Thank Your Intelligent Mother for Your Big Brain

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Inventors, artists, and scientists are the usual suspects for symbolizing and celebrating the brainy human primate. But what if babies, mothers and other caregivers were the real stars in the story of human intelligence? That is one implication of a new study in PNAS from Piantadosi and Kidd (1).

Among primates, greater adult brain size and behavioral complexity are correlated with heightened offspring dependency, which are all exaggerated in humans. Scientists have long emphasized the significance of the co-evolution of those traits in humans (2,3,4), and now Piantadosi and Kidd have provided new insight regarding how that co-evolution occurred.

First, they modeled their assumptions of hominin evolution: those with larger heads grow faster after birth than those with smaller heads; those with larger heads have a greater drop-off in survival as gestation lengthens; those with larger heads have a higher probability of survival throughout development because of greater parental intelligence.

Then Piantadosi and Kidd built those assumptions into an evolutionary fitness landscape in which a child's probability of survival to reproductive age was highest in two regions: one where pregnancy is long and neonatal heads are small and another where pregnancy is short and neonatal heads are large. The latter phenomenon fits with the hypothesis that larger-brained hominin species bore their infants earlier in development. So, based on the models, Piantadosi and Kidd provide a scenario for the evolution of human intelligence and infant dependency. They are inevitable adaptations to one another. This type of "runaway" selection would have occurred if natural selection for big, intelligent adult brains meant that hominin babies were born with relatively small brains and, because this diminished brain size rendered them more dependent, they benefited from the care of intelligent, big-brained hominin parents who had even smaller-brained babies. And so on. Starting as early as the genus *Australopithecus* and then gradually over the roughly 2.5 million years of the fossil record for the genus *Homo*, adult hominin brain size increased while artifacts indicate that behavioral complexity did too. These hallmarks of humanity could have been ratcheted up accordingly.

This spin on well-known patterns of variation and development among primates and fossil hominins raises questions specific to the study and beyond, new and old. For instance, what renders human babies helpless? Is it all just relative brain size? And, why must an increase in adult brain size require a decrease in neonatal brain size? Finally, is human parenthood more intelligent than that in other primates?

Today, neonatal humans have the largest absolute brain and overall body mass for primates and are born after a longer than expected gestation for a mother primate of our body size (5). So the notion that humans are born early is not supported by maternal investment. Most often, the claim that human babies are underdeveloped is based on their relative brain size. Because adult humans are so encephalized, human babies have the smallest relative brain size of all the primates. With only about 30% of brain growth achieved at the time of birth, humans experience more brain maturation while under the care of others than our closest relatives do. With a gestation length nearly as long as ours, chimpanzees have the next smallest relative newborn brain among primates at only about 40%, and they too are burdens on their intelligent caregivers. Capuchin monkeys, known to be quite brainy, are born with only 50% of their adult brain mass and are notably needy as infants as well, lagging in thermoregulation, for example. So regardless of whether it is fair to say that humans are born "early," the link that Piantadosi and Kidd make between relative brain size at birth and intensity of parenthood is a fair one. But is the neonatal brain the entire cause of human offspring neediness?

The loss of the grasping foot must have played a role in the evolution of hominin parental care because it would have limited an infant's ability to cling, especially to an upright standing, walking, and running mother. Nonhuman primate mothers count on their ability to remain hands-free while carrying their dependent infant(s) for months to years, and grasping infant feet are part of this equation. According to fossil footprints in Tanzania, grasping feet were gone from part of the hominin clade by 3.6 million years ago. This is the genus *Australopithecus*, which may have also birthed large infants (6). A big, heavy baby ups the parental ante, both as an organism to nourish with milk and as a load to carry, and that's even when it has clingy feet. So, following Piantadosi and Kidd's arguments, it may not be coincidence that adult hominin brain size took its first steps toward remarkability (suggesting that intelligence did too) around this time in the Pliocene epoch when hominin infants may have become more costly.

The evolution of hominin parental behavior was surely more complicated than the evolution of neonatal brain size alone. But we are still left wondering why offspring independence and brain size should decrease just because adult brain size increases.

The most prominent hypothesis for a limit on human neonatal brain size is the "obstetrical dilemma," whereby the birth canal constrains fetal growth because it is limited by anatomical adaptations for bipedal locomotion. Thus, it is often assumed that the male pelvis—which is narrower in the dimensions that make up the birth canal—is better adapted to bipedalism. Observations of the difficulty of human childbirth lead many to hypothesize that the bipedal pelvis was a unique selective pressure on fetal brain size while brains were expanding in hominin history. However, there is another, non-pelvic explanation for why neonatal brain size decreases when adult brain size does.

Unlike humans, our closest relatives chimpanzees do not give birth when the fetal cranium is approaching the limits of the birth canal. Yet, they have the next smallest relative brain size at birth among primates. So if the pelvis isn't limiting chimpanzee gestation and fetal growth it is possible that something else is, and it is possible that humans share it with our evolutionary kin. It is difficult to measure so it remains to be learned whether it works this way in chimpanzees or other primates, but humans give birth just before fetal energetic demands outstrip a mother's metabolic ceiling—the sustainable limit to her physiology (5). So although a mother increases her basal metabolic rate during her pregnancy, she reaches a point where she cannot continue to increase it further to accommodate any more fetal growth, especially metabolically expensive brain tissue. If metabolism is the fundamental constraint on pregnancy, then birth canal dimensions need only remain adequate for childbirth.

So, if brains are just too metabolically or energetically costly to increase in utero, then at a certain point encephalization would occur postnatally. And this is what we see: the larger the mother's brain, the smaller the fraction of hers that emerges from her womb. So, whether one applies the pelvic or the metabolic explanation for neonatal brain size or both, one is left wondering whether a runaway scenario focused on parenting is necessary, given the many existing hypotheses for hominin encephalization.

In support of the runaway hypothesis, Piantadosi and Kidd plot nonhuman primate intelligence and time-to-weaning, showing that the former predicts the latter, and as one increases so does the other. So, among nonhuman primates, caring for offspring appears to be a brainy activity. But, although time to weaning is a sound measure of infant dependency, *Homo sapiens* deviates from the pattern by weaning infants early not late for an ape of our body size—between 2.5-3 years, estimated from traditional societies. And that shorter time-to-weaning is marked by fast-paced infant growth and a high cost of lactation. But to really compare human dependence to that of nonhuman primates, we need to build in the time and cost of growing children after they are weaned—something that's comparatively absent in nonhuman primates. Both the human brand of offspring dependency and intelligence make direct comparisons with nonhuman primates difficult. Thus, much of what links the runaway scenario to the supporting evidence is the untested assumption that human parental intelligence is especially important. To explore further on this issue, we can continue our consideration of the costliness of human babies.

Whether the trend actually began, with *Australopithecus* or with early *Homo*, human offspring are exceptionally large. As discussed already, for a primate of our body size, humans are born after a long gestation, are remarkably fat, and are larger than expected in body and brain size. It is likely that pregnant mothers are able to endure this costly experience, at least partly, because humans have a higher basal metabolic rate and expend the more energy per day than other apes (about 400 kcal/day more than chimpanzees and bonobos; 7). This heightened metabolism may factor into both parties in the human lactation relationship too, given that the fastest brain growth rate occurs during the first three years of life (8) while babies are gaining calories, fat, and many other important factors from mother's milk prior to weaning. Such a high cost of a rapidly growing infant brain is likely contributing to our early weaning relative to other apes (9), despite additional resources available to and from human mothers. What is more, the high energy human condition, buffered by enhanced fat deposition, may support the physical costs of carrying absolutely big, heavy babies. It may also support the excessive costs of provisioning weaned children who are too immature in their musculoskeletal and cognitive development to forage for and process food entirely for themselves (10).

Childhood's slow period of post-weaning growth is argued to be a hallmark biocultural adaptation in humans because it eases a mother's burden and allows her to invest relatively sooner in her next costly infant, and because factors like kinship and marriage are significant factors in childcare (4). These and other benefits and complexities to a long period of juvenile dependency are missing from the runaway scenario, but they should not be ignored.

The accelerated human metabolism likely fuels the big parental brain (7) which is associated with significant diet-related behavioral shifts during hominin evolutionary history. Processing (or pre-digesting) foods with stone tools (11), increasing acquisition of fat- and protein-rich animals in the diet (12), and cooking (13) may have been the most beneficial to the lives of the youngest, most dependent, most vulnerable members of hominin societies, while being the most beneficial to their parents' and related caregivers' fitness. It is commonly assumed that these technological and ecological behavioral shifts arose in conjunction with enhanced cognitive ability. What's more, the highly social and emotional nature of human reproduction both between child and caregiver and also between caregivers—a situation often referred to as communal or cooperative breeding –would benefit from an energy-fueled brain, including its role in the development of language (14). It is too easy to emphasize a baby's deficient motor skills and, thus, to forget how intelligent and unlike other primates they are from the very earliest moments of life. Although they are relatively small, neonatal human brains are the absolute largest for primates, as previously stated. So, if brain size is linked to intelligence in adults, why not in babies? Through gaze, facial expressions, gestures, and more, human infants and young children manipulate parents and other caregivers into investing so carefully and intensely (2). Perhaps hominin babies have cleverly manipulated their intelligent caregivers into relaxing selection on many of the traits that would benefit survival if they were not born into such a handy and intelligent species. Runaway intelligence, indeed.

Given the large literature dedicated to the territory covered here, Piantadosi and Kidd's powerful scenario is probably too simple to depict the complex evolutionary processes that brought us big brains, intelligence, and costly babies. Regardless, their research underscores the importance of child-rearing in the evolution of humankind—an importance that is often overlooked. Likewise, the work that goes into raising children is woefully undervalued both socially and economically in the United States. It is unlikely that an evolutionary appreciation for childcare will lead to massive culture and societal change, but it may give rise by a slow and gradual process.

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