trapped. My research pointed to the latter and I visited one of its major proponents, Nick Lane, at University College London. His theory is complex, and I did my best to describe it. The bottom line is that the replicating molecules trapped in rock pores generated a membrane that encased their innards. Once that happened, they were able to survive outside of the pores. One kind of these managed to survive long enough to divide, and this kind is said to be the last universal common ancestor of all of life (LUCA).

LUCA marks the beginning of life at about 3.7 billion years ago. Its descendants included the first bacteria, progeny of which we live with today. There are many more bacteria on Earth than humans, and many more bacteria in your body than there are human cells.

One of the many kinds of bacteria to diverge from the original one was archaeobacteria, now known as archaea. They were sufficiently different that they and bacteria are now classified as separate Kingdoms of life. The DNA of these so-called prokaryotic cells is free floating in the cell body.

The next Kingdom, Protista, arrived about two billion years ago. These came about after a bacterial cell ended up inside an archaeal cell, and they figured out how to coexist – this is called the theory of endosymbiosis. Through division of labor, the archaeal cell's DNA came to be surrounded by a membrane, creating a cell nucleus, and the bacterial cell became the

energy machine (mitochondria). Such cells are referred to as eukaryotes. They are famous for having invented sexual reproduction, which contrasts with the cell division reproductive method of prokaryotes. Eukaryotes were also the first predators.

In a single cell microbe, obviously, all the cell functions have to be taken care of by the individual cell. But sometimes microbes of a particular type adhere together to form colonies that function like a multicellular organism. Through division of labor, some cells take care of reproduction, others locomotion, and others feeding. This is achieved by chemical interactions that regulate gene expression. Specifically, by turning off all functions but one in each cell, different cells become specialists rather than generalists. Unlike in a multicell organism though, if the cell defects from the colony, all of its functions return. By contrast, in a true multicellular organism, cells come with a good deal of genetic specialization. For example, a human reproductive cell can't suddenly become a sensory or muscle cell. Because the cells of a multicellular organism are interdependent, they cannot live on their own.

Colonies are not organisms. They are collections of cells with different genomes. Multicellular organisms are entities that have a single genome, and in which all of the cells work together to keep the entity, the organism, alive.

In a typical colony, the cells are not necessarily siblings and thus do not have a common genome. But there is a kind of eukaryotic colony in which all the cells have the same parent and genome. These are called clonal colonies. Plants, fungi and animals, the three multicellular Kingdoms of life, resulted from separate kinds of clonal colonies. Animals, for example, evolved from a colony consisting of a kind of protozoa. The present-day protozoan called choanoflagellates shares a protozoan ancestor with all of animal life. Because the cells of multicell organisms are all eukaryotic, multicell organisms are also eukaryotic organisms.

The Arrival and Expansion of Animals

Animals are defined by how they differ from the other multicellular organisms. One way is in terms of energy metabolism. Animals get their energy from consuming and digesting carbon-containing compounds and breaking it down to make glucose as part of their metabolic process. Fungi digest food externally and then absorb it to get fuel from glucose. Plants get energy from the sun and use it to make glucose.

Another difference is that animals are “animated” (motile). Plants and fungi are mostly stationary, making only slow movements that are best seen with slow-motion video. In an animal, stimulus information reaches one part of the body to cause a part of the body far away from the point of stimulation to react in a fraction of a second. This is because in all of life, animals, and only animals, have nervous systems.

Like most things in evolution, nervous systems did not suddenly appear. They arose by small changes over time, where existing capacities were co-opted to make new capacities. For example, the core signaling mechanism of neurons, the action potential, arose in microbes as a way to facilitate the repair of damaged parts of the cell wall – electrical sparks at the site of the injury attracted healing chemicals.

The first animals, sponges, appeared about 700 or 800 millions of years or so ago. Present day ones don't have a nervous system (early ones may have) and as adults they are sessile. But in their larval phase they are, like their protozoan ancestors, quite motile. In general, the evolutionary history of an organism is better reflected early than in later stages. From the beginning, the body unfolds under the influence of natural selection on DNA, but each step is more and more influenced by the way genes are expressed as a result of individual factors, especially interactions with the environment.

A major group that evolved from sponges was Cnidaria, which includes jellyfish. They have what is called a radial body (top and bottom, but no front-back or left-right axis), and possess a nervous system consisting of a diffuse net of interconnected neurons. From them bilateral animals, which possessed a front-back, left-right, and top-bottom axes, evolved. An early kind of bilateral animal was the flatworm. Most animals alive today have bilaterally symmetric bodies, and are descendants of flatworms that lived about 630 million years ago. In contrast to Cnidaria, the flatworm had brain that provided centralized control over the nervous system.

The two main bilateral groups that evolved from the flatworm ancestor are invertebrates such as mollusks, crabs, bugs, spiders, and so on, and vertebrates, which include fish, amphibians, reptiles and mammals. This is a highly simplified version of the vertebrate history as there was a transition invertebrate group called chordates from which vertebrates evolved. Both invertebrates and vertebrates went through explosive evolution during the Cambrian period, which started about 540 million years ago, spurred on by predator-prey competition and the development of associative learning capacities.

Vertebrates and Their Brains

Jawless fish, lamprey, are the oldest living example of early vertebrates. They arrived more than 500 million years ago with skeletons made of cartilage. Cartilaginous fish with jaws, such as skates, rays and sharks, came next, followed by fish with the kinds of boney skeletons most vertebrates today possess.

Life was aquatic until about 465 million years ago when plants colonized the land. Their respiratory output generated an increase in atmospheric oxygen, which allowed some invertebrates to transition to the land and feed on vegetation. Some 350 million years ago, vertebrates invaded the land in the form of amphibians that could live aquatically or terrestrially. Their

land-dwelling descendants, amniotes, spawned reptiles about 300 million years ago and mammals about 210 million years ago.

The first mammals were tiny nocturnal creatures. They were preyed upon by large, vicious dinosaurs. When dinosaurs became extinct about 65 million years ago due to climatic changes, the low energy needs of smaller mammals allowed them to flourish. Mammals then invaded all areas of the earth and all habitats. Primates evolved from early mammals 70 million years ago, apes from them 25 million years ago, and humans from apes about 8 million years ago.

Despite this diversity of vertebrates, there is a profound similarity in their brains. All vertebrate brain consists of three major zones: hindbrain, mid-brain and forebrain. Of particular interest is the forebrain, which changed the most over the course of vertebrate evolution. However, the implications of this were misunderstood throughout much of the twentieth century,

The problem began in the early 20th century when the German anatomist Ludwig Edinger proposed a ladder metaphor to understand brain evolution, arguing that the human forebrain reflects a *mélange* of ancestral vertebrate brains stacked on top of one another – a reptilian brain, an early mammalian (non-primate) brain, and a new mammalian (primate) brain. Edinger's line of thought was adopted by leading anatomists in the early 20th century and reached a crescent of popularity the 1950s through Paul Maclean's famous "limbic system" and "triune brain" theories. The over-arching conclusion was that "man" reflects the apex or pinnacle of brain evolution – that we are the pride and joy of mother nature.

I have long been critical of the limbic system/triune brain theory. One key issue, amongst many, is that modern research has shown that lower vertebrates (fish and amphibians) possess primitive equivalents (precursors) of the brain areas that MacLean said were unique inventions of lower mammals (limbic areas) and of primates (neocortex). In fact, fish, amphibians, and reptiles have all of the major brain regions that mammals possess, just in more primitive forms. Yet, the intuitive appeal of MacLean's ideas allowed the limbic system and triune brain theories to survive both as a scientific construct and cultural memes.

One consequence of the popularity of the limbic system theory was that the inaccurate portrayal of brain evolution made its way into what is called basic emotions theory, a modern day version of Darwin's 1872 paper on emotions in man and animals, which argued that we humans inherited emotional states of mind and related body expressions from our mammalian ancestors, by way of having inherited features of their nervous system. It has been said that Darwin was a great biologist but not so good a psychologist. His ideas about emotions were meant to help his theory of body evolution, which was not doing so well, as it challenged cherished religious beliefs of Victorian England's Protestant populace. He therefore

began to focus on the behavioral and mental implications of natural selection. He did this by applying common sense (folk psychological) assumptions about the mind to explain the evolution of emotions. For example, since we feel fear when we flee from danger, an animal fleeing from danger must feel fear as well. Why else would they flee? He noted humans could see jealousy, scorn, pride and contempt in dogs and other mammals. Elizabeth Knoll says he justified this approach by saying it was “a more cheerful view” than assuming humans have animal- qualities, and the public was more likely to accept it. The numerous examples of anthropomorphic analogies in his book, according to Knoll, were indeed a factor that helped Victorian England come to accept Darwin’s theory of evolution. But by conflating causation with correlation, he set animal psychology on a track that was so anthropomorphic that it led early 20th century behaviorists to ban mental states from psychology for many decades. MacLean, being a brain scientist, was not subject to behaviorist dictums, and placed Darwinian emotions in the limbic system. Later basic emotions researchers, such as Jaak Panksepp, sustained the out-dated Edinger/Maclean view of brain evolution by promoting the idea that different emotional feelings are the products of limbic systems circuits.

Primitive behaviors such as withdrawal and approach are universal, life-sustaining capacities of all organisms, from bacteria to people. As a result, such behaviors may simply exist as part of the homeostatic survival toolkit of cells. All organisms have to manage energy resources, regulate intracellular fluids, defend against harm, and reproduce, but the way any one organism does these things depends on the kind of body its species evolved. That is, survival requirements depend on the kind of body the organism has. For example, different mammalian species flee from danger by running, flying, or swimming, depending on the kind of locomotory capacities that evolved with their bodies. In other words, behaviors are bauplan-dependent (species-specific) survival implementations of universal (species-general) survival requirements. And survival circuits are the species-specific neural implementation by which the behavioral implementation of the universal requirement is achieved in each animal.

All vertebrates have an amygdala. A key, but certainly not the only, role of this brain area, and especially its component circuits, is to detect and respond to dangers they encounter in the course of everyday life.

While we often hear that the amygdala is the brain’s fear center, I think this is incorrect. The defensive survival functions of the amygdala that we inherited from our vertebrate ancestors is, I believe, the present-day manifestation of a survival imperative that has existed since the beginning of life. Yes, we are often afraid when in danger, but that does not mean fear bubbling up out of the amygdala causes the experience. This long history strongly implies that defensive behavior evolved to keep early cells alive at

least long enough to replicate, and pass their defensive and other survival functions on to their progeny. While we humans, and perhaps our mammalian ancestors, and maybe some animals, have some kind of subjective experiences of fear when in danger, the implication is the primordial function of defense was not to make the organism feel fear, but to give it a behavioral tool for dealing with danger. The same can be said of the pleasure or satisfaction we have when we engage in energy management (eating), fluid/electrolyte balance (drinking), and reproduction (sex). I will discuss how subjective emotional experiences come about later in relation to consciousness.

The Rise of Cognition

Behaviorists, of course, rejected cognition, whether in humans, monkeys, rats or pigeons, because it was internal and thus unobservable. But an early behaviorist, Edward Tolman promoted the idea that lower mammals are purposive or goal directed – that they used cognitive maps to navigate when foraging for food or escaping from harm. Hard-core behaviorists clung to the idea that learned associations accounted for such actions. The so-called cognitive revolution in the mid 20th century freed human researchers from behaviorist dogma, and even made Tolman a hero, but animal behaviorists, at least initially, clung to non-cognitive, associative explanations. Eventually, rodent researchers, using reinforcer devaluation paradigms, showed that Tolman was correct. That even lowly rats are not simply stimulus-response habit machines but instead are also creatures that chose actions based on the value of expected outcomes. This does not mean that non-mammals lack cognition, but the evidence, at least at this point in time, suggests that they do not seem to have cognition in the way it is usually defined in mammals – in terms of internal representations and mental models.

A major development in human cognitive psychology was Alan Baddeley's transformation of short-term memory into working memory. That is, a cognitive workspace with executive control over behavior. This gave psychology an anchoring point for cognition. Working memory has ever since been viewed as ground zero for cognitive models. Even goal-directed behavior in rats came to be thought of as being dependent on their more limited version of working memory.

The classic view was that working memory was a product of the lateral prefrontal cortex (PFC). It receives and integrates inputs from sensory and memory cortex and holds the information in temporary storage while deciding how to respond to it. A more recent view is that working memory involves a collation between PFC, sensory and memory areas that collectively hold information temporarily while the executive memory, which includes PFC and parietal networks make decisions.

While all mammals have some working memory capacity, the cognitive abilities of primates outstrip those of lower mammals, and those of humans outstrip those of other primates, including apes. This parallels the expansion of the PFC that took place in primates. Lower (i.e., non-primate) mammals mainly have medial, agranular PFC areas, while primates added granular areas located mostly on the lateral surface of PFC. And in humans the lateral granular areas expanded. There is, in fact, a lateral granular region in humans that other primates lack. It is a region of the frontal pole, the anterior most part of the brain. The reason that this structural feature (granulation) is important is that working memory and hierarchical relational reasoning crucially depend on granular PFC.

While areas are important, they do nothing on their own. Function comes from connectivity. An important feature of the granular PFC in primates is its wide range of inputs from posterior cortical areas that process sensory and memory information. This allows the granular PFC to integrate diverse kinds of information in the formation of complex abstract conceptions. In humans, this connectivity of granular PFC is even more robust. Additionally, all these connections also converge in the frontal pole, which is reciprocally connected with lateral PFC, giving the frontal pole unparalleled capacity for conceptualization and reasoning.

Consciousness

I first became interested in consciousness through work I did in the mid 1970s with my PhD advisor, Michael Gazzaniga. From our studies of human patients, we concluded that conscious experiences are the result of cognitive interpretation situations in an effort to help maintain a sense of mental unity in the face of the neural diversity of non-conscious behavioral control systems in our brain. In so doing, we drew heavily from attribution and appraisal models in social psychology at the time, in particular Leon Festinger's theory of cognitive dissonance, Stanley Schachter and Jerome Singer's attribution theory of emotion, and Richard Nisbett and Timothy Wilson's work on "telling more than we can know".

Contemporary discussions of consciousness often treat it as a single kind of thing. But it is not. It is important to distinguish, at the very least, "creature consciousness" and "mental state consciousness." Creature consciousness refers to the condition of being awake and behaviorally responsive to environmental stimuli and applies to the vast majority of animals. Mental state consciousness, on the other hand, is the condition of having experience with actual content about the world and/or oneself.

Theories of mental state consciousness come in two broad forms. One, called first-order theory, assumes that the sensory systems that process external events are all that is needed to have mental state experiences

about those events. Higher-order theories, on the other hand, argue that local sensory processing is not sufficient – that the information needs to be further processed – to be re-represented. I am a proponent of high-order theory and focused on it in *Deep History*.

In the brain, the hypothetical higher-order network involves regions of granular PFC, including dorsal and ventral lateral PFC, and the lateral and medial frontal pole. For example, the conscious experience of an apple, in this theory, reflects lateral PFC re-representation (in a sense conceptualization) of lower-order visual cortex states.

Theories of consciousness, including most higher-order theories, seldom consider the role of memory in consciousness. But without semantic memory, and especially memory-based schema, the sensory representation of an apple is not meaningful (is not conceptualized) as an instance of the fruit of that name. Conceptualization occurs in perception independently of whether the perception becomes conscious. \. But David Rosenthal's higher-order thought gives conceptualization a key role since thoughts are conceptual in nature.

My multistate hierarchical representation model, which is a variant of Rosenthal's theory, makes memory and conceptualization an essential underpinning of higher-order consciousness. This model is based on the connectivity of sensory and memory circuits with PFC. One set of connections is with granular PFC areas, such as the dorsal and ventral lateral PFC. Another set of connections is with agranular medial PFC areas (orbital, ventral medial, medial, anterior cingulate and insula cortex). By way of various intra-PFC connections, granular and agranular PFC areas interact and, in my scheme, constitute a higher-order consciousness network that is crucially conceptual in nature.

So far, I have discussed mental state consciousness as if it were a single thing. But I believe that a partition suggested by Endel Tulving can greatly facilitate progress. Tulving distinguished between three forms of mental state consciousness in humans. These are auto-noetic (explicit self-awareness of one's existence over time), noetic (explicit awareness of facts and concepts about the world or one's self), and anoetic (implicit awareness of the world). The first two are based on episodic and semantic explicit memory and the third is based on implicit procedural learning. The fact that these are each based on a kind of memory that has been extensively studied offers important neural anchors for pursuing kinds of consciousness in the brain.

In *Deep History*, I mainly emphasized auto-noetic and noetic. But in more recent writings, as discussed later, I have come to understand the crucial role of anoetic consciousness.

Emotional Consciousness

If the amygdala defensive survival circuit is not the way the conscious feeling of fear comes about, what is? My view is that it comes about much

like any other conscious mental state, as a higher-order interpretation of lower-order information.

It is sometimes said that emotions such as fear are universal. But I argue that it is danger, not fear, that is universal. I define fear as a personal, schema-based, narrative-driven, culturally shaped, subjective experience that occurs in a biologically or psychologically significant situation. Schemas are collections of memories about specific kinds of situations that underlie our thoughts, feelings, and actions in life.

The key idea is that conscious experience, whether emotional or not, is always preceded by non-conscious (pre-conscious) cognitive processing of sensations and memories, including schema, that results in a mental model of the situation. In an emotional situation, such as fear, brain and body consequences of threat-elicited survival circuit activation become part of the model. The brain becomes aroused in a general way that supports energy mobilization but also in specific ways tailored to the situation.

In *Deep History*, I argued that human emotions could not exist in the form we experience them without our early human ancestors having evolved language, hierarchical relational reasoning, noetic consciousness, and reflective auto-noetic consciousness. Our emotions thereby became the mental center of gravity of the human brain, fodder for narratives and folktales, and the basis of culture, religion, art, literature and relations with others and our world – of all that matters in life as we know it.

The picture of emotion and consciousness I painted was extremely human centered. Human auto-noetic consciousness depends on un-paralleled cognitive processes that are entwined with language and culture, and is enabled by circuits with unique properties. The evolutionary past of auto-noetic consciousness, in particular, is quite shallow. Yet it did not arise in a void. Fundamental cognitive underpinnings of auto-noetic consciousness, such as episodic-like memory and working memory, were present in our primate ancestors. But what seems to be missing is the ability of even our closest ape relatives to be robustly self-aware and to engage in mental time travel. But even if methodical impediments to measuring these could be overcome, their version of auto-noetic consciousness would likely pale in complexity to what humans experience. The most obvious difference would be how language allows us to parse our subjective experiences, but I suspect even without language, human cognition would make human consciousness different.

Like all other species, we are special because we are different. Our differences are important to us because they are ours. They give us capacities that other animals don't have. But other animals have capacities we lack. As I discuss, our differences do not make us superior or better adapted. They just make us different. Our differences are mere footnotes in a four-billion-year-old saga. Only by knowing the whole story can we truly understand who we are, and how we came to be that way.

Epilogue: Surviving Ourselves

Autonoetic consciousness is the basis of the conceptions that underlie our greatest achievements as a species – art, music, architecture, literature, science – and our ability to appreciate them. But consciousness, especially autooiesis, has a dark side – it is the enabler of selfishness and greed, mental features that could be our undoing. The Earth has persisted despite geophysical disasters and mass extinctions, and will likely continue to persist as a planet in the solar system. But if we don't make corrections soon, it may not persist in a way that will support the current configuration of organisms living on Earth, including, and especially, us.

Autonoetic consciousness is about one's self. It is, by definition, personal, and thus selfish, and sometimes narcissistic. And, it may well be our evolutionary Achilles' Heel. We persist as individuals only if we persist as a species. We don't have time for biological evolution to come to the rescue – it's too slow. We have to depend on the more rapid avenues of change – cognitive and cultural evolution, which, in turn, depend on our autooetic brains. Whether we perish or persist is in our hands, and thus in our autooetic minds.

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