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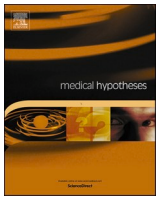

Auto-domestication hypothesis and the rise in mental disorders in modern humans

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ABSTRACT

Domestication is a process of protecting a particular set of individuals from some influences of their natural environment and managing their reproduction to suit particular needs of a domesticator. Biological characteristics of modern humans are a result of the process of auto-domestication that is continuing. Thus, they include disadvantages occurring in domesticated species: poor ability to cope with the external environment, reduced central nervous system plagued by mental abnormalities, gastrointestinal and metabolic deficiencies including reduced dentition, and musculoskeletal limitations. Since the process of autodomestication is continuing, these disadvantages will increase in future generations. At this stage of our bio-cultural evolution, we are being confronted by a pandemic of mental disorders which we are ill-equipped to address. This paper briefly discusses reasons why modern humans are more susceptible to mental disorders due to auto-domestication.

Introduction: Auto-domestication hypothesis in human evolution

There are two possible scenarios to account for the demonstrated change from robust to gracile hominin morphology in the Late Pleistocene. One is that of speciation and replacement, in which a new, more gracile mutation appeared in some part of the world that was unable to breed with other humans and then began replacing all robust people of the world. This replacement or 'African Eve' model, initially proposed by Protsch [1,2], and Bräuer [3], is the only alternative to the multiregional model, of which many variations are possible [4,5,6]. The proposal by geneticists that modern humans comprise genes from at least three robust subspecies (one of which remains unidentified) refutes the 'African Eve hoax' [7,8] because it implies that all known humans of the Late Pleistocene and even somewhat earlier are variants of one species [9]. That includes the diminutive human remains from Liang Bua in Flores [10]. However, the Eve advocates, who have entirely dominated the discussion since the 1980 s, continue to reject multiregionalism [11]—which proposes that recent hominins evolved as an interconnected network in various continents [12,6]—and have recently chosen to limit the term 'humans' to what they define as 'anatomically modern humans'. This illustrates the considerable disparities in this field: we believe *Homo* includes all hominins of at least the last 2 million years.

The replacement model has been derived initially from the false dating results Protsch and colleagues reported from many human fossils [13] and numerous subsequent misapplications of data, as well as from the common modern experience of Europeans spreading to other continents ruthlessly replacing their inhabitants. Its most debilitating feature is that it seeks to define human modernity, yet it explains virtually none of the many factors accounting for it. For instance, the model does not explain the sudden reversal of hominin encephalization around 40 ka (40,000 years) ago and the ensuing rapid atrophy of the brain [14,15] related to the generalized gracilization of the entire body [16]. It fails to consider the process of equally swift neotenization in humans and ignores the accumulation of literally thousands of detrimental disorders during the same period. Nor does it account for the rise in neurodegenerative or mental diseases of which other primates are virtually free of or explain why they involve primarily those areas of the brain that are the phylogenetically most recent. The replacement model

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also does not explain any aspects of the unique modern human strategies in matters of reproduction. Most notably, it has no rationalization of human menopause, a counter-reproductive-success phenomenon found in only two other mammals. It cannot account for the loss of estrus in human females or the preservation of exclusive homosexuality. Similarly, it cannot explain why males of all contemporary societies express a pronounced preference for neotenous females, one of so many features unique to modern humans. Nor would it even attempt to account for why we are the only species of which the males select females, based explicitly on cultural variables such as attractiveness. Another variable separating *Homo sapiens sapiens* from all other species on the planet is our dependency on exograms (memory traces external to the brain) to the degree that their skilled use has become a crucial selection criterion. The replacement model also fails to explain why a reduction not only in brain volume but also in muscle bulk and physical strength, bone robusticity, prognathism or dentition size should have been an evolutionary advantage during the Pleistocene. However, all the listed characteristics are comprehensively accounted for by the second potential explanation of modern human origins, the auto-domestication theory [17,18,19].

Most of the robust to gracile human changes were biologically detrimental to the species, whereas the replacement advocates perceive them as teleological, ignoring that evolution is a fundamentally dysteleological process. This is already an indicator that the transformation from robust to gracile humans was not an evolutionary process in the sense of Darwinian evolution. That the revolution took place in a geological instant is precisely why the replacement backers were convinced that only a speciation event could explain it. However, they overlooked another genetic process that can prompt far more drastic changes to a species in much shorter times. The domestication syndrome [20,21,22] can transform members of a species dramatically, including their skeletal morphology, within a millennium or two—50 to 100 generations—[23]. In vertebrates, the domestication syndrome includes gracilization in craniofacial morphology, reductions in tooth size, depigmentation, more frequent and non-seasonal estrus cycles or their elimination, alterations in adrenocorticotropic hormone levels, changed concentrations of several neurotransmitters, prolongation in juvenile behavior and several other neotenous effects, increased docility and tameness, and reductions in both total brain size and of specific brain regions [24]. It never occurred to those advocating hominin replacement that this list of variables coincides precisely with those we attribute to the development from robust to “modern” humans.

Hypothesis

Biological characteristics of modern humans are a result of the process of auto-domestication that is continuing. Thus, they include disadvantages occurring in domesticated species: poor ability to cope with the external environment, reduced central nervous system plagued by mental abnormalities, gastrointestinal and metabolic deficiencies including reduced dentition, and musculoskeletal limitations. Since the process of autodomestication is continuing, these disadvantages will increase in future generations.

Auto-domestication: morphological/physiological changes and maladaptions

Domestication is a process of protecting a particular set of individuals from some influences of their natural environment and managing their reproduction to suit particular needs of a domesticator. In the modern world humans play the role of a domesticator most often, though there are known instances of domestication of animals, plants and fungi by vertebrates or invertebrates [25,26,27]. Thus, domestication is a natural biological phenomenon. Auto-domestication is a process where members of a species act in a way that manages contact of other members with the natural environment and guides their reproductive activities. For as long as the genus *Homo* exists, if not even a bit earlier, humans managed resources in their environment [28] and, as far as the vast ethnographic literature shows, they directed reproductive activities of society’s members by restricting or enhancing coital opportunities and frequencies of related or unrelated individuals and regulating rejection or acceptance of newly conceived individuals into communities (cf. marital customs, rules of abortion, infanticide or acceptance of neonates such as baptism). Management of resources, present among *Homo* from early on, became especially enhanced with the advent of food production (agriculture/animal husbandry) and exacerbated by the industrial revolution. In human evolution a primary role is played by the set of autocatalytic feedbacks between human biological characters, the environment, technology and social organization [29]. As food procurement and later production required new technologies, changed the environment and influenced social organization, it was inevitable that changes have occurred in human biological characteristics. Organized food acquisition allowed for increased size of local communities. This increase led to the appearance of social structure with diversified roles of individuals, providing greater protection against external dangers and regulating interindividual relations, including reproductive ones. Thus, basic conditions of domestication developed: protection of individuals against the external environment and management of reproductive performance. With hierarchical social structure, it was mainly the “elite” acting as domesticators of the people, albeit individuals of equal status also influenced each other’s well-being and regulated reproductive activities. Changed conditions of human biological existence resulted in morphological and physiological changes. The most general of them were: gracilization, i.e. loss of body robusticity, thus reduced muscle mass and bone strength, tooth size decrease (approximately ~ 15% in Europe between Upper Paleolithic and modern times [30], and loss of brain size (~10%, see below) while in terms of physiology changes were related to altered food availability, especially replacement of animal protein with carbohydrates, use of milk and dairy and changes in fat consumption. (Fig. 1).

Due to the increase of body size (height and weight) in the last century it is less known that when 18th–19th centuries measurements are considered, in the last 35 ka body height declined by ~10 cm (6%) and body mass by 20 kg (25%) [31]. (Fig. 2).

Domestication effects of both environment protection and reproductive management result from pleiotropy. It occurs when selection for a particular gene or set of traits that are beneficial for the actor of domestication, influences seemingly unrelated phenotypic traits [34]. For instance, selection for docility might prompt changes in craniomorphology and many other somatic or behavioral modifications. The uniformity of these effects among mammals is remarkable, and some of them, such as brain size reduction, apply even to fish [35] and birds. That effect is particularly confounding in humans because it occurred during a time the demand on cognitive and intellectual resources is assumed to have risen exponentially. From 4.5 Ma until the Holocene brain size increased at a rate of +0.32 Darwins while in the Holocene it decreased at the rate of −10.80 Darwins (about 33 times faster; [30]. Bearing in mind that the human brain atrophy of the last forty millennia occurred at a rate dozens of times greater than the previous phase of millions of years of apparently continuous encephalization, and the great emphasis in paleoanthropology on brain volume increase, it is astonishing that this factor was disregarded—except by very few [14,15,36,37].

It is even more astounding that so many years after the auto-domestication theory was first presented, it remains entirely ignored by the replacement advocates. This is despite its confirmation in recent years by the accumulating genetic evidence validating the domestication of humans [18,19,38,39,40,41,42,43]. Not only does the theory explain all the differences between robust hominins and their gracile descendants, but it also offers the only possible explanation for many of them. For instance, the Keller and Miller paradox [44], emphasized in the present paper, permits no alternative explanation. Keller and Miller

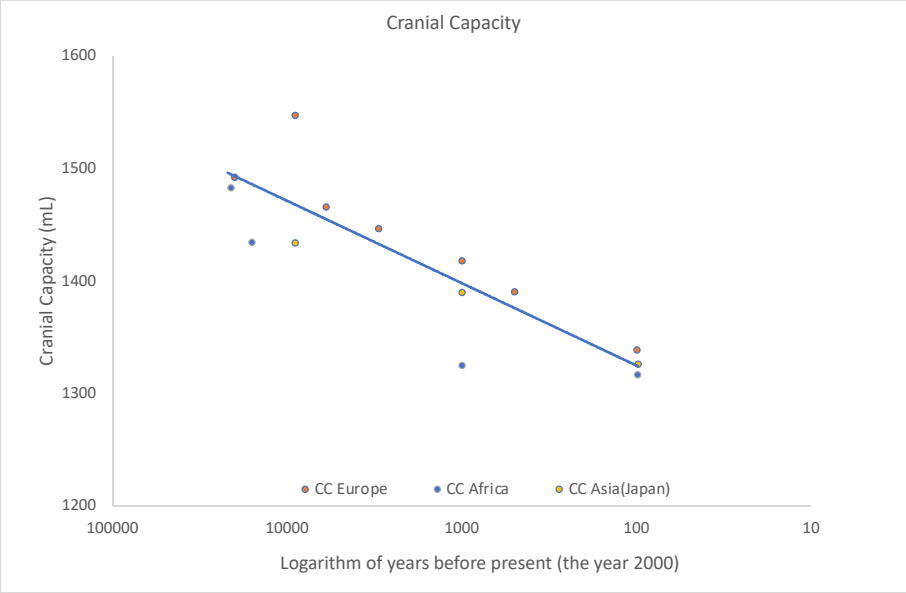

Fig. 1. Changes in human cranial capacity from Upper Pleistocene to 1900. Time scale is logarithmic. Data averaged for both sexes from [14,15].

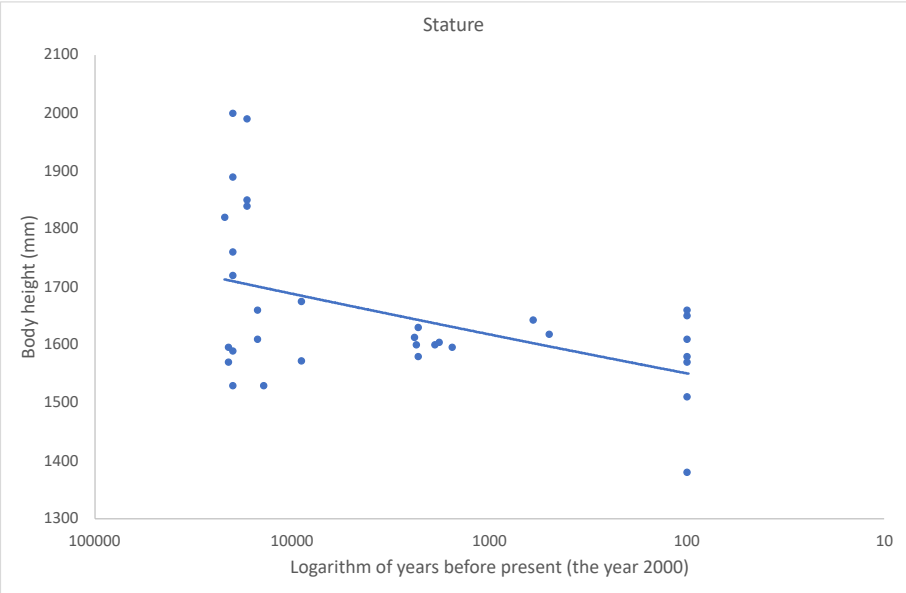

Fig. 2. Changes in human body height from the Upper Palaeolithic to 1900. Time scale is logarithmic. Data averaged for both sexes from [31] and supplemented by [32,33].

prompted an intensive debate of why natural selection, which is so effective in optimizing complex adaptations, seems unable to eliminate genes that predispose humans to common, harmful, and heritable mental disorders. Indeed, they considered such disorders as the very embodiment of maladaptive traits and reviewed three potential explanations for the paradox: (1) ancestral neutrality (susceptibility alleles were not harmful among ancestors); (2) balancing selection (susceptibility alleles sometimes increased fitness); and (3) polygenic mutation-selection balance (mental disorders reflect the inevitable mutational load on the thousands of genes underlying human behavior). After extensive debate, they concluded that there are no compelling explanations of why human brains seem to malfunction so often today and why these malfunctions are both heritable and disastrous to survival and reproduction. However, the paradox of why natural selection failed to select against the thousands of deleterious or disadvantageous genetic mutations that define present-day humans is easily resolved by the auto-domestication theory. It is the inevitable outcome of the domestication syndrome, as are all characteristics of human modernity.

Consequences of altered omega-3 intake in modern humans and increasing mental disorders

The human genome evolved during the Paleolithic period (2.5 Ma–12 ka ago) in which ancestral hominins were exposed to various evolutionary environments. While the Paleolithic period represents over 120,000 generations of *Homo*, only 466 generations of *Homo* have existed during the Holocene period (12 ka–present) [45]. In percentage, this represents 99.5% and 0.5%, respectively [46]. Consequently, it was mainly during the Paleolithic period in which natural selection informed modern human characteristics.

Skeletal and archeological findings reveal that ancestral humans were omnivorous, and had varied diets depending on the geography, climate and food availability [47]. So, what did ancestral human diets consist of? Whatever that was edible; plants (terrestrial and aquatic grasses, nuts, berries, tubers, leaves); animals (reptiles, mammals, avians, mollusks, fish, insects), eggs and honey. The important point is that ancestral diets were characterized by a high omega-3 fatty acid intake. Lipids in the form of omega-3 fatty acids α-linoleic acid (ALA) and docosahexaenoic acid (DHA) constitute ~ 20% of total brain weight [48]. Additionally, in the adult brain, DHA makes up 30% of the lipid section of grey matter [49].

It has been speculated that the ratio of omega-3 (α-linoleic acid) and omega-6 (linoleic acid) was ~1:1[50]. This is in stark contrast to many modern diets where there is a disproportionate omega-3/omega-6 ratio of 20:1 [51]. Due to their neuro-trophic and neuro-protective benefits, omega-3 fatty acids would have been positively selected since they improved cognitive functioning. The bottom line is that from the Paleolithic period the human brain required a regular source of omega-3 fatty acids in order to maintain optimal cognitive performance [52].

The Agricultural Revolution (11 ka ago) accelerated auto-domestication via significantly changing hunter/gatherer diet and lifestyle that had informed the human genome [46]. According to skeletal samples data of Neolithic people, the gradual shift to cultivated plants and domesticated animal foods had marked health deficits in many Neolithic societies [53]. These included loss of height and musculoskeletal mass, increasing dental caries, malnutrition, infections, arthritis, and reduced longevity [54,55,56].

The combination of a nutritionally monotonous diet which favored omega-6 fatty acids, loss of robusticity, less physically active lifestyle and overall decline in health status of Neolithic populations would have also promoted the onset of mental disorders which were rarely seen in Paleolithic ancestors [19]. For example, omega-3 fatty acids are important in the production of Brain Derived Neurotrophic Factor (BDNF) which regulates neuronal plasticity, growth, neurotransmitter modulation, neurogenesis, that are vital for memory, learning and mental well-being [57]. Clinical studies have shown that low levels of BDNF are strongly correlated with major depressive disorder in humans [58]. Also, reduced BDNF in the pre-frontal cortex is associated with psychiatric disorders [59]. Thus, omega-3 fatty acids are involved in a series of complex neuro-hormonal feedback mechanisms that enhance physical performance which in turn fosters BDNF production with subsequent neuro-behavioral regulation. The radical alterations to high omega-3 Paleolithic diet, as well as, at least periodically, lowered physical activity levels (PAL) beginning in the Agricultural Revolution would have fostered the condition for various psychiatric markers which were evident by the time of the Bronze Age (5 ka ago).

However, the 19th century facilitated a precipitous move towards refined sugars, inflammatory omega-6 oils, and processed carbohydrates, as well as a marked decline in omega-3 fatty acid consumption. This has led to numerous chronic health outcomes [46,47,48]. This development may have resulted in a significant increase in mental disorders which we are currently witnessing [48].

In the last twenty years there have been numerous studies on the role of omega-3 fatty acids and their association with mental disorders including depressive disorder, schizophrenia, bi-polar disorder, attention disorder hyperactive disorder, and autism. While the findings of several studies have been inconsistent due to confounding variables and lack of knowledge regarding the time when omega-3 supplementation is most effective, epidemiological studies and other reports have revealed an association between fish intake and risk/prevalence of depression, unipolar and bi-polar disorder, as well as fish oil benefits for individuals with mood disorders and schizophrenia [48,60,61]. Moreover, it has been shown that first episode patients with psychosis have noticeable deficits in omega-3 concentration in red blood cells; second, some authors claim that omega-3 therapy for males with schizophrenia may reduce the severity of their symptoms, further confirming the association between omega-3 fatty acids and mental disorders [62,63].

Another link between auto-domestication, omega-3 consumption and mental disorders in extant humans is in relation to preterm births. There is an increasing prevalence of preterm births in many countries. From 2000 to 2004 preterm births increased from 9.8% to 10.6% [64]. Swanson et al. [65] have endorsed the inclusion of omega-3 to pregnant mothers in reducing preterm births. These authors reason that omega-3 may reduce inflammation of the uterus which may trigger pre-term labor. Considerable amounts of DHA are absorbed in fetal tissue during the third trimester [66]. Much of this DHA infiltration is concentrated in the fetal brain and retina [67]. Possibly, for this reason preterm birth compromises the amount of omega-3 fatty acid uptake in fetal brain development. Modern mothers with reduced omega-3 fatty acid dietary intake have a higher risk for preterm babies who may be more vulnerable for developing autistic spectrum disorder and ADHD [68,69]. Evidence supports that the development of these mental disorders is further increased where preterm birth is combined with low birth weight [65]. It seems that when women are given eicosapentaenoic acid (EPA) and DHA supplementation, they generally maintain optimal length of pregnancy, thus, reducing the risk of psychiatric morbidities associated with preterm birth [65,70].

Given the discordance between current and evolutionary omega-3/omega-6 dietary ratio, there is a strong argument that the continuing auto-domestication of humans with its high consumption of omega-6 industrial processed foods and concomitant reduction in omega-3 foods is contributing to the global prevalence of mental disorders.

Implications of the auto-domestication hypothesis

The implications of the auto-domestication hypothesis are that the significant maladaptive genetic changes the process began introducing between 30 and 40 ka ago are in all probability irreversible. This is suggested by the apparent irreversibility of the corresponding changes in other species affected by the domestication syndrome. In addition, these detrimental alleles have been augmented by the effects of further modifications in more recent times, such as significant dietary changes throughout the Holocene. Therefore, humans would require high levels of care both for their physical and mental well-being. Living conditions should be modified to limit disadvantageous results of domestication but this is highly unlikely to occur at an adequate level to arrest the ongoing process.

The change in human diet from the Neolithic onwards caused micro-evolutionary changes in human populations. Many papers have focused on dietary changes and the anatomical and physiological costs for straying from our Paleolithic diets. This has been an intriguing area. According to Zuk [71] humans have during the Holocene Period developed adaptations to changes in diet and lifestyle such as high altitude adaptation, lactose persistence and gene mutations to reduce malarial morbidity (e.g. sickle cell anemia, thalassemia). While these adaptations have been positively selected, we are challenged to find examples of positive selection of brain/mind during the same period. On the contrary, many studies have argued that increasing domestication in humans, especially our departure from our omega-3 rich ancestral diets has had a deleterious impact on our mental wellbeing. Our hypothesis highlights that due to complex neuro-hormonal processes the brain is considerably vulnerable to environmental/cultural changes, especially where they outpace biological evolution.

At this stage of our bio-cultural evolution, we are being confronted by a pandemic of mental disorders which we are ill-equipped to address. To what degree will ‘genetic load’ inform mental disorders for future humanity? Due to relaxation of natural selection in *Homo*, will medical interventions be able to ‘rescue our minds’? The auto-domestication hypothesis offers a way for interrogating these questions and others. Our willingness to address our current psycho-social dilemma will be instrumental in shaping our future mental trajectories.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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