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Mammalian brain development and our grandmothering life history

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ABSTRACT

Among mammals, including humans, adult brain size and the relative size of brain components depend precisely on the duration of a highly regular process of neural development. Much wider variation is seen in rates of body growth and the state of neural maturation at life history events like birth and weaning. Large brains result from slow maturation, which in humans is accompanied by weaning early with respect to both neural maturation and longevity. The grandmother hypothesis proposes this distinctive combination of life history features evolved as ancestral populations began to depend on foods that just weaned juveniles couldn't handle. Here we trace possible reciprocal connections between brain development and life history, highlighting the resulting extended neural plasticity in a wider cognitive ecology of allomaternal care that distinguishes human ontogeny with consequences for other peculiarities of our lineage.

1. Introduction

Evolutionary anthropologists, developmental psychologists and neurobiologists all have something to say about human development and evolution, but differ profoundly in what they hope to explain. Academic fields exist in part for the pragmatic reason that no scientist can routinely consider the advanced details of all realms of knowledge. Idiosyncratic x- and y-axes generate each field's data representations, their customary "independent" versus "dependent" variables profoundly influencing the questions they focus on and each field's views of how causal arrows point. Periodic attempts at alignment and integration are therefore essential. Here we propose to align evolutionary anthropology, psychology and neurobiology on the general subject of human development and demographic life history. In particular, we will describe the regularities in brain development across placental mammals including humans. We will connect those regularities to life history associations between duration of development and longevity, privileging the hypothesis that human post-menopausal longevity evolved as a consequence of allomaternal subsidies from ancestral grandmothers. Subsidies allowed mothers to wean infants still very dependent and so widened the cast of interacting characters at an early point in their neural development. Each field has produced its insights and narratives on this central subject in relative independence. As co-authors from different fields, we are not always in agreement, except on the importance of integrating these different lines of evidence about human development and evolution.

1.1. *Anthropology versus psychology*

Two contemporary misalignments, observed informally, will illustrate the divergence independent lines of explanation have produced. If an evolutionary anthropologist asks a group of psychologists how early development might differ between humans and non-human primates, the psychologists will typically center on the importance of the mother-infant bond for social and cognitive adjustment. If they are asked then to guess how early or late humans are weaned compared to other great apes, they will map "importance" onto duration, and hazard that human infants are dependent longer and so must require greater maternal effort, spend a longer time with their mothers and therefore nurse longer. Yet, evolutionary anthropologists comparing humans to our closest living relatives, the great apes have recognized for more that two decades that humans wean earlier, and space births more closely than they do [134].

For a converse example, if cognitive scientists ask anthropologists how large human brains have evolved, anthropologists will most often invoke selection on the size or properties of individual cortical areas, which highlights the critical role of selection over evolutionary time on particular behavioral competencies. Understanding improvement in a particular behavioral competency as selection on the size of a particular brain region can trace its lineage to Jerison's idea of "proper mass" (1973) [74] coupled with the earliest examples of lesion-symptom mapping in neurology.

Therefore, for example, increase in the size of "Broca's area" and immediately associated tracts in the cerebral cortex might be used as an

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index of selection on language competency [10,122]. The distributed, overlapping and network-based views of neural mechanisms arising in current neurology, cognitive and computational neuroscience, however, are increasingly at odds with this modular view [5,114,135].

1.2. Evolution of life histories, developmental neurobiology and evo-devo

The general accumulation and systematization of knowledge about the progress of life from conception, birth, development, sexual maturity and death across vertebrates will be found across multiple academic departments, principally different aspects of biology. As we will be discussing features of human life history in the context of primates, and great apes, and more generally mammals, we will be considering general control of growth and behavioral development, as well as specific events like birth, weaning, duration of childhood, sexual maturity, menopause and death, as they are typically studied in anthropology departments. This research concerns itself with description of basic commonality and diversity in strategies; interaction of life histories with particular ecologies; and costs, benefits, and contests in resource allocation. Theorizing in this area typically involves discovering the ecological and social determinates of developmental trajectories, where energetics have long been of special interest for human evolution (e.g., [1,69,70,93,94]) and are increasingly described more precisely [89,115,116]. But the mechanisms of development, except as realized, for example, in the energetic requirements of producing a brain of a certain size over a certain time, are not considered.

Developmental neurobiology, for the most of its history, did not focus on the evolution and the production of diversity among organisms. The generation and placement of neurons, wiring them up, placing them in environments and specifying initial parameters typically take place in a generic fruit fly-mouse-rhesus nervous system.

In the last twenty years, this gap in integration has been bridged by the joint study of evolution and development, “evo-devo”. Many insights have been generated, but the central one we address here is what Kirschner and Gerhart [84] have called the “third pillar of Darwinism.”

“Darwin's all-encompassing theory of evolution was based on three major supports: a theory of natural selection, a theory of heredity, and a theory of the generation of variation in the organism”.

The first two pillars have been extensively studied, ever since Darwin. The last pillar, examination of and theorizing about the variation offered to selection by the organism, became structurally significant to our understanding when rapid cataloguing of the genome across organisms became possible. The first rudimentary steps in decoding the mechanistic path from genome to phenotype produced major surprises. The variation offered for selection by the genomes of existing creatures was anything but random. Random, point-by-point mutations of single DNA base-pairs, first guessed to be the main cause of variation, from “genetic drift” to “hopeful monsters” did occur, but their effects are typically made negligible by recurring replication of local sequences, large segments, and even entirety of the genome. Some fundamental components, notably the Hox and similar regulatory genes, which specify the major axes and components of the body and brain plans, have been conserved across invertebrates and vertebrates [110].

Moreover, evolution progressively filtered developmental mechanisms toward suites of control mechanisms that produced functional outcomes in the face of normal variation, either variation produced by the developing animal itself, or the environmental variation the animal will encounter. For example, in producing a limb, linking the generation of bone and muscle mass, vascularization and neural innervation to each other by molecular recognition and trophic interactions rather than separately generating and linking them post hoc is more efficient and less prone to end-stage failure [83]; in producing an eye, the length of the eye and the power of the lens and cornea are matched only roughly by genetics, but are brought to focus as the retina's activity (a measure of focus) slows eye growth as external light activates photoreceptors [143]. A single species may encounter resource-rich, stable environments or resource-poor unpredictable ones in its phylogenetic history, and come to be equipped with environment-appropriate multicomponent “game plans” executed after environmental quality is ascertained. This phenomenon has been much studied, but particularly as epigenetic responses to stress is another example [72].

“Evolvability” is the concept spanning these particular types of genomic variability and environmental interaction. The best way to describe the extreme conservation of basic body plan and organ structure, developmental programs coordinating functional systems, and prediction of environmental variability is under hot debate, as expected for a young research area [83]. Stable information may be distributed across genome and environment. It is not only the province of genes.

The overall goal of this article is to first, align basic facts about brains and life histories across the views of anthropology, psychology and neurobiology. Second, to the extent possible, we will try to integrate the views of anthropological examinations of life history and evo-devo approaches with each other. A review that spans G-proteins to grandmothers will present a different combination of challenge and boredom to each reader, but we will attempt to underline the relevance of the various necessary bodies of data to the eventual integration as we go.

Specifically, the features of human evolution we will consider in the frames of our disciplines are the following. First, human brains are very large, both absolutely and relatively compared to all mammals [74]. For primates overall, the best account of the evolutionary progression of brain size and body size is that body size was first reduced, producing relatively large brain sizes, and subsequently, in some radiations, larger brains evolved, placing those brains in the range of largest mammalian brains in both relative and absolute size [133]. Bodies are small for both age at maturity and longevity compared to non-primate mammals [20]. Since *relatively* larger brain size can arise from selection for smaller body size [133], widely used measures of brain size relative to body size, like encephalization indices, that incorporate both effects can obscure the separate roles of each. Our own hominid radiation, which includes great apes and humans, has the largest brains and bodies, longest offspring dependence, slowest maturations, and greatest longevities among all the primates [134]. Maturation is even slower in humans than other hominids, where it occurs in an intensely social context that varies across cultures [67]. Human females have unique and superficially contradictory life history features compared to other hominids: relatively earlier weaning with higher fertility, combined with longer duration of development and notably greater longevity even though latest last births occur at about the same age in women as in other great apes [59,134].

We will begin from developmental neurobiology, and present evidence about what mechanisms generate large brains, and what components these brains consist of. We will be interested in the interrelationships of the rate of brain growth, final brain mass, somatic growth, apparent maturational state both in morphology and behavior, and overall longevity. We will discuss what features like “extended maturation” or “critical” or “sensitive” periods might correspond to structurally for complex abilities like language, or elaborated cognitive control. In the context of a changed social niche produced by changes in life history, we will highlight new evidence about comparative differences in brains other than size that could enable evolving humans to be maximally attentive to and able to learn from their changed social niche [28,45,141].

We aim to link this information from developmental neuroscience with theoretical and empirical work in demographic life history evolution. Life history theoreticians use stable population theory, which relies on the Euler-Lotka equation to explain the necessary interdependence of age- specific fertility and mortality rates throughout the lifespan [16,136]. Since the size of each cohort of newborns in age-structured populations depends on the number of females in the fertile ages and their rates of offspring production, and those females come