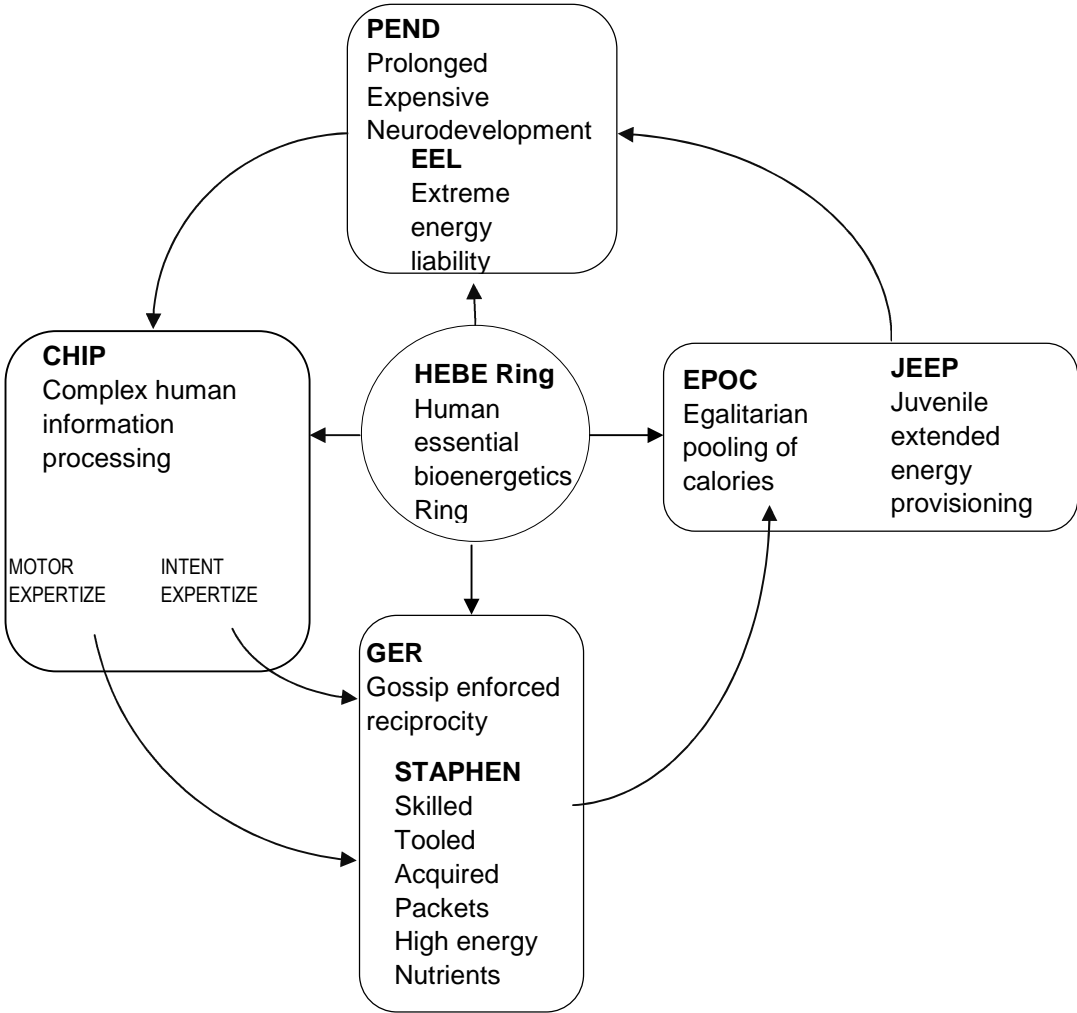Human neuromaturation, juvenile extreme energy liability, and adult cognition/ cooperation

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Human childhood and adolescence is the period in which adult cognitive competences (including those that create the unique cooperativeness of humans) are acquired. It is also a period when neural development puts a juvenile's survival at risk due to the high vulnerability of their brain to energy shortage. The brain of a 4 year-old human uses ≈50% of its total energy expenditure (TEE) (cf. adult ≈12%). This brain expensiveness is due to (1) the brain making up ≈6% of a 4 year-old body compared to 2% in an adult, and (2) increased energy metabolism that is ≈100% greater in the gray matter of a child than in an adult (a result of the extra costs of synaptic neuromaturation). The high absolute number of neurons in the human brain requires as part of learning a prolonged neurodevelopment. This refines inter- and intraarea neural networks so they become structured with economical "small world" connectivity attributes (such as hub organization and high cross-brain differentiation/integration). Once acquired, this connectivity enables highly complex adult cognitive capacities. Humans evolved as hunter-gatherers. Contemporary hunter-gatherers (and it is also likely Middle Paleolithic ones) pool high energy foods in an egalitarian manner that reliably supported mothers and juveniles with high energy intake. This type of sharing unique to humans protects against energy shortage happening to the immature brain. This cooperation that protects neuromaturation arises from adults having the capacity to communicate and evaluate social reputation, cognitive skills that exist as a result of extended neuromaturation. Human biology is therefore characterized by a presently overlooked bioenergetic-cognition loop (called here the "HEBE ring") by which extended neuromaturation creates the cooperative abilities in adults that support juveniles through the potentially vulnerable period of the neurodevelopment needed to become such adults.

HUMAN NEUROMATURATION, JUVENILE EXTREME ENERGY LIABILITY, AND ADULT COGNITION/ COOPERATION   **1**

1. INTRODUCTION

1.1. Human exceptionality and energy liability
　　　　The evolutionary origins of the human exceptionality in cooperation and cognition are unknown. The absolute large size of the adult human brain and its high relative size compared to the human body (high encephalization index) (Jerison, 1973), however, are usually considered critical to these aspects of human uniqueness (Sherwood et al., 2008). But the nature of the relationships between brain size uniqueness and human cooperative and cognitive abilities are poorly understood.
　　　　Another concern is the nature of the process by which the unique traits of the human brain and human cognition were selected during the Middle Paleolithic. One potentially relevant but presently unreviewed area for exploring these issues is the bioenergetic liability during neuromaturation that affects the human brain while acquiring adult cognitive capabilities. The complexity of cognitive faculties links not only brain size but also to the nature and period length of neuromaturation, while the energy utilization, duration and liability of this neuromaturation links, in turn, to brain size and neuron number—moreover, support of juveniles is known from anthropological research to link to human cognition particularly human social cooperativeness. Thus, the ingredients exist for an intergenerational bioenergetics loop between the extreme energy liability of juveniles and a concomitant parallel buffering energy provisioning given to them by adults enabled by such neuromaturation. This review argues for the key centrality of such a loop to the scientific study of humans. This is because the proposed intergenerational biological loop could have shaped the survival of Middle Paleolithic humans, and through its affects upon adaptive selection, the physiology, behavior and neurobiology of humans as a biological species.
　　　　This proposal is motivated by three shifts in how the novelty of the human brain is understood.
　　　　First, the human brain is now appreciated to combine large size/encephalization with a high neuron density that results in it having a particularly high neuron number (due to the peculiarly low neuron number-brain size scaling factor found in primates) (Herculano-Houzel, 2009; Herculano-Houzel et al., 2007). Thus, while the human brain is not the largest one in nature (those of elephants and certain whales are much larger), high neuron density results in it either being the animal brain with the most or near equal most neurons (Herculano-Houzel, 2009; Roth and Dicke, 2005). This causes the human brain to be neurocomputationally unique in that it contains not only the highest, or the near highest numbers of neurons but it does so within an unusually compact computational space: a rodent brain, for example, scaled with a human number of neurons would have a volume of 34 L not 1.5 L. A perfect 34 L sphere has a diameter distance of 40 cm not the 7 cm maximum separation distance of a 1.5 L one (taking 1 kg of brain ≈1 L). As a result of this compactness, the connections of the interarea networks across the brain are physically close together in terms of their processing links. This is neurocomputationally important since it reduces time delays between them allowing for the neurodevelopment of novel types of computational network organization and though this, the potential to acquire more complex forms of cognition. Neural speed is known to be important to human cognition, for example, greater intelligence is linked to quicker reaction and inspection times. A brain with the same number of neurons as that of a human but volume scaled with that of a rodent would not be capable of developing human cognition due to its greater separation of neurons and

concomitant greater time delays.

Second, volumetric MRI has shown that human neurodevelopment involves a complex and extended neuromaturation in which there is the refinement in its network connectivity of "small world" attributes such as interarea differentiation and integration around connectivity hubs (particularly involving the prefrontal cortex), and that these are linked to the acquisition of human specific cognitive capabilities including executive faculties.

Third, the size and neuromaturation expense of the juvenile human brain is now appreciated to impose an extreme energy liability upon human juveniles that would prevent their survival if it were not also that they live in the energy supportive circumstances created in human communities that protects juveniles against energy shortages. Humans are atypical as animals in that human juveniles (at least when members of hunter-gatherer bands) are raised in egalitarian cooperative breeding groups. While other animals such as meerkats, tamarins and marmosets also engage in cooperative breeding, humans do so with the unique trait of food pooling in an egalitarian manner. This creates a group equality in energy intake (known anthropologically as "nutritional homogeneity" (Sherry and Marlowe, 2007)). This food pooling has the effect of directing shared energy so it results in an increase in the energy support of all immature members in a group and their neurodevelopment. In contrast, in ranked cooperative breeding animals this food sharing predominately results in increasing the reproductive fertility of the dominant female. The atypical and unique aspect of human child and adolescent support raises the possibility that the evolution of juveniles with large brains is critically dependent upon juvenile's existing in the social cooperative circumstances that provide high quality energy support during their complex and prolonged neuromaturation.

These three shifts in how the novelty of the human brain is understood suggests that its bioenergetics arose in the context of a peculiar energy developmental problem and a peculiar energy provisioning solution. Not only is this problem and solution unique to humans as a species but they determine in many ways human, particularly juvenile, biology.

The human neurodevelopmental problem arises from the unique character of the human brains that forces an extreme endogenous energy liability upon juveniles. This liability exists because the large immature human brain occurs in a small body making it dominate factor upon juvenile energy needs. This is important to survival since the external situation of a young individual when they first become independent following the ending of lactation is usually one in which they face difficulty in acquiring energy. Several factors contributes to this situation. Endogenously, high encephalization makes the brain a large part of the body's total energy expenditure budget. Moreover, due to neuromaturation, their brains have greater energy needs than those of adults. Exogenously, this greater need for energy is exuberated by the situation that energy input is limited for immature individuals by such factors as inefficiency in their food forging. Thus, the human brain's combination of a large, highly encephalized and neuron dense brain is a potential disadvantage as it causes the immature juvenile brain to have a peculiarly extreme liability to energy shortage at a time when they are least able to obtain food themselves. Moreover, this high liability is one that needs to be extended for many years if the human brain is to be able to acquire its full information processing potential.

The provisioning solution is that large but compact neuron dense human brains

when adult have the cognitions that allow them to obtain high energy foods through hunter-gathering and to organize the social reciprocity by which such food, (particularly that which has been hunted, "packageable", and so easily distributed), can be pooled to meet the energy needs of juveniles. (Mothers are also be provided by such pooling with the energy needed to have the high energy cost pregnancy and lactation that supports fetuses and infants with such large brains.)

   This situation of problem and solution can be expressed in the form of an intergenerational loop here referred to as the **h**uman **e**ssential **bio**energetics (HEBE) ring (see fig. 1). The acronym makes references to the Greek goddess of youth, Hebe, an appropriate connotation since the bioenergetics so essential to humans concerns that which occur in juveniles (Hebe, is the Greek equivalent of the Roman goddess, Juventas). The ring visually communicates the situation by which the juvenile energy liability potentially entailed by the neuromaturation of the human brain does not in fact impair juvenile survival due to adult cooperative behavior created as a result of such neuromaturation. This feedback situation is proposed to be (i) a core aspect of human biology that was (ii) critical to human evolution as a selection event and (iii) biologically defines the nature of humans as an animal species.
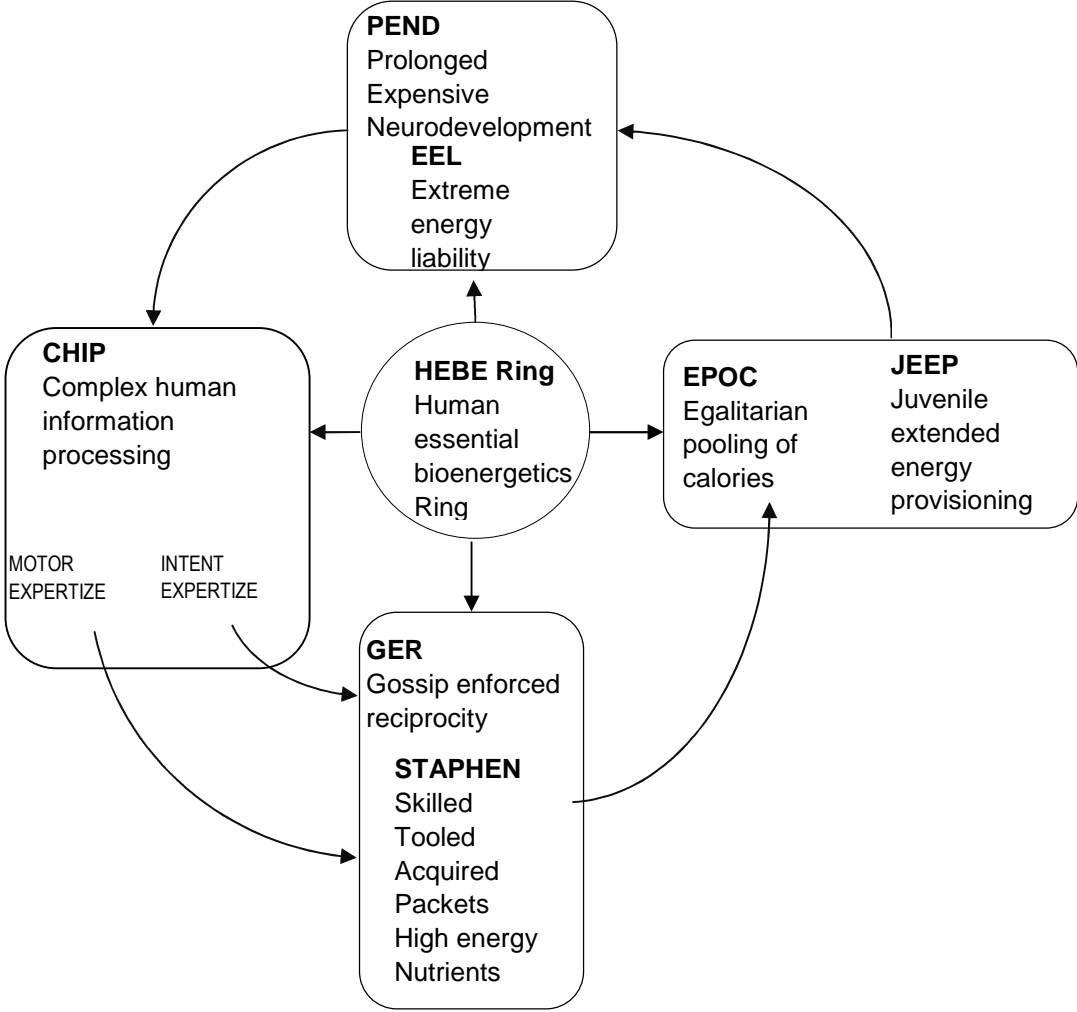

Fig. 1. The HEBE Ring showing the contingent relationships of its main components

1.2. Human essential bioenergetics ring

This paper reviews the human brain energy liability situation that gives rise to the HEBE ring and its separate components. This ring it is argued to have arisen in its present form with Middle Paleolithic hunter-gatherer humans and continues with some changes (such as type of social cooperation and food sources) to underlie in a modified manner the biology of contemporary people. It presents in a unified biology the fitting together of an intergenerational process constituted out of a previously overlooked set of human bioenergetic, neurodevelopmental, social cooperation and food energy related issues and phenomena.

The argument of this paper requires both review and interpretation of the various stages of the HEBE cycle. To aid discussion they are given acronymic related names. Humans have a prolonged energy expensive neurodevelopment (PEND) and this is directly responsible for creating adult complex human information processing (CHIP). The cognitive abilities it provides underlies the ability of hunter-gatherer humans for skilled tooled acquisition of packageable high energy nutrition (STAPHEN) which are then shared to juveniles in regard to gossip enforced reciprocity (GER). This sharing of packageable—i.e. large enough to be passed around—food is radically unlike that of other cooperative breeding animals since instead of supporting dominant females and their young, the group offers egalitarian support to the young of all females by means of the egalitarian pooling of calories (EPOC). This creates the situation of juvenile extended energy provisioning (JEEP), and this ensures that the extreme energy liability (EEL) of humans while creating the possibility of impairing human survival, rarely compromises juvenile survival.

The loop which these stages create is presented in terms in two types of theoretical discussion made in the context of each other. First, a theoretically fitting together of diverse facts acquired in different disciplines involved in the study of the traits that characterize humans. This paper reviews the evidence for the existence of each of these HEBE ring components. Second, a theoretical demonstration of the biological necessity of these links in human evolution. It is possible that the ring components might associate due to incidental connections. For example, it might be that the prolonged period of human juvenility is unrelated to acquiring adult cognitions but instead secondarily due to another factor such as a life history extension of immaturity in regard to the general prolongation of the period of human life. Likewise the egalitarianism and food pooling which characterizes human hunter-gatherers, (and which is noticeably not present in most agrarian and modern societies), could be merely an incidental aspect of the way of life of hunter-gatherers. Moreover, though humans engage in cooperation to provision juveniles to support their prolonged neuromaturation, it might be conceivable that this may not be is a necessary requirement if humans are to acquire the complex cognitions needed for such cooperation.

The core concern of this paper is to go beyond describing the ring in terms of mutually fitting components and argue that its components are biologically necessary linkages. It is not just the case that animals with larger brains have a correlated longer

neuromaturation, it is argued, but it is a necessary consequence if such large neuron dense brains are to develop fully the information processing capacities of which they are capable and which might compensate adaptively for the extra costs entailed by their great size. Nor is it an incidental factor of human hunter-gatherers that they cooperative pool food together but that this is necessary to the circumstances of surviving in their hunter-gather ecological niche.

The components of the HEBE ring, as noted, are presented using acronymic terms. These are created not just for brevity but also clarity in that the concepts behind them are defined by their place in the HEBE ring. For example, complex human information processing (CHIP) is not exactly the same concept as the sophisticated adult cognition found and studied in contemporary humans since it concerns specifically those information processing capacities that produce cooperation and the ability to obtain high energy foods in Middle Paleolithic hunter-gatherers. Moreover, it concerns cognitions that are dependent upon the earlier stage of prolonged expensive neurodevelopment (PEND). While CHIP is closely related to adult cognition as it occurs in contemporary people, it is also theoretically distinct from it as adult cognition in contemporary people is also a product of many and diverse factors such as education, cultural systems (such as writing) and modern technologies that were not present for Middle Paleolithic hunter-gatherers. Thus, CHIP is not necessarily the same as the adult cognition that characterizes contemporary humans as instead it concerns the general competence for cognition that was acquired and relevant for the foraging and social skills that had an utility in the circumstances of Middle Paleolithic hunter-gatherer survival. Separate to that, changes have occurred in human cognition in the later periods of the epipalaeolithic, farming and variously named "ages" and eras of human history up to and including contemporary societies. These later cognitions can inform us about these earlier Middle Paleolithic cognitive abilities but they are biologically a distinct phenomena. PEND is not exactly the same as energy expensive neuromaturation since it also covers all energy costs linked to the acquisition of adult cognitions covered by CHIP, and for which juveniles need to receive energy support. Thus, PEND encompasses not only the direct energy costs of expensive brain development but also those indirect costs needed to engage in costly learning activities in terms of the energy which they use, and in the food acquisition opportunity costs of not foraging while active in them. PEND also more broadly concerns not just the expense but the associated liability that associates with the high energy needs of the juvenile brain.

The human biology discussed in this paper, it should be emphasized, concerns specifically that of humans during the Middle Paleolithic period in which human first evolved as a species. Humans, unusually for a biological species, have markedly diverged in their ways of life from the circumstances in which their biology was selected. Not only are contemporary humans in many obvious respects different from humans 100,000 to 200,000 BP but even the apparently simple hunter-gatherers such as the !Kung that survived into the twentieth century that were studied by anthropologists are distinct from these early hunter-gatherers, for example, in regard to population density, and in the use of bows and arrows and other technologies. This also applies to the humans during South Africa Middle Stone of the Howiesons Poort and Sibudu

African periods in 72 - 60 ka. These technology sophisticated human arose at periods considerable later than the evolutionary origins of the human species. The terms modern humans, and *Homo sapiens sapiens* are used to cover the species including these early humans and present people. The term contemporary humans concerns only those modern humans that live in the food provision, social and educational circumstances found in modern industrial states.

1.3. What this paper seeks to achieve

Section 2, of this paper reviews evidence that humans generally, and human juveniles more specifically, have extreme physiological liability in energy requirements and that this is a particularly predominant aspect of their biology. Extreme energy liability is distinct from the idea that human brains are energy expensive—a notion that motivates such theories as the expensive tissue hypothesis which argue that the human brain challenges human survival due to its high energy costs and requires special adaptations such as reduced gut size, musculature and high energy diets. Liability concerns the sensitivity and resilience to shortages and so the circumstances in which energy is obtainable in a manner that is reliable. The brain as an organ, particularly when large, is peculiarly vulnerable due to energy shortage. This review details the situation in which the HEBE ring components arise as parts of an interdependent intergeneration loop from this high energy liability of juveniles. Section 3 reviews the consequence of this liability for human biology and one previous theory, the Brain Malnutrition Risk Hypothesis.

In section 4, review is made of the link between the prolonged period of human immaturity and the acquisition of complex human information processing. This link is shown to be necessary and not incidental. At present the status of the prolonged period of human immaturity is treated as an observed variable of human life history but is here identified as critical to human origins. This section shows that the constraints of the high neuron human brain forces it to have prolonged neuromaturation—at least if it is to optimally acquire the information processing capacities of which its high neuron number makes it potentially capable. Section 5 examines the evidence that prolonged neuromaturation links to human specific cognitions including those needed for human unique forms of cooperation.

Section 6 reviews the biological novelty of cooperative energy provisioning provided to human juveniles that enables the extended period of human neuromaturation. Several researchers have noted that humans are cooperative breeders. However, such accounts of cooperative breeding fail to highlight the biological novelty of this cooperation in regard to that humans provide is egalitarian not ranked in its support to juveniles. This equalitarian/ranked difference is critical since ranked cooperative breeding allocates energy predominately to mothers to enhance her fertility and only to a lesser extent to juvenile neuromaturation, whereas this relationship is reversed when such cooperation is egalitarian.

Section 7 establishes that the human indirect reciprocity that underlies hunter-gatherer egalitarianism depends upon such reputation related activities as gossip and credit assignment. These depend for their existence upon expert awareness of others behavior, executive skills such as cognitive control, and descriptive communication. The existence of such reputation creating cognitions are dependent upon a prolonged period of acquisition and extended child and adolescent neuromaturation. Section 8

concludes by discussing the importance of these interactions of the HEBE ring for appreciating the novelty and evolutionary foundations of human biology.

2. HUMAN BRAIN ENERGY LIABILITY

2.1. The brain large or small is a high energy labile organ

The energy liability of an organ concerns the degree to which it is vulnerable following energy shortage to functional disruption and cellular death. This reflects factors intrinsic and extrinsic to the organ both in the body and external to it in its environment. Liability concerns the lack of resilience of an organ to energy deficits and the ability of external factors both of the body and outside it to buffer or prevent such shortages.

The brain as an organ has is an unusually high energy liability organ due to several intrinsic physiological factors listed below.

- Limited energy reserves. Glycogen is present but at much lower concentrations (3–12 μ mol/g) tissue and than in the liver (100–500 μ mol/g). 3 μ mol/g of glycogen can sustain the brain for about ten minutes.
- High energy consumption.
- With the exception of hibernation, the brain lacks an off or rest state. Even slow wave sleep only reduces its energy consumption by 25% (that of REM sleep does not at all).
- The brain suffers dysfunction quickly following energy shortage and this rapidly leads to irreversible damage and cell death.
- The brain does not utilize short chained fatty acids (triglycerides) as an energy source due to limits in their ability to cross the blood brain barrier. Glucose is the predominate energy source though lactate can replace up to 35% of the energy needs. Ketone bodies can also be used as an energy substrate though these are not neutral to its functioning i.e. inhibiting glutamate functioning.

A sign of the brain's potential liability is that though overall energy consumption is fairly constant irrespective of activity or rest state, this reflects wide internal shifts in the local allocation of energy consumption with the extra energy of activate areas being compensated by reduced energy consumption in inactive ones.

A high energy utilizing organ will tend to make greater energy demands of available energy supplies and so impose more severe challenges on the body's abilities to meet its requirements. But high energy utilization does not of itself necessarily entail an organ will have high liability if it has the capacity to radically reduce its energy consumption without impairment. A low energy demanding organ, in contrast, might have high liability if even small reductions in its intake impair its functioning or physiological support external to it lacks the capacity to buffer it against even minor shortages.

2.2. Adult human brain liability

The human brain both when mature and immature utilizes the largest share of any endothermic vertebrate energy budget due to its large physical size and its large size in relation to the human body (high encephalization). This is an important factor in its unique sensitivity to energy shortage. Its percentage share of energy utilization in terms of adult BMR (which includes energy consumption at rest and excluding digression) is ≈20% (Mink et al., 1981). Two factors are relevant here: brain energy scales with brain

volume with an exponent of approximately 0.86 (Karbowski, 2007)). The human encephalization quotient (EQ) which takes account of the fact that brains in larger animals are proportionately smaller than in smaller ones, is the largest amongst all mammals with only dolphins and other great apes being comparably large (Marino, 1998). Using Jerison's formula for EQ (Jerison, 1973), humans have an EQ of 7.0 while that of next highest animal, the Tucuxi dolphin, (*Sotalia fluviatilis*) has one of 4.6, and that of the highest primate, the chimpanzee (Pan troglodytes) one of 2.3 (Marino, 1998). Other primates have much lower EQS, Callitrichinae (tamarins and marmosets), a family of cooperative breeding primates discussed later on have one of ≈1.6.

The general liability of CNS neural tissue (the brain and the spinal cord) is reflected in the conservativeness of the share it takes of the energy budget across adult vertebrates (in terms of the proportion of the body BMR devoted to the CNS). This proportion is 2.7-7.7% (mean 5.3%), largely irrespective of such factors as vertebrate class (sharks to mammals), size (goldfish to elephants) and thermoregulatory status (homeothermy 5.5±0.7%, or ectothermy 4.8±0.6%) (Mink et al., 1981). (This size BMR allometric function is proportional due to it being to the power one (Mink et al., 1981) allowing discussion of percentages independent of body size.) The proportion of energy allocated to the adult CNS (due to the large relative size of the brain) however markedly increased in primates (>10%) and particularly in modern humans (≈20%) (Mink et al., 1981) having a body mass that is optimal in terms of maximum life expectancy (Peters et al., 2010). Gnathonemii, such as the Peters' elephantnose fish (*Gnathonemus petersii*), are the only exception to the human brain having the highest relative energy consumption to its body. This links to the peculiarities of this genus being an electroceptive fresh water fish with an expanded high energy utilizing "gigantocerebellum" but a low energy consuming ectotherm body (Nilsson, 1996).

2.3. Developing brain liability

There are five main areas in which the immature human brain differs in its energy utilization from that of the adult that increase its potential liability:

- The greater energy expenditure of the child and adolescent brain per unit (which may be expressed either in terms of mass, 100 g or volume 1 mm^3) relative to that of the adult (section 2.3).
- The greater expenditure of it in terms of its share of the total energy expenditure of the body (section 2.4).
- The different energy costs of different stages of brain development—brain formation and its neuromaturation (synaptic, myelination)—and the nature of the factors shaping or in other ways relevant to them (2.5).
- The neuromaturational energy costs of the gray matter and the white matter components of the immature cerebral hemispheres (2.6).
- The greater energy vulnerability of the immature brain to neuroglycopenia and so the heightened need of juveniles for reliable food intake energy nutrition (2.7).

These issues are important since greater liability in them must be matched by greater buffering of energy supply. Such buffering can be internal (greater reserve glycogenolysis and gluconeogenesis production potential— many by the liver) or external (access and availability to energy foods of a reliable nature). The later factor includes not only the ability of an animal to acquire foods through their own efforts but the social cooperation it has with conspecifics such that they will provision it when required with food stuffs.

2.4. Total energy developing brain consumption

Chugani and colleagues (1987, table 2) provide the data gathered below in table 1 for the percentage energy increase in children of different ages relative to those of adults. If the data for brain energy consumption are combined with data about their adult metabolism (also given in (Chugani et al., 1987)), and those for the volumetric size of these areas in children and adults (Caviness et al., 1996; Filipek et al., 1994), they reveal that the total energy utilization of the child's brain between 3-8 years-of-age is greater than the adult by ≈177%. For the period between 8-15 years-of-age, brain energy utilization is greater by ≈149%. This is illustrated in fig. 2.
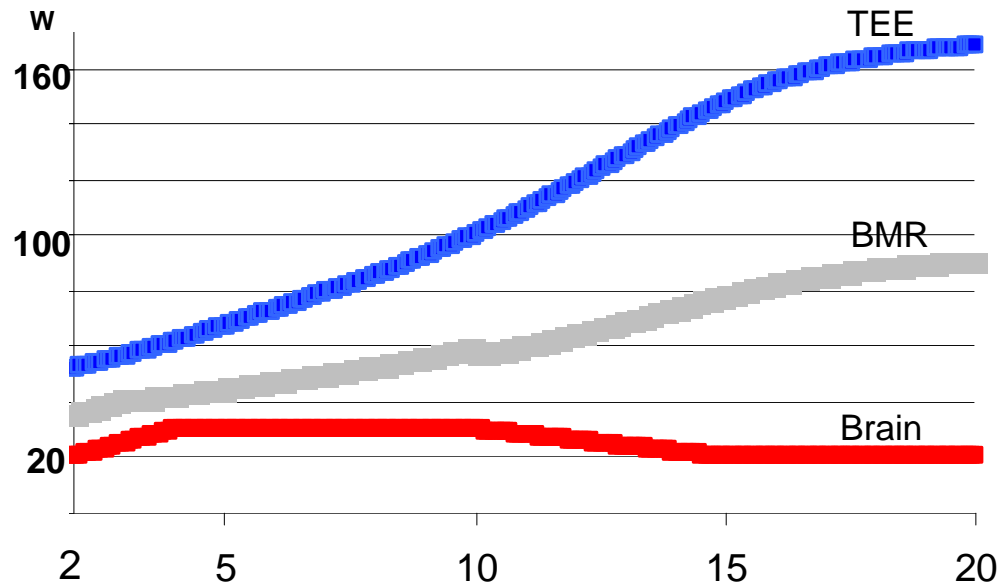
Fig. 2. The total energy expenditure (TEE) of the body, basal metabolic rate (BMR) and the brain energy consumption as they change from two years-of-age to 20 years-of-age. TEE is based upon the predictive equations for boys and men in (Torun, 2005). BMR is based upon the predictive equations in (Henry, 2005). The slight irregularity in the BMR line around 10 years-of-age is due to two equations for different age partitions that do not exactly match at this transition. Brain consumption is based on children between 4 and 9 years-of-age having a 50% higher metabolic rate than adults, and that this smoothly declines between 10 and 15 years-of-age to adult levels. Energy is expressed in watts. Note, the energy consumption appears slightly higher than the total energy expenditure in figure 4. However, the graph line for this in men in figure 4 continues upwards and reaches 157 W, which is in a similar range to that in figure 2. It also, moreover, concerns hunter-gatherers from Ache, Hiwi, and Hadaza groups that tend to have smaller body sizes than those populations used to create the TEE and BMR predictive curves.

Table 1 Childhood and adolescent brain energy consumption as percent relative to that of adults in four brain areas, Chugani et al. (1987).

	0-1 years	1-2 years	3-8 years	9-15 years
cerebral cortex	0.72-0.93	0.99-1.25	1.85-2.24	1.52-1.78
brainstem	0.89	1.06	1.46	1.45
cerebellum	0.93	1.03	1.71	1.45
basal ganglia	0.75	0.93	1.55	1.41

An alternative assessment of the energy usage of a child's brain can be made by calculating the various BMRs of different organs and the whole body then estimating what remains to be accounted for by the brain. Hsu and colleagues provide the relevant data for body organs of an average child of nine years-of-age weighing 30.5 kg and provide a measure of their total BMR (Hsu et al., 2003). The total BMR was 59.2 W which is near that calculated using predictive equations for children of this age and weight (Henry, 2005). Of that 27.6 W are accounted for by the BMR of nonbrain components (liver 6.6 W; heart 2.6 W; kidney 3.9 W; skeletal muscle 7.7 W; adipose 1.4 W; smaller organs and tissues such as spleen, pancreas, thyroid gland, and skin 5.3 W). At the age of 9, a child grows by 3.6 kg year^{-1} (growth chart spreadsheet data, Centers for Disease Control and Prevention) which requires 5.3 kJ g^{-1} (Webster, 1980), suggesting that the energy for body growth adds another 6.2 W. This implies that the child's brain consumes around 26 W. The child's brain BMR if it had an adult metabolic rate would be 17.5 W. The difference between the calculated child and adult brain metabolic rates here—149%—roughly matches that measured by Chugani directly for this age (though Chugani's research group found higher wattage values).

The information given in table 1 and used in this calculation provides a rough estimate that is conservative since it ignores metabolic differences between immature and mature white matter. This estimate is consistent with those found using older techniques in the 1950s (Kennedy and Sokoloff, 1957) that measured an 180% increase for cerebral flow and an 130% change for cerebral oxygen utilization. It should be noted that these increases do not link to smaller cerebral cortex gray matter mass in the child than in the adult as its volume starts to overlap with the lower adult range of volumes from the age of around 4 years-of-age (Courchesne et al., 2000). The gray matter of the average child's brain increases by 6-7% after this to reach a maximum volume around 6 to 9 years-of-age (it then declines after this by 13-15% by the age of 18) (Courchesne et al., 2000, figure 3a). However, since white matter increases with a different trajectory, it is several more years after the peak of gray matter volume before total brain volume in the average person reaches its maximum (Courchesne et al., 2000).

The raised period of inverted U energy consumption of a child's brain broadly correlates with other metabolic related changes suggesting a period of still partially understood potential neurophysiology vulnerability in the juvenile brain. There is increased blood volume flow into the brain (Kennedy and Sokoloff, 1957): 130% between 3 and 6 years-of-age that declines to near adult levels at 15 years-of-age. Parallel to this there is an increased rate (50%-85% higher in children than adults) of blood flow per unit gram of the brain (Chiron et al., 1992). Biomolecular changes occur such as the ratio of N-acetyl aspartate (a molecular water pump in myelinated neurons) to choline (used to make cell membranes of dendrites) which reaches a peak at 10 years-of-age (Horska et al., 2002), and the capacity to synthesize serotonin changes in a pattern that is similar to that of changing energy metabolism (Chugani et al., 1999). Though energy liability is the focus of this paper, it should be noted other forms of greater liability also affect the juvenile brain concomitant with these neurophysiological differences. The juvenile brain has increased vulnerable to injury compared to the adult in that when concussed it suffers longer neurological impairment (Kirkwood et al., 2006), particularly in memory (Sim et al., 2008), and is at greater risk of death from "second impact syndrome" (McCrory and Berkovic, 1998). Other factors such as hypoxia, dehydration, hyperthermia and hyperammonemia are covered in (Skoyles, 2008).

2.5. Brain body percentage

The juvenile human brain not only utilizes more energy than the adult one but is a much larger organ relative to the rest of the body. As a result, juvenile brain consumes, *ceteris paribus*, a higher percentage of the total body energy costs exposing it to much higher risk of energy malnutrition.

An initial high brain body ratio (encephalization) is not peculiar to humans: developmentally, due to the initial large size of the immature brain (even if it is smaller in absolute size than in the adult), the brain to body ratio in all animals starts off relatively high after birth and then decreases, often abruptly (Kobayashi, 1963). For example, the mouse brain is roughly 6% of the mouse body weight at birth until 14 days old, as the brain size during this time increases in line with that of body growth. At 14 days however it stops further growth—while the body continues to increase weight—resulting in the adult brain being only 1.1% of body weight (Kobayashi, 1963). This brain/body relationship varies with species including the human one. In the rat, the brain after birth grows faster than the body, so while it is 4.6% at birth it rises to 7.1% at 10 days only to decline to 0.73% as an adult. Rabbits after a day are 3.8% declining to 3.1% at 13 days and then dropping quickly to 2% at 15 days and finally as adults to 0.036%.
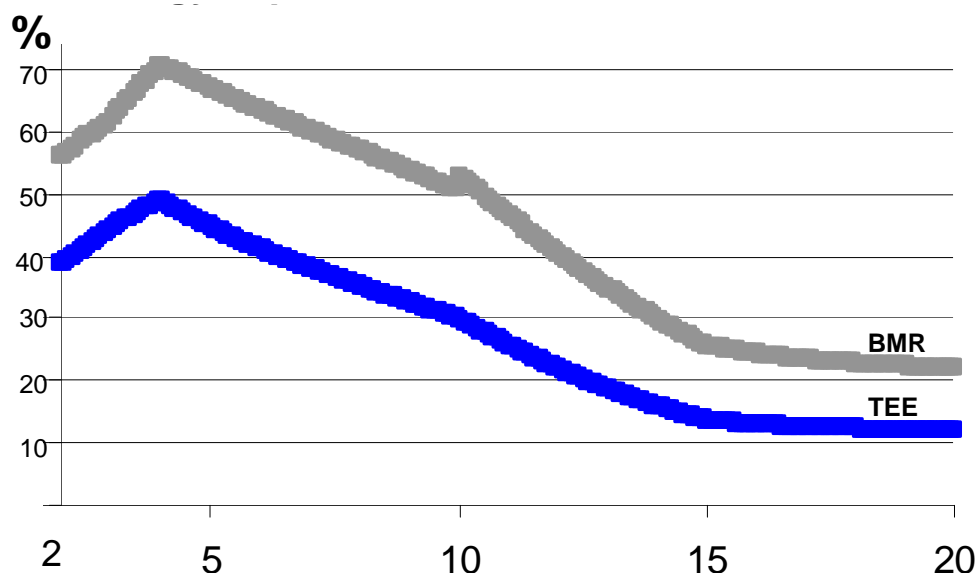
Fig. 3. TEE and BMR energy consumption: the data used to create the lines of TEE and BMR energy consumption in figure 1 against age are replotted to show how they change as a percentage of total energy consumption of the body between 2 and 20 years-of-age.

Juvenile encephalization is particularly high for humans since juvenile body growth is delayed relative to brain growth (Vinicius, 2005). At birth it is 10.1%, this decreases to 7% at six months but slightly rises to 8% at two years then declines back to 6% at six years-of-age, 4% at 11 years-of age and then 2% when adult (all percentages from figure 4 in Kobayashi, 1963). These differences relate to an unique pattern of growth in humans: "In all precocial mammals other than humans at around the time of birth there is a striking switch in brain growth relative to body growth. During intrauterine development, fetal brain size typically increases substantially as body size increases. Following birth, on the other hand, increase in brain size is far more limited

as the body grows in size…. [and moreover that] Humans show a major difference from all other mammals in that the fetal pattern of substantial brain growth relative to body growth continues for approximately a year after birth" (Martin, 2007, p. 74.). The size of the brain relative to the body is important in regard to the energy costs of the immature brain since in addition to its absolute size, a proportionately larger brain to body ratio, will require such a brain to take a larger percentage of the body's total energy expenditure. As a result, a high brain/body ratio continues to keep the human brain's share of body energy budget at a high level with concomitant high liability to energy intake shortages into its period of neuromaturation.

2.6. Brain formation

The development of the mammalian brain can be divided into two broad biological stages in regard to its energy utilization, energy sources and evolutionary change: brain formation and neuromaturation. Brain formation creates broadly the neuron-axon substrate of neural networks (Zilles and Amunts, 2012), while neuromaturation refines broadly their information processing capacities so they provide biologically important cognitive competences. Brain formation itself can be roughly separated into a neurogenesis stage in which neurons are created and gliaogenesis one after this in which supporting glial cells are created. Concomitant with this there is the formation of a grid like axon layout (Zilles and Amunts, 2012). Brain maturation can itself be further and roughly divided into local network area synapse refinement in gray matter which cognitive functions are acquired, and myelination cross-brain network stage of refinement of small world network attributes in white matter that enhances executive control and other top down regulative processes that integrates and regulates these functions. All these divisions are approximate with processes overlapping.

Brain formation necessary occurs before immature individuals become independent of maternally supplied energy. The reason is that energy independence requires the cognitive and behavioral capabilities that only result from the neuromaturation that occurs subsequent to brain formation.

A brief review is needed of these stages related to cellular development and changes in volume before their energy costs and the implications of these for the acquisition of information processing can be examined. This is because such volume changes affect the size of the brain in terms of its size as a share of the body and its share of the body's energy budget. This discussion is also relevant to understanding the volumetric evidence about neuromaturation and intelligence discussed below.

Brain formation is similar to the formation of other organs and other parts of the nervous system such as the spinal cord and periphery nervous system (Hua and Smith, 2004; Purves and Lichtman, 1980) in being initially carried out by a cell exuberance that is later reduced by programmed cell death (apoptosis) (Doseff, 2004). This pattern of exuberance-elimination occurs during brain formation to neurons and axons (Innocenti and Price, 2005). Around 70% of the brain's initial neurons (Rabinowicz et al., 1996) and a roughly equal percentage of long range axons (LaMantia and Rakic, 1990) are formed only then to be eliminated in development (in the case of neurons by apoptosis and with axons by retraction).

The physical mass of the brain's neurons, after it arises in the fetus, moreover, contains nearly all of the neurons that will later form it as an adult organ. In humans the peak of the brain's neuron production is at 15-20 weeks gestation, and that of glial cells from 30 weeks to the end of first year (Dobbing, 1970, fig 2). With certain neurogenesis

exceptions (Eriksson et al., 1998), no large number of neurons compared to those already present are created after birth (Bhardwaj et al., 2006; Gould, 2007), though there is a continual turnover in glial cells (Bhardwaj et al., 2006). The early immature brain, as a result, may have three to four times more neurons than the adult brain, even though the newborn brain takes up only 24% to 31% of the volume of the adult one (Vinicius, 2005). Since the energy consumption of neurons is mediated through adjacent glial cells, the later development of the latter would suggest energy metabolism of the brain would increase (as observed) following the initial phase of gliogenesis.

Human brain formation when compared to that in other primates is advanced (even if it still continues to grow in size after birth) since "despite the somatic immaturity of the human infant, the human brain is relatively developed at birth. Two months prior to parturition, humans are at or above the neural maturational level of newborn macaques, and more neurally developed than a week-old kitten or a 2-week-old rat." (Clancy et al., 2001, p. 14.). It is also more nearly formed in size compared to other body organs. The newborn human brain is 24-31% of its adult weight (Vinicius, 2005), but the heart is only 6-8% and the skeletal muscles 2.7-4.6% (International Commission on Radiological Protection, 2002, table 2.8). At one year-of-age, the brain is 66-73% of the adult, the heart is 15-20%, and skeletal muscle 6.6-11% (International Commission on Radiological Protection, 2002, table 2.8).

Critically, the energy for brain formation comes from the mother. As noted by Martin, "The brain is unusual among body organs in that most of its growth is completed at a very early stage, and hence resources provided by the mother during pregnancy and lactation" (Martin, 1996, p. 154). The energy utilization of the neonate brain per 100 g is less (72-93%) than in the adult, and less than half that of 3 to 8 year old children (see table 2) (Chugani et al., 1987). It is therefore not a cost that needs to be supported by the juvenile or the provisioning of allomothers and other individuals (though as noted, its large size requires adipose tissue for energy reserves and this does create substantial cost to its mother in pregnancy and during lactation).

2.7. Neuromaturation

The maturation of the mammalian brain, once its underlying basic cellular neuron-axon structure is formed, is unlike the maturation of its other organs in that it does not concern a size increase that scales with the growth of the body (such as the mammalian heart, liver or kidneys). It is in this respect different to the development of the brains of fish, amphibians and reptiles in which the continual addition of neurons plays an important role in neuromaturation (Kaslin et al., 2008). Instead, the maturation of the mammalian brain involves the remodeling and reorganization of its local neural networks and their connectivity. It should be noted that while such synapse and myelination changes dominate brain maturation, processes involving them also have roles earlier in brain formation (Bourgeois et al., 1994; Innocenti, 1995; Innocenti and Price, 2005). These, however, lack their later important energy consequences (infant and earlier brains have a lower energy consumption per 100 g than adults (Chugani et al., 1987, table 2)). In what follows, the discussion of neuromaturation mainly refers to the cerebral hemispheres due to their predominance in primates (they make up all but ≈14% of the adult human brain (Filipek et al., 1994)).

2.7.1. Gray matter maturation

The neuromaturation of gray matter occurs in a period of synapse exuberance in

which synapses double in number to what they are at birth and during adulthood (Huttenlocher, 2002; Huttenlocher and Dabholkar, 1997). This increase is reflected in markers of synapse numbers such as synaptophysin that increase in the prefrontal cortex in terms of its "integrated optical density" that is initially low, rises and peaks between 6 and 10 years-of-age and then declines during adolescence to adult levels (Glantz et al., 2007). This exuberance is needed to allow the synapse removal required for neural network refinement (Innocenti, 1995; Innocenti and Price, 2005). Synapses and associated processes, moreover, are energy consuming. 80% of energy consumption even in the adult cerebral cortex could concern synaptic activity (Sibson et al., 1998) or related neuronal signaling (Jolivet et al., 2009). However much uncertainty exists in regard to data used in making estimates with synapses being suggested to consume 34% in rodents and speculatively "perhaps 74% in humans" (Attwell and Laughlin, 2001, p. 1143).

A strong link exists between the energy consumption of the brain during the period of its most intense cognitive development, and the period of its greatest absolute number of synapses. For example, the energy demands per 100 g of the human cerebral hemispheres between birth and one year of age is 87% of the human adult (Chugani et al., 1987, table 2), this corresponds to the limited number of its synapses (Huttenlocher, 2002; Huttenlocher and Dabholkar, 1997), and the limited learning done at this age by the neonate brain. However, the energy demands per 100 g of the human cerebral hemispheres between the ages of 3 and 15, during which children are most engaged in intense learning, jumps respectively to 198% (between the ages of 3 and 8) and 162% (between the ages of 9 and 15) (Chugani et al., 1987, table 2). This change in energy consumption parallels the increased numbers, at these ages, of synapses (Glantz et al., 2007; Huttenlocher, 2002; Huttenlocher and Dabholkar, 1997).

There are also electroencephalography (EEG) associated changes that parallel with these synapse and metabolic shifts suggesting the existence of profound changes in brain functioning during juvenility. Slow-wave band EEG activity correlates with changes in gray matter density in children and adolescents (Whitford et al., 2007), metabolism (Feinberg et al., 1990) and synaptic density (Feinberg et al., 1990). This is also the case with the power of delta and theta bands of eye-open EEG and metabolism (Boord et al., 2007). Research finds that the delta EEG component of non-rapid eye movement (NREM) sleep declines by 50% between 10 and 20 years-of-age, with half that happening between 12 and 14 years-of-age (Campbell and Feinberg, 2009; Feinberg et al., 2006). This delta EEG component during sleep has been suggested to reverse in a homeostatic manner the effects of neuron during waking suggesting decline of such metabolic activity towards the end of neuromaturation (Feinberg et al., 2006).

2.7.1.1. Gray matter volume changes

Parallel to energy, synapse and myelination changes, there are macro level changes in gray matter thickness. These are important since they provide when measured by MRI a researchable proxy to the otherwise (except for rare clinical and postmortem circumstances) inaccessible metabolic and cellular level changes. Small MRI volume alterations of ≈8% over juvenility happen to gray matter (Lenroot and Giedd, 2006; Shaw, 2007; Shaw et al., 2008; Sowell et al., 2002). There are also volume changes to white matter together with microstructural organization in fiber direction detectable as shifts in MRI fractional anisotropy (FA) (Lebel et al., 2008). These MRI differences provide a noninvasive window through which stages in brain maturation in

human children and adolescents can in nonclinical contexts be investigated (Mabbott et al., 2006; Schmithorst et al., 2005; Shaw, 2007; Shaw et al., 2008; Sowell et al., 2003).

Gray matter changes in volume broadly have an inverted U shape that is particularly marked and delayed for those of "superior intelligence" (121–149 IQ range) (Shaw et al., 2006). Initially cortical thickness expands and then after puberty it thins during adolescence (Shaw, 2007; Shaw et al., 2008; Sowell et al., 2003). This invented U shape occurs not only with the cerebral hemispheres but also in terms of total volume to the lobes of the cerebellum with which the cerebral hemispheres interact (Tiemeier et al., 2009).

2.7.1.2. Gray matter neuropil

Gray matter volume changes link not to neuron expansion nor neuron number reduction (since these are completed by this age) but instead primarily to neuropil changes in the synapse energy supporting glial cells and capillaries. Neuropil (broadly defined) consists of the dendritic arbors upon which synapses exist, and the microvascular capillaries and glial cells that provide synapses with their metabolic support (Pellerin and Magistretti, 1994; Pellerin et al., 1998). Thus changes in them provide a proxy to changes in local area energy utilization.

Neuropil components make up a substantial proportion of gray matter. In the adult human cerebral cortex, roughly three glial cells exist for every two neurons, depending upon the layer (Azevedo et al., 2009). They increase during development: there is an over three-fold rise (at least in the mediodorsal thalamus where the numbers have been counted) between the newborn and the human adult (Abitz et al., 2007). Glial cells and their processes are estimated to make up from 15% (Williams et al., 1980) to 20-25% (Wolff, 1970) of the volume of the adult cat's gray matter. The percentage in humans can reasonably be taken to be greater since the glial-to-neuron index increases with brain size (Jehee and Murre, 2008). Further reflecting this, primates have a high glial cell neuron ratio linked to increased brain size with humans having the largest brain amongst primates (Sherwood et al., 2006). Glial cells are also larger with a 16.5-fold greater volume in humans than in rodents (Oberheim et al., 2009).

Glial cells increase in number and size depending upon neuron activation and the metabolic demands of activated neurons. The cortex in animals stimulated to learn by enriched environments are thicker by 3.3-7%, and this associates with an increase in glial cell numbers per neuron of 12-14% (Diamond et al., 1964; Diamond et al., 1966). When such synapses numbers increase, the area directly between glial cells and synapses expands by 19% (Jones and Greenough, 1996), and the synapses that exist tend be big (Sirevaag and Greenough, 1985): "In addition to having larger synaptic contacts.. EC [environment complex] rats exhibited a population of very large synapses not seen at all in the IC [isolated condition] in layer IV" (Sirevaag and Greenough, 1985, p. 216). Moreover, the volume of glial cell nuclei for each synapse is also higher by 37.5%. Environmental enrichment produced in one study a 23.1% increase in dendrite length that was associated with wider capillaries (4.35 μm compared to 4.15 μm in controls) and shorter distance between any part of the neuropil and a capillary (27.6 μm compared to 34.6 μm) (based on figures in Sirevaag and Greenough, 1987). The mean volume of mitochondria per neuron was also 20% greater (1599 μm^3 compared to 1280 μm^3) and the volume of glial cell nuclei for each neuron was 63% higher (Sirevaag and Greenough, 1987).

Such energy related changes are also reflected in volumetric measures of human

gray matter. The subgenual part of Brodmann's area 24 is reduced in size in those with bipolar disorder (controls: 214.7 mm^2 gray matter, major depressive disorder, MDD: 177.9 mm^2), and this correlates with reduced glial cell numbers (controls: 8.43×10^6 glial cells; MDD, 3.90×10^6) but not reduced neuron numbers (controls: 5.24×10^6 neurons; MDD, 5.97×10^6) (Ongur et al., 1998). PET also finds both reduced blood flow and reduced metabolism in this area in such individuals (Drevets et al., 1997).

Increases in basal metabolic demand also augments the density of capillaries (Weber et al., 2008). The potential for microvascular capillary expansion in response to greater oxygen and energy supply needs is extensive as there are 40 cm of capillaries for every 1 mm^3 (Kreczmanski et al., 2005). Blood also itself makes up around 3.93% (Bulte et al., 2007) to 5.2% (Leenders et al., 1990) of adult gray matter volume. Increasing glucose and oxygen supply associates with parallel increases in capillary density (Borowsky and Collins, 1989; Weber et al., 2008).

A possible explanation for cortical thickening and thinning could be that the dendritic arbor itself expands. This, however, is unlikely to be a major factor in gray matter increase, though certain elements of it might increase in some neurons during childhood, see the data reported for layer IIIC pyramidal neurons in (Petanjek et al., 2008) and during adolescence for neuron soma in layers 2 and 5 (Rabinowicz et al., 2009). As Petanjek and colleagues however note, the data only suggest "slight dendritic growth might occur at that time [childhood and adolescence]" (Petanjek et al., 2008, p. 926). Further, along with this increase in neurons in some layers in adolescence goes decreases in other layers such as 3, 4 and 6 (Rabinowicz et al., 2009). It has also been noted that while dendritic branches become more complex and long in enriched environments, "the increased dendritic branching tends to take place within the volume already occupied" (Greenough and Volkmar, 1973, p. 499). Extensive change to dendritic dimensions, moreover, is also unlikely, since this might change the "cable" related electrical properties of dendrites that determine the spread of forward and back propagating currents that underlie their information processing (Segev and London, 2000): related to this, the morphological dimensions of dendrites are under tight homeostatic regulation (Samsonovich and Ascoli, 2006).

2.7.2. White matter maturation

White matter maturation, in general, involves the reorganization of connections between groups of such areas across the brain in terms of small world network attributes (Bullmore and Sporns, 2009; Bullmore et al., 2009). This entails axons being initially unmyelinated to allow their selective myelination and diameter expansion during neuromaturation. This creates neuromaturation related energy costs due to the inefficient energy transmission that happens through unmyelinated and small diameter axons (Wang et al., 2008).

Cerebral cortex axons can broadly be separated into three types with different relationships to myelination and white matter. (1) Intracortical 1-3 mm unmyelinated ones within the gray matter; (2) short-distance 10-30 mm fibers below the gray matter and (3) long 30-170 mm distance fasciculi in the deep white matter. The numbers of connections greatly reduces with distance (Schuz and Braitenberg, 2002). These cerebral cortex connections differ in regard to developmental myelination, and so their contribution to white matter volume change. The intracortical component, due to its lack of myelination, does not developmentally expand white matter. However the short and fasciculi myelinated axons that make up the white matter undergo maturational change

as information transmission refines axons that link neural networks by selectively myelinating a small fraction of them. This process (though selective) leads to volume expansion and because of this, it can be detected as white matter volume change (Mabbott et al., 2006; Schmithorst et al., 2005; Shaw, 2007; Shaw et al., 2008; Sowell et al., 2003). Another factor is that neuromaturation can result in changes in its microstructural directional organization, and this can produce increases in diffusion tensor imaging MRI measured fractional anisotropy (FA) (Lebel et al., 2008). Many of these changes occur late in neuromaturation, with white matter having a delayed growth in adolescence relative to gray matter. Within this delay, white matter increase is broadly inverse to that of gray matter decrease (Giorgio et al., 2009; Lebel et al., 2008). The change, though, does not seem to be due to the increased myelination of lower cortical layers shifting them in neuroimage classification from gray matter to white matter (Tamnes et al., 2010).

The myelination that occurs as a result of neuromaturation makes axon transmission more energy efficient: for the passage of each spike, a 0.5 μm unmyelinated axon costs about 12-fold more in energy than when that spike is passed through a myelinated one (Wang et al., 2008). White matter, however, has only a minor impact upon total brain energy cost as its metabolism in humans is about two fifths that of gray matter (Leenders et al., 1990) while it makes up just ≈38% of the cerebrum (Filipek et al., 1994). Myelination related costs (about which costs are less investigated), like those of synapse neuromaturation, also seem to have the pattern of being initially low at birth then high and then reducing with maturation, at least this is the case in the macaque (0.233 μ mol glucose min^{-1} gm^{-1}, birth-59 days; 0.503 μ mol glucose min^{-1} gm^{-1}, 60-179 days; 0.271 μ mol glucose min^{-1} gm^{-1}, 180 days-adult) (Jacobs et al., 1995, table. 2.).

The neuromaturational trajectory of myelination differs from that involving synapses in that it is not an inverted U in shape being instead one of linear increase, and in that it can extend for a much longer period, a situation reflected in the continued expansion into the third decade in terms of white matter volume (Lebel et al., 2008; Sowell et al., 2003, fig. 6; Yakovlev and Lecours, 1967) and increased fractional anisotropy (Hasan et al., 2009; Lebel et al., 2008). This relative delay of myelination maturation is also consistent with small world connectivity refinement occurring particularly in the later stages of neuromaturation during adolescence, in which distant connections are pruned to create a more hub based connectivity (Fair et al., 2009; Fair et al., 2008).

2.8. Neuroglycopenia vulnerability and the juvenile brain

The brain, including that of juveniles, is in a privileged position to regulate metabolically its own energy supply (Gobel et al., 1010; Peters et al., 2004). The main source of its energy is plasma glucose produced by glycogenolysis and gluconeogenesis in the liver (Haymond and Sunehag, 1999). The hepatic production of glucose is closely linked to that of brain size in growing nonhuman animals such as the pig (Flecknell et al., 1980), as well as in growing humans (Haymond and Sunehag, 1999, see their fig. 4B). By 3-4 years-of-age, as a result of the high human brain/body ratio (and its high energy consuming cerebral cortex component), hepatic glucose production in spite of the much smaller child body size approaches and overlaps that of adults (Bier et al., 1977).

The high pediatric brain percentage consumption of the body's glucose

production causes it to have increased vulnerability to hypoglycemia. Following temporary fast, circulating plasma glucose in children drops to hypoglycemia levels after 24-36 hours—levels that are not found in adults even after 2.5-3 days of fasting (Cahill, 2006; Haymond and Sunehag, 1999). Another important factor is that children are neurologically impaired (neuroglycopenia) from hypoglycemia at higher blood glucose levels (3.6 to 4.2 mmol L^{-1}) than adults (lower than 3.0 mmol L^{-1}) (Jones et al., 1995). Thus, the juvenile human body lacks the physiological capacity to buffer itself against short-term energy interruptions to its brain that can be tolerated by adults. This considerably increases the juvenile brain vulnerability to any, even short-term, interruptions in its external nutritional supply. As far as can be ascertained, no previous note has been made in the paleoanthropology literature of the extreme vulnerability of the juvenile brain to hypoglycemia following interruptions in food supply. It would seem (together with the parallel need for highly reliable food energy supply to juveniles) to be a very critical factor determining the evolution of high encephalization in humans.

2.9. Juvenile learning and neuromaturation

Brain maturation also has increased energy costs related to its close relationship to learning related feedback. This information trains cognitive abilities upon specialized neural networks in different neural areas and refining the cross-brain connectivity between them. A key feature of adult cognition is highly refined competence in assignment of credit—the ability to ask and answer why?. While this is important to social cooperation, it plays a key role in learning by enabling the brain to identify those aspects of its performance that need change from those that do not. A major aspect of initial human learning is acquiring the abilities to acquire more effective abilities to assign credit as to why a skill was successful or not. These include language and the interaction reciprocity that allows an individual to be tutored.

Performance feedback and diverse experiences are important to efficacious neuromaturation—if such experiences are limited, the capacity of the brain to acquire information processing useful to an adult's survival will be reduced. Acquiring such information however has energy costs.

The importance of learning stimulation and associated energy needs occurs with rats in enriched environments where it results in them engaging in more physical activity (Bennett et al., 1964). The IQ in human 11 years-olds links to how much they had as a child at three years-of-age sought and engaged in stimulation (Raine et al., 2002). The stimulation of education upon neuromaturation has been shown to raise IQ (Ceci, 1991) by about 2.3 to 5 IQ points for each extra year spent in school rather than elsewhere (Ceci, 1991; Winship and Korenman, 1997). Play occurs for motor skill acquisition during the peak period of synaptogenesis and their neuromaturation (Byers and Walker, 1995). Moreover, such stimulation seems to be more important for large brained orders of mammals than smaller brained ones since play occurs more often in them and is more complex (Iwaniuk et al., 2001).

As a consequence, neuromaturation has energy costs linked to physically engaging in learning experiences, or that result from doing this at the cost of missed opportunities to forage. These can potentially conflict with providing the energy needed for neuromaturation. Play, for example, can be limited by energy shortage, or the need to fully devote time to food acquisition, since it is increased in food provisioned animals (Nunes et al., 1999), and in better quality habitats that require less time for feeding (Li

and Rogers, 2004).

Such learning and neuromaturation cannot neurobiologically be brought forward so it happens earlier when the brain is supported by its mother in pregnancy or early in lactation. The optimal time for neural network training experiences occurs when the brain exists in an adult-like body (even if it is smaller such as is the case with most juvenile animals). This is because the body must have matured sufficiently to be somewhat adult-like so it can engage in adult-like behaviors. This necessitates therefore that neuromaturation takes place when the brain occupies a juvenile body, not a fetal nor infant one. As a result, such neuromaturation and learning is usually forced to be timed when the young individual is independent of maternal energy support, and so at risk of energy malnutrition (Deaner et al., 2003).

3. THE HUMAN BRAIN AND ADAPTATIONS TO EXTREME ENERGY LIABILITY (EEL)

3.1. Molecular adaptation

Energy consumption adaptations related to neural energy liability exist at multiple levels in primates. Later and separately discussed adaptations exist in regard to changes in nonneural expensive tissue (gut, skeletal muscle) body composition and food diet intake/support. However, evidence of the need for such adaptations exists at all levels including the molecular one.

The mitochondrial processing in the electron carrier molecule cytochrome c, for example, "underwent two periods of increase amino acid replacement: the first occurred early in vertebrate evolution and the second occurred at the stem of the anthropoid primates" (Grossman et al., 2004, p. 582). Molecular differences exist that are specific to humans and their brains: the human cytochrome c gene is expressed at a higher level in human cerebral tissue than in chimpanzees or gorillas (Uddin et al., 2008). Other energy related proteins, such as carbonic anhydrase II, also show regulatory changes in the adult human cortex that suggest selection has occurred to support the metabolic processes needed for evolutionarily higher neuronal activity in the human cerebral cortex (Caceres et al., 2003). The human brain, compared to that of chimpanzees, further shows the expression of transcription factors that cluster into regulatory networks that consist of two distinct but interlinked modules. One of these clusters includes among other functions many linked to neuromaturation such as axon or dendrite outgrowth, axonal transport, and synaptic transmission, while the other cluster concerns pathways linked to energy metabolism (Nowick et al., 2009).

This suggests that a major factor shaping the molecular evolution of the human brain as a primate and more recently as a Hominidae has been its exceptionally high energy utilization including that in neuromaturation. The presence of other adaptations at other levels of biology such as the proposed ring therefore is part of a wider adaptation to the peculiar energy entailments consequent to the size and body size relationship of the human brain.

3.2. Prejuvenile liability adaptation

The immature human brain has high energy needs and liability. This has been already theorized in regard to its formation in terms of the general selection and maternal inputs (Isler and Van Schaik, 2009b; Martin, 1989; Martin, 1996; Martin, 2007). Such investment in humans includes the need to provide the infant with

sufficient energy reserves to buffer against temporary energy shortages or energy utilization increase (as happen during fevers). This requires that the body mass gain that occurs in the last trimester of fetal development and in the first 18 months of neonate existence is primarily devoted to increasing adipose tissue. Human juveniles show slow growth: this is usually noted to occur after weaning since human infants show rapid increase in body mass after birth. However, slow growth in fact also characteristic of in human neonates if the contribution of adipose tissue increase is excluded. Though the argument of this paper is the key role of energy pooling for juvenile support, such support also occurs indirectly through that given to females, and this provides the energy required for the creation of neonates with such energy reserves. It is these energy reserves linked to increased brain size, rather than brain size itself (which is a relatively minor cost), that makes human pregnancy and lactation so expensive.

3.3. Cost related factors in neurodevelopment

The energy costs of brain formation are predominantly costs incurred during embryo, fetal and (if the newborn is altricial) postnatal stages involved in the formation of its neurons and axons. These costs are borne by the mother during gestation and (if a mammal is altricial) during lactation and in a few cases, food provisioning. This maternal energy supply does not generally support the total cost of neuromaturation, since this usually occurs when the animal is newly independent from its mother, and so dependent upon other adults or its own ability to provide energy for its own development. The cost of brain formation, moreover, in absolute terms, is small, compared to this latter one of neuromaturation.

Nonetheless, adaptations exist to protect the brain. Newborns and one year infants have increased adipose tissue which provides an energy reserve to buffering periods of temporary energy shortage (such as its mother being absent) and extra energy consumption such as incurred during fever.

3.3.1. Life history constraints from energy inputs

A major life history variable is the energy an animal can obtain from its own foraging or the provisioning of others. Juveniles are less successful at foraging than adults and this increases their risk mortality (Janson and van Schaik, 1993). At the onset of independent foraging, for example, juvenile red foxes, *Vulpes vulpes*, are forced to subsist upon easy-to-catch prey such as earthworms and insects that do not require well-coordinated capture skills. Since rain determines the abundance of such prey, chance factors such as weather determine survival and body growth in such young animals (Soulsbury et al., 2008). Further, in many species, young immature individuals have to compete disadvantageously with more experienced, larger and usually higher status or more dominant adults. As a result, access to food will often be reduced since a juvenile cannot fend off or compete with such adults. It has even been suggested that these skill and competition problems have selected reduced growth rate in juvenile primates as a means to reduce their metabolic need for energy (Janson and van Schaik, 1993).

A potential conflict can exist therefore between the bioenergetic needs of brain maturation and the immaturity of an animal's forging skills since the latter can result in limited intake of energy after independence (Daunt et al., 2007; Soulsbury et al., 2008).

3.3.2. Independence constraints from encephalization

The energy-neuromaturation conflict could be expected to be a particularly

powerful factor upon the evolution of neuromaturation in highly encephalized and large brained animals such as humans. This is because brain energy consumption remains a large part of the juvenile child's or adolescent's total energy budget (figures 2 and 3, for that in humans). Moreover, due to its size and numerous brain areas, large brains also at such time have more to gain from neuromaturation and continued learning. Notably, due to their greater numbers of cortical areas they have greater scope between them for small world network neuroreorganization. Such reorganization in humans is particularly active during adolescence as at this stage neural connectivity maturation shifts to creating greater segregation and integration of links between brain areas (Fair et al., 2009; Fair et al., 2008). This is only possible because human neuromaturation is so protracted. Thus, a big brained and highly encephalized juvenile with a limited ability to acquire food could be expected to fail to fully develop its potential cognition as a mature adult due to neuromaturation being curtailed by energy deficiency.

In contrast, energy independence of juvenility is not a crucial constraint upon neuromaturation in low encephalized animal species even if they have large brains (such as elephants and whales) since by the time their brains are fully formed, they will be consuming only a relatively small percentage of that animal's total energy budget. In contrast, for highly encephalized animal species, the increased per unit costs of neuromaturation will keep the brain's energy costs a major factor in its energy budget, even though at this period in its life history, its energy will have changed to less reliable nonmaternal sources. This is particularly the case where their brains are absolutely large since these need prolonged neuromaturation. In humans this continued dominance of brain energy costs during juvenility upon total body energy expenditure can be seen in figure 3 where at the age of five, 55% of such body expenditure is devoted to the brain, with it still being 30% at the age of ten. Thus, natural selection might be expected to limit neuromaturation more strongly in regard to costs, the greater an animal is highly encephalized and large brained. Evolutionarily, this creates a potential bioenergetics ceiling upon the selection of such brains. Indeed, it has been even suggested that brain size of nonhuman Hominidae is near a ceiling for further expansion without further help (Isler and Van Schaik, 2009b).

3.3.3. Vegetarianism and carnivory and life history developmental constraints

Packaging. One key biological variable upon energy availability to young juveniles is whether an animal primarily gains its energy from vegetable or animal resources. In the former, food stuffs, particularly those with large package size but low energy such as leaves, require limited skills for their acquisition and cannot be easily given to others. In contrast, for the latter, food stuffs irrespective of size will provide higher density sources of energy but to obtain them requires more highly developed hunting or scavenging skills. (The latter might be carnivory or hypercarnivory [no alternatives to meet]; the difference between omniovority and carnivority is that the latter involves locomotive, butchery and skill specializations for meat acquisition—a fox may eat vegetation but unlike a pig that might animal flesh it also adapted to chasing, capturing and breaking apart prey.)

Immature skills. Carnivory because it requires expertise that only is acquired after practice needs the food support of juveniles since young animals after lactation lack the effective hunting skills of mature animals. This necessitates a period of support either by its mother (in non social carnivores) or cooperative helpers (as in social carnivores). This leads carnivores to distribute food sources either by regurgitation or

carrying it to their young. In the latter case it requires they have sufficiently large "package" size to be carried. This point is important in the context of humans since human hunter-gatherers only share foods of large package size gained from butchered animals. Food of smaller size such as gathered fruits, and other vegetable matter is not (Kaplan and Hill, 1985).

Human evolution. Humans arose from australopiths that show dental and isotope evidence of being primarily vegetarian (Spoonheimer et al., 2006; Strait et al., 2009; Teaford and Ungar, 2000) like other nonhuman Hominidae (Milton, 2003). Homo, moreover shows anatomical adaptations, isotope and other evidence of a shift to a partial meat based nutrition (whether scavenged or hunted) (Braun et al., 2010; Foley, 2002; Milton, 2003; Stanford, 1999). Ecologically, this makes Homo akin to social carnivores such as lions (Schaller and Lowther, 1969) and wolves (Hall and Sharp, 1978) and omnivorous Callitrichidae primates (Hrdy, 2009).

3.3.4. Allomaternal juvenile provisioning and life history variables

Allomaternal help is another factor affecting energy availability for juveniles such as being raised by pair bonded parents (paternal assistance) or group support (allohelpers) (Hrdy, 2009; Isler and Van Schaik, 2009b). Such allomaternal help in terms of food provisioning depends upon the acquisition of foods that are high energy and packageable and so sharable.

3.4. Brain Malnutrition Risk Hypothesis

The "Brain Malnutrition Risk Hypothesis" (Deaner et al., 2003) has linked the issues of energy support needs of juveniles to the survival situation of their brain. It identifies energy constraints upon the evolution of large brains through increased risks upon survival as such enlargement leads to greater energy consumption in the context of the limited ability of juveniles to acquire energy making them "highly vulnerable to temporal dips in the energy supply". To reduce this survival risk, the "Brain Malnutrition Risk Hypothesis" identifies that they have large body mass as neonates and or are raised with allomaternal support in cooperative breeding. This theory expands upon an already existing theoretical literature upon the question of how maternal energy provided to offspring determines the size of neonates and their brains (Isler and Van Schaik, 2009b; Martin, 1989; Martin, 1996; Martin, 2007) (fig. 1. A), and the question of how adult brain size (which links to its neonatal brain size) affects the capacity for social bonding and cooperation (Dunbar, 2009; Shultz and Dunbar, 2007) and cognitive abilities (Deaner et al., 2007; Sol, 2009). Large brains need extra energy and this has been proposed to arise from a reallocation of it from other high energy consuming tissues (Isler and van Schaik, 2009a) such as the gut (Aiello and Wheeler, 1995) and skeletal muscle (Isler and van Schaik, 2006; Leonard et al., 2003) (fig. 1. B), together with a higher quality diet (Fish and Lockwood, 2003; Leonard and Robertson, 1994). Moreover, a correlation using multiple recession and independent contrasts has been found between greater encephalization in primates and increased duration of juvenility (Barrickman et al., 2008). The "Brain Malnutrition Risk Hypothesis" (Deaner et al., 2003), expands upon this work by noting the energy problems of the juvenile brain given its size and the limited ability of juveniles to acquire energy.

However, Brain Malnutrition Risk Hypothesis as presented proposed fails to integrate into this analysis the special energy needs of juveniles linked to the neuromaturation of adult cognitions and how these in turn play a critical role in creating

the circumstances by which malnutrition risk is not encountered by human juveniles. This review seeks in part to address this omission. The evidence for this exists but requires a detailed account of the energy costs involved in neuromaturation and how this result in juvenile energy liability.

4. PROLONGED EXPENSIVE NEURODEVELOPMENT (PEND)

4.1. Why the prolongation of PEND is theoretically important

Neuromaturation in humans not only increases energy liability but also causes this period of vulnerability to be prolonged. This makes it evolutionarily a potential problem since it keeps an individual at risk to energy shortage for an extended duration.

Arguments have already made by others that immaturity and its protraction in animals, human and nonhuman, is in general terms advantageous for acquiring cognitive abilities (Bjorklund, 1997; Joffe, 1997; Johnston, 1982; Pagel and Harvey, 1993; Pereira and Altmann, 1985; Walker et al., 2006). Further, the duration of juvenility (which associates with neuromaturation) is protracted in primates and associates instead of cognition acquisition with increased brain size (Charnov and Berrigan, 1993). It has been suggested for example that due to the slow growth of primates "energy demands for growing and supporting big brains ... the long primate lifespan follows from the cost, rather than some cognitive benefit, of having a big brain" (Charnov and Berrigan, 1993: p. 193). It is argued here that prolongation of neuromaturation is not necessary to large brains rather that large brains due to their greater size gain a potential for cognition that for its acquisition depends for its realization upon extended neuromaturation. It is thus possible that large brains could have a shorter period of neuromaturation but this would be at the cost of not acquiring the cognitive competences which it might acquire. Since large brains have a large adaptive cost in regard to increased energy intake needs, selection for large brain in regard to such the cognitive capabilities that offset them will require a prolonged neuromaturation—otherwise adults will not be advantaged to develop them.

4.2. The problem of neuron large brains and learning

The human brain is unique in containing a very high number of neurons in a compact volume. That is due to humans having the largest primate brain. Brain expansion in primates scales with increased neuron number in a particularly economical manner (Herculano-Houzel, 2009)—to the power of $10^{1.056}$ rather than $10^{1.55}$ as in rodents—so giving large primate brains high rather than low neuron density (Herculano-Houzel, 2009). One of the reasons for this is that primates are arboreal living animals and so at risk for brain injury and concussion following falls. Evidence suggests that such injuries can be frequent and that their impact upon the brain is linked to brain size. Limited brain size expansion with increased neuron number would also be advantaged since concomitant increase in head size might impair head movements.

As a result of this difference in scaling, a rodent brain of human size would have 34 kg mass. This is important since increases in neuron number links to increased needs in connection neurons both locally in areas (their number increases with neuron number) and between areas. Compactness is important since this reduces the length distance across the brain and so time delays in neural communication between separated brain areas over which such connections are made.

Two central scaling constancies in brain structure are invariant area-infiltration

(the connectivity invariance between neuron links in a local brain area) and invariant area-interconnectedness (the connectivity invariance of links between neurons in different areas) (Changizi, 2006). The number of synapses on neurons increases with to the 1/3 power with brain size (Changizi, 2009). Connectivity of neural networks within areas and for network formed across between such areas is under selective pressure to have an invariant degree of interconnectedness to the square root of the number of neurons (Changizi, 2009). This creates a need for selecting "economical well-connectedness" provided by connection economical small world network attributes.

Identifying these interactions faces a fine-tuning task that increases with to the size of the network being refined. As a result, it requires their brains to have a more prolonged and elaborate neuromaturation. Since synapse and myelination neuromaturational are energy expensive, high neuron number brain thus require prolonged expensive neurodevelopment to acquire their full potential information processing abilities.

There are two broad issues in regard to how the complex and species specific cognitions of humans might be the result of such prolonged human neuromaturation.

Neuromaturation increases neural information processing capabilities by refining local networks and reorganizing their connectivity across the brain. Therefore, increasing the duration of neuromaturation could be evolutionarily crucial since it allows time for changes in connectivity reorganization across the brain to feedback and modify earlier network refinement. This could create new development stages that can build upon each other thus enabling novel types of cognitive capabilities while increasing the information processing competence in already existing ones.

Heterogeneity of neuromaturation is important. If refinement and reorganization occurs in a short period then it will be forced to happen near-synchronously in different cortical areas. But if it is prolonged, the opportunity arises for differentiated timing and so complex patterns of interactions of development across the brain that might result in the ability to acquire more sophisticated adult information processing competences. Such differentiation of neuromaturation would create enhanced cognition through the addition of extra stages to cognitive development, and the sequencing of maturation (sensory before higher cognition ones that then can modify sensory ones). If these spatial temporal patterns of area maturation across the brain were inheritable, particularly effective maturational patterns could be selected, thus advantaging further prolongation of the neuromaturation period.

One reason for prolongation is the acquisition of skills that can feedback and refine and enhance already developed cognitions. One key factor upon learning is assignment of credit by which the particular aspect of a performance can be linked to the component or factor that affected it. Effective assignment of credit allows accidental factors to be disregard from interfering in learning with attention being confined to those that have the potential to improve cognition. For example, a hunting throw that misses an animal target because the animal was frightened by another animal unrelated to the hunting performance should be ignored but one that links to a failure to aim with sufficient distance requires adjustment of the throw timing in regard to perceived distance between the arm and the target. Several factors enhance and refine assignment of credit and they develop after initial cognition. Important factors are executive skills that enable multiple factors to be analyzed separately from each other. Another is the

ability to identify and ignore peripheral or salient but irrelevant factors and the ability to isolate and control subaspects of cognition. A major factor outside the brain is communication as this allows the experience of better skilled individuals to identify factors that need or not to be attended.

4.3. Network function and neuromaturation

Research upon artificial neural networks shows that network connections modified with appropriate training (Buonomano and Merzenich, 1995; Hopfield, 1982; Maass et al., 2007; Rumelhart and McCIelland, 1986) enable diverse information processing competences, including those needed for sensory and motor processes (Guigon et al., 1994) and also for complex cognitions, including those that are human specific such as syntax (Elman, 2005). Fundamental to this refinement is that it occurs in an enormous maturational "space" of possible patterns of connections, some of which create effective information processing, but most do not. The realization of diverse functions depends upon finding the effective information processing connections within this realm of sparse connectivity (Felch and Granger, 2008).

In the brain such network refinement depends upon the synaptic pruning that "rewires" the local area neural networks formed between neighboring area neurons (Chklovskii et al., 2004; Le Be and Markram, 2006). The size of the potential information processing space for connecting up neurons that needs to be explored is enormous: synapse pruning even without significant growth of axonal or dendritic arbors allows neuron rewiring changes of 3-4 bits per synapse and so $\approx 9 \times 10^4$ bits per dendritic arbor (Chklovskii et al., 2004). With the growth of new axonal and dendritic branches (as when the neuron is developing) its rewiring potential with other neurons could be 23 bits per synapse and so $\approx 6 \times 10^5$ bits per dendritic arbor (Chklovskii et al., 2004). The informational storage capacity of each neuron's arbor synaptic connections has been modeled as being as high as 2.7×10^4 bits (Poirazi and Mel, 2001). This opportunity for refining neural network connections allows for neural network information processing capacities to be enhanced provided the right connections are found and established.

Neural networks therefore might have in theory considerable computational potential. But this is only a sufficient factor: due the vast development space in which it exists, its actual realization in any maturing brain is far from necessary—or even probable. The right connections need to be discovered. This makes the effectiveness of learning processes and learning experiences that explore this space central to the quality of neuromaturation as they act to select the most efficacious network connections for doing information processing. Without this learning aided identification of synapse connections, there can be no optimal pruning or modification of them (Barbato and Kinouchi, 2000). How learning contributes to this pruning and selection in neuromaturation is far from a trivial problem. It is reasonable, however, to suggest that it is advantaged by extending its period of duration and so allowing more elaborate processes of development that can better explore and so exploit the computational potential "hidden" in neural networks.

Some evidence for this comes from expert skills. These exist in a wide range of activities such as chess and instrument playing. What is notably about expertise is that its acquisition requires prolonged (ten year) daily (several hours) deliberative practice (Ericsson and Lehmann, 1996). Such expertise correlates with area linked volumetric changes in the cerebral cortex gray and white matter (Elbert et al., 1995; Schlaug et al.,

1995). Crucially, such volumetric changes are greater the earlier such deliberative practice starts—whether childhood or later—in a young individual's neuromaturation (Elbert et al., 1995; Schlaug et al., 1995).

4.4. Neural network connectivity maturation and complex cognition

In addition to synapses joining neighboring neurons into local networks, axons connect such networks with other local neural networks and networks in distant brain areas. This "enbrains" local networks (Mareschal et al., 2007) while creating an integration and segregation within the brain of its functional and anatomical cross-brain connectivity.

Integration here involves the capacity of the brain to combine different localized functional abilities together into more complex cognitive capabilities, while segregation/differentiation concerns its capacity to isolate particular localized abilities from less relevant ones so they can be combined in an optimal manner (Dosenbach et al., 2008; Fair et al., 2008; Fair et al., 2007). The organization of neural network connectivity across the brain is a topic of considerable recent theoretical and empirical investigation. Properties studied in such connectivity include self-similarity (Bassett et al., 2006; Bullmore et al., 2009), critical cascades (Bullmore et al., 2009), modularization (Bullmore et al., 2009) and small world attributes such as clustering coefficient, path length connectedness and degree density of network connectivity (Bullmore and Sporns, 2009; Bullmore et al., 2009; Watts and Strogatz, 1998). The human brain shows a strong capacity to create such small world connectivity attributes in its integration and segregation, not only anatomically through axons, but also functionally through synchronization, clustering and coupling of networks activation at multiple frequency bands (Bassett et al., 2006).

The maturational efficiency of network connectivity links to such cross-brain segregation/integration network properties with the brain being efficient when its "components show simultaneous evidence of independence in small subsets and increasing dependence in subsets of increasing size" (Tononi et al., 1994, p. 5034.). People with brains in which its connectivity shows shorter small world network path length and a higher global efficiency have higher intelligence (Li et al., 2009). Another factor aiding efficiency is when groups of areas show "dense intrinsic or intramodular connectivity and relatively sparse extrinsic or intermodular connectivity" (Bullmore et al., 2009, p. 1131.). Related ideas have been suggested by child psychologists about cognitive development occurring through "integration and dissociation" (Johnson and Munakata, 2005, p. 155).

Such integration and segregation of connectivity (and how it changes with neuromaturation and increased cognitive competence) can be detected from the analysis of functional imaging of brain area activations. Neural interactions across the brains of 7-9 years-of-age children compared to adults are not so functionally segregated and integrated (Fair et al., 2008; Fair et al., 2007). These are more dominated by short-range functional connectivity than long-range functional connectivity (Supekar et al., 2009). Also compared to adults, their primary sensory, association and paralimbic areas are more connected with subcortical areas while less strong connections exist between cortical areas (Supekar et al., 2009). Adults in semantic and syntactic tasks activate specific areas in the superior temporal gyrus and frontal operculum while 5 and 6 year old children engage in large overlapping activations while also recruiting further additional areas (Brauer and Friederici, 2007). Such changes relate to enhancement in

cognitive abilities. For example, people having high performance under cognitive overload (compared to those with low performance) have the ability to restrict the spreading of local area activity beyond that required by a task (Jaeggi et al., 2007).

Another age competence related process that can be observed is that of a higher level hub control by which areas including the prefrontal and cingulate cortices organize integration and differentiation (Fair et al., 2008; Fair et al., 2007). Such hub regions develop later than the ones that they coordinate (Gogtay et al., 2004; Huttenlocher and Dabholkar, 1997; Lenroot and Giedd, 2006; Shaw, 2007; Shaw et al., 2006; Shaw et al., 2008) and degree of their development links to IQ (van den Heuvel et al., 2009). The development of response inhibition skills in adolescents links to connectivity changes that replace local focused processing with fronto-parietal integration (Stevens et al., 2009). EEG studies also find that after the age of four and until adulthood that an increase happens to integration of local domains with a parallel increase in differentiation in their long distance connections (Thatcher et al., 2008). With increasing maturity, these changes in the frontal lobes occur with increases in long distance connectivity to the posterior areas of the brain (Thatcher et al., 2009).

Complementary to these neurological changes, research upon human cognitive maturation inspired by the ideas by Jean Piaget (1952) identifies that human cognition develops in stages. Initially, child development refines early sensory-motor functioning. Then as these functions mature into adolescence, they get cognitively extended by symbols and representations, and then later enhancement by strategic control made possible by metacognitive abstractions/awareness (Fischer, 1980; Karmiloff-Smith, 1986; Mareschal et al., 2007). The relationship of these to neuromaturation at present is unknown but it would appear that the existence of such developmental stages is permitted by the having an extended period of synaptic and connection immaturity.

4.5. Language and neuromaturation

Language is the chief informative means of communication in the extant human species. It is evolutionarily unique to humans and could provide novel opportunities if given sufficient developmental time to affect neuromaturation and so neural network refinement and connectivity reorganization.

- This is because in addition to enabling external communication, human language also supports other information processes such as internal "private speech". This internal cognitive process has an ability to reorganize brain function and so its development. For language to effect the brain, however, in this way requires that neuromaturation is increased in duration both to allow for language abilities to develop, and also to give it an opportunity then to reshape cognitive development.

- Language allows for the refinement and the reorganization of the brain to be changed by external experience that enters the brain from or with the aid of descriptive language, both in the form of tuition, and more generally in the form of culture. In both cases, such effects would be advantaged by the prolongation of neuromaturation and cognitive development.

4.5.1. Language and brain changes

Language is unique to human neurobiology. It contains diverse subcomponent processes related to production and perception involving syntax, semantics and

pragmatics. These language components are spread across the brain. In the cerebral cortex they occur in the inferior frontal (Broca's area) and superior temporal (Wernicke's area) regions and elsewhere such as the basal temporal region (Luders et al., 1991) and insular (Dronkers, 1996). Subcortically they occur in cerebellum and basal ganglia (Booth et al., 2007). An added level of complexity is that homologous areas in the right and left hemispheres make different contributions to language processing (Berman et al., 2003; Lindell, 2006). Language development could be expected to depend upon extended human neuromaturation to enable the connection refinement between such areas—indeed the pathway between the Broca's area and the Wernicke's area matures strongly during juvenility (Brauer et al., 2010; Friederici, 2009). Significantly, this pathway is one that is poorly developed in nonhuman primates (Friederici, 2009).

Language involves expertise in many subskills several of which continue to mature into adolescence and up into adulthood. This applies to even those abilities that are apparently simple such as the kinematics of speech production (Smith and Zelaznik, 2004) and the planning of sentences (Sadagopan and Smith, 2008). However the most critical neuromaturation of language is tied particularly to changes before puberty. Deaf children (6–8 years-of-age) exposed to language can show normal syntax as adults but not when they acquire language at older ages (9–13 years-of-age) (Mayberry and Lock, 2003). The ability to learn a new language without a foreign accent also changes: 68% of children between 1 and 6 years-of-age achieve a near-native pronunciation but this drops to 41% between the ages of 7 and 12, and is only found in 7% of children after the age of 13 (Asher and García, 1969). A sensitive period exists after auditory deprivation in which cochlear implants can lead to normal neural responses to speech that ends between 3.5 and 7 years-of-age (Sharma et al., 2002). Parallel to these age effects are ones in the maturing brain. Brain pathology after the age of five has a much greater effect upon language than that acquired before this age (Liegeois et al., 2008; Mariotti et al., 1998). Learning two languages when young uses the same brain areas but learning a second one after 11 years-of-age results in separated development in the Broca's language area (Kim et al., 1997).

4.5.2. *Language direct impact upon neuromaturation*

Language itself plays a critical rile in the neuromaturation of the brain since neural networks do not only mature in respect to external stimulation but also internally in terms of language stimulations created by the brain itself—particularly as human children grow older and more language immersed. Stanley Rapoport has for example noted the existence of a top-down stimulation upon the brain from idea generation and attention that can "stimulate widespread brain association areas . . [and so] synaptic stabilization secondary to adaptive thought processes . . New primate species may create new cognitive, social or cultural stresses which in turn can accelerate brain evolution" (Rapoport, 1999, p.160). This adds to the human neuromaturation learning experiences that result from direct interaction with the environment.

Such internal stimulation might be particularly important if it aided the integration and differentiation of the human brain's large number of cortical areas. Though language is usually discussed in terms of enhancing interpersonal communication, language also has been found to provide internal cognitive scaffolding (Luria, 1979; Vygotsky, 1986). A related idea is that language provides a "cognitive niche" or a "material scaffolding" (Clark, 2006). Such internal language organization

takes place in what is variously called "private speech" or "internal speech" which coordinates and activates thought and mental processes (Sokolov, 1972).

Language through such developmental processes modifies human cognition in diverse and only partially understood ways. Spatial words enhance spatial perception (Pyers et al., 2010), and languages that describe objects in relative coordinate spatial frameworks, compared to doing so in absolute terms, reshape in this manner, spatial perception (Majid et al., 2004), and tense description words structure likewise the temporal perception of events (Boroditsky et al., 2002). Functional imaging shows that language even shapes low-level perceptual cognition such as decision processes in the visual cortex (Tan et al., 2008), color discrimination (Ting Siok et al., 2009) and nonverbal perceptual processes in regard to size and color categorization of objects (Lupyan, 2009). Jerison in his ideas about intelligence and brain size (Jerison, 1973), attributed a key role of language also to the maintenance of "perceptual invariance", as do other authors in regard to perceptual categorization such as Harnad (Cangelosi and Harnad, 2000). If children are not exposed to intentional state words—such as want, know or believe—this subsequently impairs and delays their ability to interpret other people's behavior in terms of them having "minds" (Peterson and Siegal, 1995; Pyers and Senghas, 2009). In the special case of written language, the internal experience of words created by literacy also shapes the functional organization of the brain (Castro-Caldas et al., 1999; Petersson et al., 2007). These phenomena suggest that language strongly affects the development and so the neuromaturation of processes across the brain, even down to the level of remolding the functional capabilities of the primary sensory cortices.

4.5.3. *Language indirect tuition impact upon neuromaturation*

This affect of language upon the brain happens in addition to its use in communication that aid tuition and the cultural transmission of cognitive skills. This communication use of language creates additional paths by which it can impact upon neuromaturation. The neural networks of the brain in neuromaturation as a result are in multiple ways "enlanguaged" (Mareschal et al., 2007).

For language, however, to have this impact upon neuromaturation, its period of duration must be protracted, as found in humans, to allow both for language acquisition itself, and for sufficient time for it then to modify the refining and reorganization of the brain, its maturing neural networks, and their cognitive abilities.

Reading and writing are language extended cognitive skills acquired in childhood. Such literacy skills, cannot be entirely separated from the effects of "schooling", the learning environment in which reading and writing is normally acquired by contemporary juveniles.

Brain imaging upon groups that differ only in regard to literacy and schooling (daughters that for social-cultural reasons did and did not receive primary education) shows that it links to volumetric changes in the white matter connections between the cerebral hemispheres (Castro-Caldas et al., 1999; Petersson et al., 2007) and the inferior parietal/ parietotemporal regions (Petersson et al., 2007). Individuals that acquire literacy as adults show different patterns of brain change than those that occur in children (Carreiras et al., 2009). These physical changes associate with functional connectivity differences in the cerebral hemispheres (Petersson et al., 2000). Consistent with these findings is that the extent of a person's education (whether less than high school, high school, or university) links (the direction of causation is not known) to

dendrite differences (more extensive higher-order branching in those with higher levels of education) (Jacobs et al., 1993).

The impact of education upon the brain during its neuromaturation is also suggested by its changes to white matter microstructure measured by fractional anisotropy, as this provides a protective reserve against Alzheimer's Disease (Teipel et al., 2009). The thinning of the cerebral cortex also in those with Alzheimer's Disease needs to be of greater degree before dementia starts in those with longer (17.4 years) than lower (12.6 years) periods of education (Querbes et al., 2009) suggest education interacts in some unknown but future protective manner in the young brain upon its neuron and neuropil development.

5. HUMAN NEUROMATURATION AND CHIP

The human brain related to its size/neuron number and high EQ, also has unique adult cognitive capacities—both species specific, such as syntax based language, and more generally, the capacity for intelligent behavior and abstract/flexible thought that is usually referred to as complex cognition (Just and Varma, 2007) or "intelligence" (Jerison, 1973). This is consistent with the finding that increased brain size across animal species usually results in them having increased cognitive abilities (Deaner et al., 2007; Jerison, 1973; Lefebvre and Sol, 2008; Ricklefs, 2004; Sol, 2009). Moreover, this link, exists to some degree among human individuals as variations in adult human brain size correlates moderately with IQ (r ≤0.51) (Andreasen et al., 1993) (but for a more complex view, see (Skoyles, 1999)). Indeed, Darwin noted, "No one, I presume, doubts that the large proportion which the size of man's brain bears to his body, compared to the same proportion in the gorilla or orang, is closely connected with his higher mental powers" (Darwin, 1871, p. 74.). It is not unreasonable therefore that greater human encephalization and human cognition should link (Sherwood et al., 2008).

Recently, neuroscience has begun to support a connection between neural network changes during human neuromaturation, and the enhanced cognitive capabilities of the human species relevant to indirect reciprocity and cooperation including language.

Human neuromaturation until recently was difficult to investigate directly since it involved either autopsy samples (for synapse estimates) or PET radionuclide tracers (direct measurement of metabolism) that can only be used in rare circumstances upon children and adolescents and their brains. The limited research that has been done shows that changes in synapse quantity (Glantz et al., 2007; Huttenlocher and de Courten, 1987) and energy consumption (Chugani et al., 1987; Muzik et al., 1999) occur in an invert U pattern across childhood and adolescence (low until 3 to 4 years-of-age, peaking around puberty and declining to adult levels during adolescence).

Volumetric MRI, a recent technology provides a proxy to such changes and can be done routinely upon brains in young people. This shows that volume changes to gray matter, like with synapse numbers and metabolism, has an inverted U trajectory of initial increase followed by decline (Lenroot and Giedd, 2006; Shaw, 2007; Shaw et al., 2008; Sowell et al., 2002).

Further, this MRI research establishes that these trajectory changes across the brain occur most elaborately in those polysensory and high-order association regions that have expanded in human evolution (Shaw et al., 2008). These polysensory and high-order association regions are also the areas that underlie the cognitive capacities

that have developed the most in human adults, including many of which are unique to humans such as language.

The acquisition of superior cognition, moreover, depends upon the shape of the thickening and thinning trajectory that occurs in different brain areas. Human specific information processing capabilities—at least in so far as such capabilities are measured by higher test scores on subtests in the Wechsler intelligence scales assessing verbal and non-verbal knowledge and reasoning correlate with a later and bigger peak in frontal cortical thickness (Shaw, 2007; Shaw et al., 2006; Shaw et al., 2008). This suggests human neuromaturation occurs with a particularly complex hierarchical unfolding of cognitive information creating stages in different areas happening at different ages.

A general factor is that human cognitions are not discrete skills that are acquired in a expert form but develop considerably with experience. Judgment, the ability to communicate and the ability to act appropriately can be more or less experienced. Humans show a marked capacity to refine their cognitive capacities and this links to neuromaturation.

6. JUVENILE EXTENDED ENERGY PROVISIONING (JEEP)

6.1. Unconstrained energy and human juveniles

Humans amongst primates are unique in several respects with regard to the availability of their juvenile's energy input. First, human adults engage in the foraging, scavenging and hunting of high energy food sources (Foley, 2002; Milton, 1999; Stanford, 1999) since at least 1.95 million years BP (Braun et al., 2010). Second, humans give such high energy foods to their young in an extended support that ceases only with adulthood. Colloquially this situation is referred to by identifying human children and adolescents as "dependents" (Kaplan, 1994). Though such energy dependency exists for modern humans, it is particularly important for human juveniles in simple hunter-gatherer bands, the ecological state in which the human species arose (as detailed in fig. 4). It is a form of allomaternal energy support (Hrdy, 2009).

In comparison, chimpanzees and other apes (Hominidae), the closest extant biological relatives to humans, although providing energy investment in their offspring, lack a human-like energy supported dependency stage. Nonlactational support to the juveniles of chimpanzees and other apes is limited as mothers rarely give food or only allow it to be "thieved" (Jaeggi et al., 2008; Nishida and Turner, 1996): "food scraps are given and difficult-to-process food rather than easy-to-process food is more likely to be taken" (Nishida and Turner, 1996).

The energy support with which human juveniles are provisioned, moreover, is biologically substantial. Following the ending of lactation human juveniles receive a large ($\approx$3.5-7 MJ day^{-1}), and extended ($\approx$15 years) energy provision that totals by the age of 18, 41×10^9 J, (Kaplan, 1994, pp. 760-763). Figure 4 details the marked contrast between energy consumption and energy production between chimpanzees and hunter-gatherer foragers during maturation from birth into adulthood. Human support is also biologically novel in the priority given to satisfying juvenile rather than adult needs, the reliability and the quality of its food stuffs (such as food preparation (Wrangham and Conklin-Brittain, 2003), and the dietary availability of the long-chain polyunsaturated fatty acids that make up neural membranes (Milligan and Bazinet, 2008). If humans are uniquely exposed to the risk of brain malnutrition, then it is also the case that they are also uniquely protected by adult food sharing from such malnutrition.

Skoyle

female energy consumption and production with age

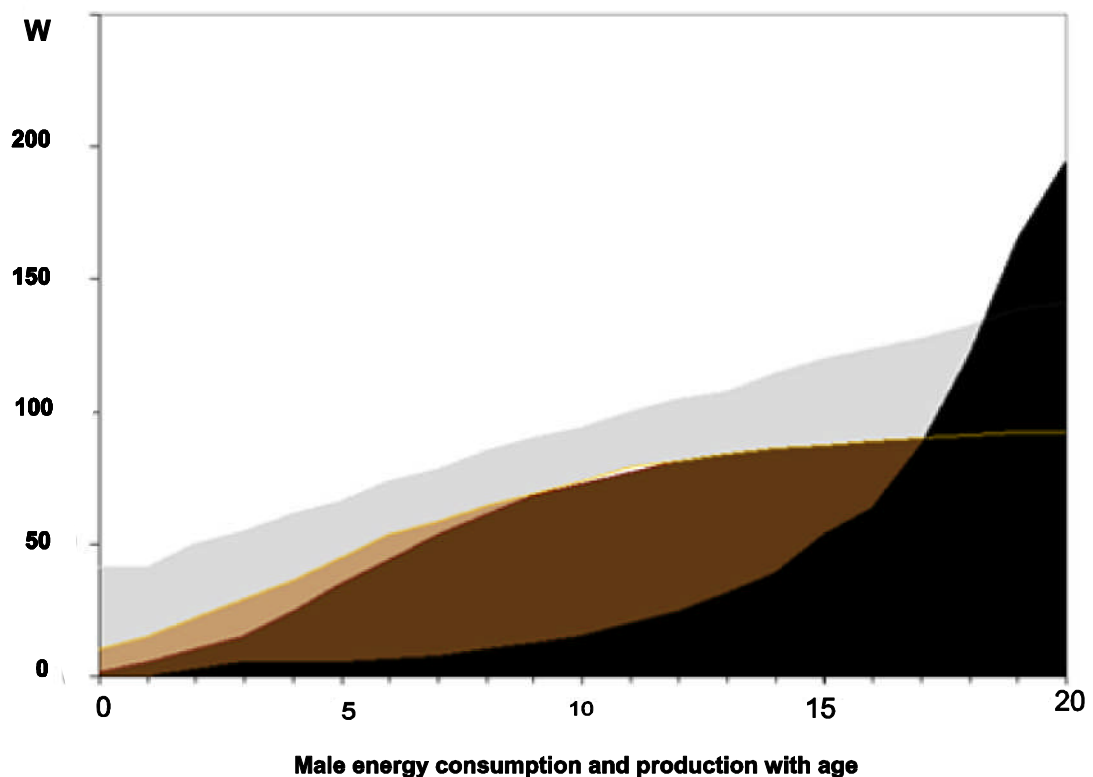**Male energy consumption and production with age**
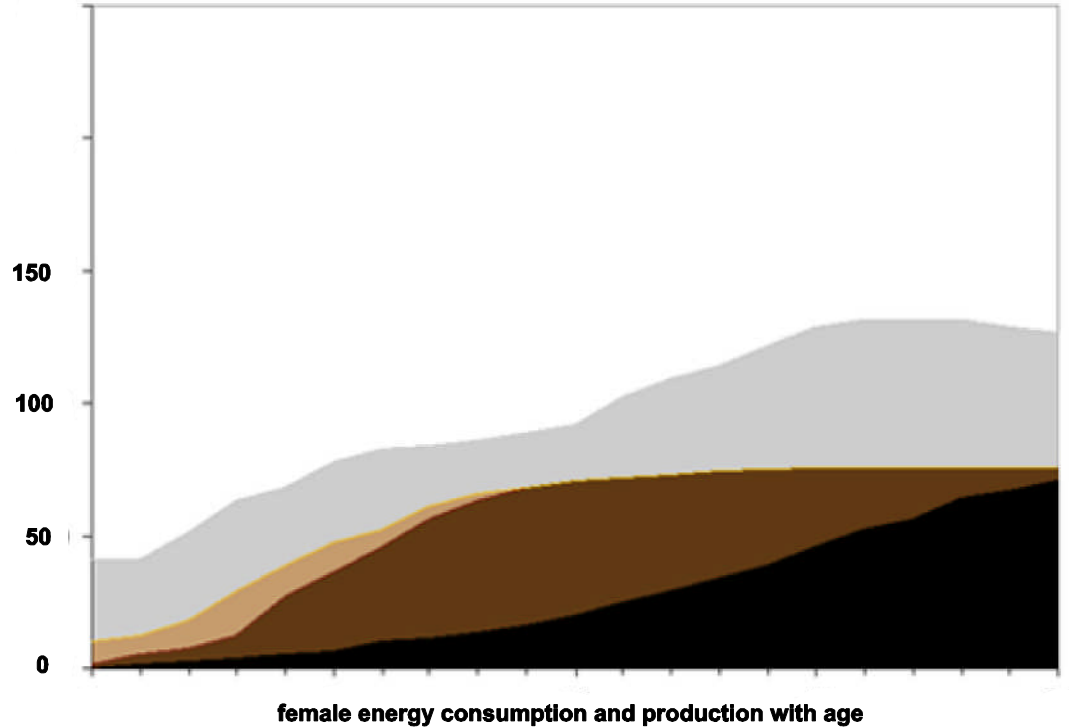
Fig. 4. The energy consumption and production of humans and chimpanzees is illustrated as it changes between birth and 20 years-of-age (females top panel, males bottom panel). The graph curves have been filled in so they appear as a "landscape" of "slopes". Humans are the very light gray (consumption) and the black (production) filled in graph slopes; chimpanzees the light brown (consumption) and the dark brown (production) ones. Energy is shown in watts to be uniform with the other graphs. Humans (very light gray) receive much more energy initially but chimpanzees (light brown) (which are slightly smaller) begin to catch up by 8 years-of-age, but this is due to their own energy production (brown) which is not the case in humans (black). Energy production only comes to equal energy consumption for men at 18 years-of-age, while for women this is delayed until 45 years-of-age when they cease to be mothers of dependent children (off graph). Based upon human data averaged for the Ache, Hiwi, and Hadaza hunter-gatherer bands and chimpanzees (Kaplan et al., 2000, fig.3).

6.2. **Human cognition, cooperation and energy provisioning**

Anthropologists find in human hunter-gatherer bands that the human dependency stage and its allomaternal energy support exists due to group food pooling behavior (Kaplan, 1994; Kaplan et al., 2000). This communal food sharing results in food being provided to all children and adolescents of a hunter-gatherer band (Kaplan, 1994; Kaplan et al., 2000; Lee, 2008). This sharing of hunted food, moreover, is only slightly biased, with a hunter's own family getting no more than a somewhat greater allocation of large kills: "successful hunter's household took, on average, about 5% of the meat from large prey weighing < 180 kg, and about 10% of the meat from prey weighing >180 kg. Other men's households took, on average, about 5% each" (Hawkes et al., 2001, p. 124.). Paleoanthropology suggests that such food sharing behavior to dependents existed at least as far back as 530,000 BP, as attested by the remains of handicapped individuals with congenital craniosynostosis (Gracia et al., 2009). Such disabled individuals could have only survived if they were provisioned with food (Gracia et al., 2009; Hublin, 2009).

Human food pooling is based upon egalitarianism, collaboration between nonkin—and critically—indirect reciprocity. In indirect reciprocity (also called third party altruism) exchange of help is not direct such as in 'You scratch my back, and I'll scratch yours', but mediated through third parties, "I help you and somebody else helps me" (Nowak and Sigmund, 2005). Indirect reciprocity is particularly useful for an animal—such as humans when hunter-gatherers—engaged in finding patchy widely dispersed high energy foods since such reciprocity allows the minimization of risk by the collective pooling of individual success and failure in obtaining such foods. It also is incompatible with dominance and submission relationships. The ability to sustain indirect reciprocity in a hunter-gatherer band is linked to human species specific cognitions—such as language, intent perception and executive functions—as these monitor, communicate and adjust people's reputation in terms of cooperation evaluations (Sanfey et al., 2003; Sommerfeld et al., 2007) such as "image scoring" (Nowak and Sigmund, 1998) and "good standing" (Sugden, 1986).

Descriptive communication is particularly important since it creates the descriptive social discourse that links a person's reputation to their cooperative behavior (Kaplan, 1994; Kaplan et al., 2000). In one hunter-gatherer band 56% of conversations involved norm enforcement criticisms, of which 49% concerned sharing or obligations (Wiessner, 2005). The community reputation needed to make such indirect reciprocity stable against free riders, moreover, depends upon the accurate ability to monitor sharing behavior (Rockenbach and Milinski, 2009). In humans, richly descriptive language does this through "gossip" which promotes and demotes an individual's social status depending upon how far their behavior is cooperative (Sommerfeld et al., 2007). Thus, descriptive communication and assessment of cooperative context has a key biological function since it socially enforces the communal cooperation that underlies the prolonged energy support received by juveniles that makes human neurodevelopment metabolically viable.

Indirect reciprocity makes food pooling in humans to juveniles distinct from the allomaternal help found in social carnivores and Callitrichidae. Human allomaternal help does not aid the offspring of a few dominant reproductive females but is entirely devoted to offspring of all reproductively capable females. This is because of the incompatibility of indirect reciprocity with power differences creates "nutritional

homogeneity" (Sherry and Marlowe, 2007). Human hunter-gatherer foragers lack within group variations in body mass index and percent body fat (except those linked to gender) (Sherry and Marlowe, 2007), and the growth of children is similar, irrespective of the advantages possessed by their parents. In foragers, "kin groups, some more powerful than others either in influence or in sheer number, were not able to gain superior access to resource and then divert them to their own children" (Daper and Howell, 2005, p. 280). This situation contrasts with other Hominidae that not only lack allomaternal help but also have marked individual differences, particularly as juveniles, in mass related to their own or their mother's ability to acquire foods, together with their mother's dominance status (Pusey et al., 2005).

6.3. Egalitarian and ranked cooperative breeding

The novelty of human food pooling is shown by its difference to the allomaternal help provided by Callitrichidae. Both primates are omnivores. But Callitrichidae do not face the neuromaturation ceiling since their brains are small and development is rapid. The largest Callitrichidae, the golden lion tamarin weights 0.7 kg while it brain weight is unknown that of marmosets weighing 0.361 kg is 7.78 g (Herculano-Houzel et al., 2007). Female Callitrichidae ovulate and can conceive by 12-17 months and males are sexually mature by 15-25 months (Digby et al., 2007). Moreover, their cooperative breeding aid is focused usually upon the offspring of a single dominant female and it helps her increase her reproduction by decreasing her inter birth interval, reducing her period of postpartum estrus, and providing her with extra birth numbers by twinning. Most females are not reproductive and while showing allomaternal care also engage in infanticide against the same offspring though this is many against the offspring of subordinate females (Digby, 2000; Digby et al., 2007). Human allomaternal care in contrast occurs for a species with a brain that requires a prolonged neuromaturation. The energy is there to be invested in it since it is shared amongst reproductive equals. As a result, it supports mostly the prolonged juvenility required by this neuromaturation (it also allows a slight shortening of the interbirth interval).

The existence of allomaternal food sharing raises the question of whether Hominidae neuromaturation contains the evolutionary opportunity to be enhanced if it receives greater juvenile energy support. Such an opportunity is theoretically important since such enhancement by creating cognitions descriptive communication and awareness of intent that support indirect reciprocity and social cooperation.

Allomaternal help in other animals involves several processes but not it seems cooperation even though cooperation can occur in other contexts. Though human allomaternal care has been described in terms of sharing a common prosociality with other animals, human sociability is distinct in involving highly skill theory of mind ability as to the motivations, beliefs and perceptions in others including second and higher order ones. While some elements of the theory of mind are found in chimpanzees they do not enable cooperation particularly over food (Skoyles, 2011). Only humans existence in cultures based upon shared intentionality. This raises the possibility that more prolonged neuromaturation has increased cognitive capabilities in humans, and that these enhanced capabilities support the cooperation need for the egalitarian and juvenile supporting type of allomaternal care found in humans.

6.6. Group food pooling behavior

The reliability of human energy provision and its support for juveniles and

mothers is due to group food pooling behavior (Kaplan and Hill, 1985). Food pooling is different to the limited food sharing occasionally found in nonhuman Hominidae as it is not necessarily linked to direct reciprocity, tolerated thief, nor focused upon kin (these issues are reviewed in Gurven, 2004; Kaplan and Hill, 1985). While human food pooling is similar to that in social carnivores, it is of longer duration and its sharing is not determined by dominance status, as humans—at least in simple hunter-gatherer groups—live together, in part due to language, within egalitarian groups (Lee, 1979).

Food pooling is important since it reduces the costs of raising children (resources are not limited to those that can be obtained by their parents). It also favors the selection of lower infant mortality. This is because remaining siblings and kin do not benefit from increased indirect fitness (Hamilton, 1964) if one of their food competitor kin dies—due to food pooling—they are not competing for the same energy intake with each other (Lee, 2008). Group food pooling, moreover, advantages higher energy consuming development (related individuals again are not competing directly with each other's energy consumption) (Lee, 2008). Further, in studies of extant human hunter-gatherers, group food pooling behavior has been found to occur in regard to a substantial proportion of high energy and lipid rich foods (Gurven and Hill, 2009; Kaplan and Hill, 1985). In contrast nonhuman primates, such as chimpanzees, show no such behavior as they fail to provide food to other nonkin group members, even when it could be done at a very low cost to themselves (Silk et al., 2005; Vonk et al., 2008).

6.7. Human high-energy food provisioning

Food pooling allows humans to build upon the high primate energy investment in young by considerably increasing its completeness, extent and reliability (Robson and Kaplan, 2003). This happened for supporting both brain formation and neuromaturation. Brain development has been changed by increases in a mother's investment during pregnancy and lactation in her young, particularly by extending pregnancy duration (Dufour and Sauther, 2002). This has considerably increased the energy needed by Homo mothers (Aiello and Key, 2002). Human immaturity, however is important and occurs over an extended dependency stage (Bogin 1997). Bogin identifies this extension with the insertion of two new stages (childhood and adolescence) in addition to what he calls "juvenility" found in nonhuman animals (Bogin 1997). (In this paper, juvenility is used to refer all stages between infancy and adulthood.)

One key innovation responsible for prolonging human neuromaturation is that while lactation is gradually replaced with weaning foods (as is the case in many other primates), these foods are to a large extent not gathered by the juvenile but provided by adults (including nonkin) (as illustrated in figure 4). Young humans as a result receive most of their energy from adults and not their own limited foraging. This allows both an extension in the period in which neuromaturation can be supported and also an increase in the time available to learn nonforaging skills such as language. Due to this, by the age of 18, young individuals in hunter-gatherer bands have taken in 55×10^9 J, with only around a quarter of this coming from their own efforts (Kaplan, 1994, pp. 760-763). This amounts to $\approx$3.5-7 MJ/day for around 15 years (Kaplan et al., 2000) after the end of weaning (2.3-3.2 years-of-age in hunter-gatherer forgers): (Marlowe, 2006; Robson et al., 2006). Crucially, such food energy is not begged for by juveniles but distributed to them as entitled dependents of a cooperative social and food pooling community.

6.8. Food pooling, and maternal and child biology

As a result of group food pooling, the metabolic support situation of those mothers that, due to their being pregnant or caring for dependents, cannot obtain by their own efforts sufficient food for their own needs, is radically changed. Human mothers receive a substantial additional energy intake ($\approx$3.5 MJ day^{-1}) (Kaplan et al., 2000, fig. 3) that more than adequately covers the cost of pregnancy (325 MJ total; for the first, second and third trimesters: 0.4 MJ day^{-1}, 1.2 MJ day^{-1}, 1.9 MJ day^{-1}) and lactation (2.6 MJ day^{-1}) (Butte and King, 2005; Sellen, 2007). This provisioning has affected human physiology: human neonates have a birth weight that approaches twice that of primates of similar size and length of gestations (humans, 3.4 kg, 267 days; chimpanzees, 1.7 kg, 235 days; orangutans, 1.7 kg , 250 days; gorillas, 2.1 kg, 260 days) (Martin, 1989). This weight is mostly due to adipose tissue that provides an energy reserve that protects the brain and its high energy needs against temporary energy intake disruption (Kuzawa, 1998). Human mothers also provide more energy early on in their lactation (Aiello and Key, 2002). This difference can be seen in figure 4 which shows the different neonatal energy consumption by chimpanzees and hunter-gatherer humans.

Increased energy support given to mothers, due to cooperative food pooling, could also have theoretically been expected to have changed the behavior of mothers to their young in ways that better support the cognitive stimulation needed by their neuromaturation. Compared to better fed captive vervet monkey mothers, ones with an energy intake that is comparable to wild ones show more rejection behaviors to their infants (Fairbanks et al., 2010). The provision by mothers of prompt, contingent and appropriate responses is known from studies upon human mothers and their infants to have important effects upon developing language abilities (Taylor et al., 2009) and prefrontal executive skills, such as working memory, impulse control, and set shifting (Bernier et al., 2010). These skills both directly and indirectly through their enhancement of theory of mind (Peterson and Siegal, 1995; Pyers and Senghas, 2009), and the ability to inhibit ones own perspective to process that of others (Nilsen and Graham, 2009) could be expected to enhance the capacity for later adult social cooperation, and so feedback upon energy support provided by future mothers.

6.9. Juvenile nutrition and adult cognition

Juvenile diet is also linked to adult cognition as human foods are usually high energy and often have high lipid content: obtaining these foods requires highly specialized adult skills. The australopith diet, like that of other hominoids, required few adult specific skills as it was predominately vegetarian (Spoonheimer et al., 2006; Teaford and Ungar, 2000). With the Homo diet this changed (Milton, 2003) to one that depended upon proficient complex forms of motor, information transmission and planning expertise, since its high-energy (such as meat and tubers) could only be acquired by adults in wide territory based hunter-gathering (Foley, 2002; Stanford, 1999) that depended upon tool manufacture/use, communication and socially cooperation. Moreover, due to the meat component it provides, juvenile humans as a result of these adult skills could receive high quantities of long-chain polyunsaturated fatty acids that go to make up the neural membranes needed for brain development (Milligan and Bazinet, 2008). It has also been suggested that encephalization might be limited as the development large brains requires nutrients such as iodine, iron and docosahexaenoic acid that have restricted dietary availability (such as molluscs and turtles) (Cunnane et al., 2007), and which humans unlike other Hominidae exploit

(Steele, 2010).

Another factor linking adult cognition to juvenile nutrition is dentition. Human children spend two to three years after they have weaned (2.3-3.2 years-of-age) (Marlowe, 2006; Robson et al., 2006) before the start of the process of acquiring adult dentition (usually begun 5.5-6 years-of-age). As a result, instead of lactation, they rely during this critical period (in which they start high energy neurodevelopment) upon food ingested with deciduous dentition (in place by 24 months) that has thin enamel and short roots, and so is easily broken and worn. Thus, for two to three years, unlike other primates that receive a much longer lactation, they are totally dependent upon ingesting high energy adult foods for which they, as juvenile primates, are not evolved and for which they have inappropriate teeth (Bogin 1997; Kennedy, 2005). Further, since their digestive tracts cannot always absorb adult foods (Bogin 1997), this requires that adults not only provision them but that they have the cognitive capabilities to select and prepare juvenile appropriate foods. At some stage, the energy and nutrition content of such foods was also enhanced through detoxification and increased digestibility enabled by adult skills in cooking (Wrangham, 2009; Wrangham and Conklin-Brittain, 2003; Wrangham et al., 1999). Thus, human juvenile nutrition is closely dependent upon complex adult cognitive capacities in a way not found in other animals.

7. COOPERATION, FOOD POOLING BEHAVIOR AND COGNITION

7.1. Indirect reciprocity and cognition

Food pooling behavior, which is central to human hunter-gatherer energy support, is an example of cooperative altruism in that an individual gives to others resources that they might have otherwise consumed themselves or not risked nor spent their time and efforts in obtaining (Nowak and Sigmund, 2005).

Considerable discussion exists upon the origins of food pooling behavior (Gurven, 2004; Kaplan and Hill, 1985). Modern theories of altruism (which underlies food pooling behavior) associate it with enhanced cognitive faculties, for example, Nowak and Sigmund (2005) link "reputation building, morality judgment and complex social interactions with ever-increasing cognitive demands". Mohtashemi and Mui (2003) relate it to social information about trustworthiness, whilst Fehr and Rockenbach (2004) to judgments about the need for punishment. Central to these processes is the capacity of humans for making and sharing richly detailed accounts of others behaviors that can affect their social reputations (Sommerfeld et al., 2007). Of 308 conversations studied in one hunter-gatherer band, 171 involved criticism linked to enforcement of norms. Of these 22% involved mocking, joking, or pantomime; 41%, outright complaint or criticism; 35%, harsh criticism; and 2% actual violence (Wiessner, 2005). The basis of human food pooling behavior is likely to be complex involving several processes (including those noted above, and diverse cultural mediated ones that extend them such as morality, notions of normal and "correct" behavior, extended kinship and forms of nonbiological "kinship" found in some cultures like as name-sharing and age-sets). The reputation, trustworthiness and punishment processes involved are also dependent upon more general cognitive abilities, such as recalling of past events and anticipating future ones.

The capacity to acquire and use this information to modify behavior is limited in nonhuman animals (Stevens and Hauser, 2004). It has, moreover, been noted that "even in cases where some of the relevant psychological components are in place, what is

missing are the interfaces between these components" (Hauser et al., 2009, p. 3264). Such abilities concern the ability "to quantify the costs and benefits, time the returns, delay gratification, assess reputation, compute the contingencies and punish cheater" (Hauser et al., 2009, p. 3264). These skills and the ability to integrate them are closely linked to developed prefrontal cortex skills—such as enhanced memory, planning and behavioral regulation—that are also poorly developed in nonhuman animals (Skoyles and Sagan, 2002). Neuroeconomic research, consistent with this, finds that the emotions such as perceptions of fairness that underlie food pooling behavior links to prefrontal activations (Sanfey et al., 2003), as does the ability to reason about other's intentions and beliefs (Liu et al., 2009). The ability to share information about the reputation of other individuals in regard to social sharing also crucially depends upon language with its rich ability to describe behavior (Sommerfeld et al., 2007). The egalitarianism and group altruism that underlie indirect reciprocity are not initially present in children and emerge around the age of seven and eight (Fehr et al., 2008) suggesting a link with late rather than early developing cognitive skills.

Theoretically, therefore, a feedback exists: enhanced cognitive capabilities enabled by food pooling directly support at a neurological level the energy funding of their own specialized neuromaturation Indirect reciprocity is more than just prosociality as shown in behaviors such helping, sharing, co-operating, and volunteering. Humans together with other animals such as Callitrichidae show this from an early age and sustain through out their lives. The prosociability of Callitrichidae however is not amongst equals but part of a complex dominance submissive social coexistence. Human prosociability—at least in the hunter-gathering is egalitarian way of life most likely to resemble that in which Homo and its various species evolved. The prosociability is fundamental since without this humans lack the nutritional homogeneity that can support larger brain and more prolonged neuromaturation—at least prior to the rise of agriculture and the far more reliable and greater supplies of food stuffs.

At present several forms of indirect reciprocity have been proposed, "image scoring" (Nowak and Sigmund, 1998), "good standing" (Sugden, 1986) and " Honor-scores" (Ohtsuki and Iwasa, 2004). These suggest the nature of some of the cognitions involved even though such indirect reciprocity as modeled with different constraints to that which exists between people (for example, interactions in hunter-gatherer bands are mostly with a small well know pool of other individuals); such scoring is without graduations.

Image scoring depends upon assessing the quality of behavior done by another whether the act of an individual helps (it goes up) or does not (it goes down). Good standing concerns the quality of the individual to whom help is given: good standing is not effected if help is refused to a person with bad reputation. Honor-scores combine both rules about the nature of the help given and the reputation of the person involved. The evaluation of good standing is more complex cognitions since it involves a judgment about intent in regard to whether refusal links or not to the other reputation. This creates the problem of errors of perception since "a large amount of second- if not third- and fourth-order information about the history of the social interactions of many potential receivers of help has to be stored and used" (Milinski et al., 2001, p. 2500) . Effective participation in indirect reciprocity will require skills that ensure individuals do not experience undue loss of reputation though the manipulations of others, engaging in nonhelpful behavior through lack of control and the ability to offer help to others that enhances their reputation.

This suggests three kinds of cognition and their integration together are important in addition to prosociability: evaluation of an individual's reputation in terms of their status of cooperators, altering behavior in regard to individual's in terms of their reputation, and communication of such reputation.

Complex capacities needed for indirect reciprocity develop in human juvenility including assessment of another's cooperation (theory of mind), the ability to change behavior in regard to such assessment (behavioral inhibition), the communication of such assessments (language) and their integration together behaviorally (executive functions). The develop of these is not independent of each other. Theory of mind notably depends upon language and executive abilities while cognitive control depends upon language. Each has the capacity to develop more complex forms. Another factor is that such assessments are informed by internalized norms and so issues of "morality" and its development.

7.1.1. Theory of mind

For indirect reciprocity to work it is crucial that such reputation is judged accurately. One factor here is that apparently noncooperative actions may not be cooperative, for example, withholding help to one individual so that another in better need of it receives it. Reputation assessment is enhanced by theory of mind skills that evaluate an action to be judged not only in terms of its behavior but the intent, knowledge and beliefs of the individual doing it. Though nonhuman animals such as chimpanzees show rudiments of theory of mind awareness, this is limited particularly in regard to false beliefs. It develops in its competence during juveniles. Children acquire primary theory of the mind by six but more sophisticated abilities such as higher order ones take longer.

7.1.2. Cognitive control

Another issue is the ability to act upon reputation information. Cooperation often involves inhibiting immediately rewarding behavior. It also involves withholding or sanctions upon others that act uncooperatively. The ability to process feedback to adjust performance on a rule switching task becomes adult-like in the lateral orbitofrontal cortex around 8-11 years-of-age, adult-like in the parietal cortex around 14-15 years-of-age and are still developing at 14-15 years-of-age in the dorsolateral prefrontal cortex (Crone et al., 2008).

7.1.3. Language

Though it has been suggest that full human language is required for indirect reciprocity, it can occur in a simple form by eavesdropping on the behavior of others (Bshary and Grutter, 2006). Though no nonhuman form of communication is adequate for communicating reputation information, this does not entail that human language as it is present is the only adequate means. Simpler forms of descriptive communication are possible, thus allowing for communication based indirect reciprocity in early Homo before the rise of full modern language. Several parts of language might be useful to communication reputation including tense, modality and agency.

7.1.4. Interactions

Another problem arise where reputation judgments are based on communication such as through gossip since this gives rise to the possibility of disinformation and

manipulation (Nakamaru and Kawata, 2004). The need to avoid such inaccuracies here requires evaluation of the motives of those engaged in communicating reputation information in terms of what they think other' think and so second order theory of the mind skills.

7.2. Absent energy cognition loop in nonhuman Hominidae

A cognitive discrepancy exists between cognition in captive and wild chimpanzees that suggests nonhuman Hominidae species failed to enter a human-like energy cognition loop in which energy provision to juveniles came to enhance their cognitive abilities. But nonhuman Hominidae were nonetheless evolutionarily near to having made this step.

Trained chimpanzees are more cognitively advanced than those found in the wild (Zihlman et al., 2004), and also grow up with better and more consistent energy support. This is because of regular and reliable artificial feeding, and the lack of the energy costs of parasitism or untreated illnesses as a result of them being constantly weighed, monitored and treated by veterinary experts, and so consequently in near optimal physical health. This energy support changes them as they show more rapid physical growth and maturation (Zihlman et al., 2004). For example, first molar eruption in captive chimpanzees occurs at 3.1 years-of-age while in the wild it happens at four years-of-age (Kelley and Schwartz, 2010). Similarly, third molar eruption occurs in captive chimpanzees at 10.5 years-of-age, while it occurs in wild chimpanzees at 10.8-14.2 years-of-age (Zihlman et al., 2004, table 1). Captive chimpanzees also have greater final body weights: compare the reports on age change in body weights in wild chimpanzees in (Pusey et al., 2005, fig. 9) to those of captive ones in (Hamada and Udono, 2002, fig. 1). Wild chimpanzee adult body weight from these graphs is about 15 kg lighter than captive ones. Further, wild chimps show considerable body weight variance when young which only fully disappears when they reach adulthood (Pusey et al., 2005, fig. 19). This argues that wild juvenile chimpanzees often grow up with an insufficient energy nutrition for optimal development, otherwise their growth would not be so stunted or delayed, and show so much developmental variability.

7.3. Origins of the energy cognition loop

This suggests energy insufficiency in juveniles could be limiting nonhuman Hominidae neuromaturation, and consequently it could have stopped them fully realizing their potential for complex cognition, that they might otherwise acquire, if they had lives (as some have when in human captivity) that offer better quality nutrition. It has, indeed, been claimed that as a result they are cognitively delayed: "field observations on social and behavioral development suggest that wild chimpanzees take up to 3 years longer to mature compared with captive animals" (Zihlman et al., 2004, p. 10541). The unreliability and low quality of the natural chimpanzee's diet might therefore be acting as a ceiling on brain development, and so stopping the selection in them of the enhanced cognitions that depend upon well supported neuromaturation. Indeed, it has already been suggested that nonHomindiae brain size has reached the maxim that can be supported without allomaternal help (Isler and Van Schaik, 2009b).

This raises the possibility that changes in ecological subsistence in the early African Pleistocene might have altered Australopithecine neuromaturation through nutrition and cooperation. This would have happened if circumstances encouraged or enhanced the opportunity for adults to acquire and share high-energy foods. Nonhuman

apes are primarily vegetarian and this limits the ability of enhanced cognition, if it was to arise, to be advantageous by improving their ability to obtain extra energy. Since vegetable matter has generally low energy, any increased in the capacity to acquire better skills would result only in a marginal increase in energy intake. A shift to meat eating (whether by hunting or scavenging), however, would not only provided more energy but also would be crucially dependent upon the ability of juveniles to acquire more sophisticated cognitive abilities given the difficulties in catching and killing prey. Chimpanzees and bonobos occasionally engage in cooperative hunting (Boesch and Boesch, 1989; Surbeck and Hohmann, 2008) and following this cooperative food sharing (Boesch and Boesch, 1989; Surbeck and Hohmann, 2008). The incipient behavioral repertoire therefore already exists in nonhuman Hominidae potentially to support, if it was to be more proficient, such a shift to a diet based upon greater meat acquisition (Stanford, 1999). Further, that occasions exist for expanding upon coordination in the sharing of high energy foods—again providing enhancement of cognitions that could support the viability of such cooperation.

Meat nutrition plays an insufficient role in nonhuman Hominidae lives to improve the energy provision given to their juveniles. This situation might have changed in hominins if the limited hunting done by chimpanzees had in australopiths altered such that its hunted meat came to be cooperatively shared. In other social carnivores with immature group members. Such cooperation focuses allomaternal help upon raising multiparious litters of a restricted number of females rather than the prolongation of neuromaturation of single births as in Hominidae to all females in a group. The existence of hunting in chimpanzees therefore makes the scenario of a shift in juvenile diet a plausible path to enhanced energy investment and cooperation in pre*Homo* hominins in the context of supporting neuromaturation.

This raises the theoretical possibility of a cognitive neuromaturation feedback loop arose amongst Australopiths in the early Pleistocene that might have led to the selection of higher energy consuming hominin and the new genera of *Homo*. Such selection might have arisen in an auto-generative manner through enhanced cognitive development feeding back and improving the conditions by which it is supported. One of these conditions is stimulation that enhances the learning of cognitions. Enriched environments can do this, for example, in the visual system of mice (Cancedda et al., 2004). In this case, the environment not only alters the brain, but also through behavioral change in the young, can lead them to modify the environment, in the case of these mice, to receive high levels of licking and so support from their mothers (Cancedda et al., 2004). An evolutionary feedback therefore could arise in which, in addition to an increase in synapse numbers, there is also greater learning opportunity, leading to more complex cognitive capabilities, and that these then, in turn, feedback and improved their own learning support. One important cognition that might auto-generate in this manner is descriptive communication since it can enhance the internal learning stimulation of the brain, and can allow better learning through tuition from those skills already acquired by others.

For such a feedback upon learning to occur, however, adults must also have the extra energy to support their young. But an increased juvenile acquisition of cognitions such as descriptive communication could also create adults better able to obtain such extra energy, including skills in cooperation built upon communication based social reputation. Thus, a loop could arise in which an increase in the abilities of adults to

acquire food resulted in better provisioned juveniles, that in turn allowed for the high energy supported neuromaturation required for the cognitive capabilities that could acquire this nutrition. Moreover, as such change involves a feedback loop, it could in the appropriate circumstances self-amplify potentially in a run-away manner producing yet greater energy provision and greater cognitive capabilities.

8 DISCUSSION

8.1. **Neuromaturation Malnutrition Ceiling Hypothesis**

Humans are a neurobiological outlier in being both highly encephalized and having absolutely large sized brains. This results in humans combining a particularly high potential to gain sophisticated cognition from prolonged expensive neuromaturation with the high potential risk that their neuromaturation might be curtailed by juvenile energy insufficiency. In humans this extra energy requirement in juveniles increases the brain's energy consumption at its peak 98% above that of the adult (Chugani et al., 1987) and extends for the ten or so years (roughly 4-16 years of age) covered by childhood and adolescence (see figs. 2 and 3). In comparison, in cats, such increase is only 60% greater, and peaks at around four months (Chugani et al., 1991). Unless removed in human evolution, this risk of malnutrition upon neuromaturation would have acted as a block upon hominins evolving larger human-sized brains, and the associated capacity to acquire complex cognitions. One might call this, following the idea of the "Brain Malnutrition Risk Hypothesis" (Deaner et al., 2003), the "Neuromaturation Malnutrition Ceiling Hypothesis".

The development of theoretical ideas in this area can be detailed as in table 2 in terms of five areas of hypothesis of which last two are the focus of this review.

Table 2. Hypotheses linking brain expansion and energy input.

Maternal Energy Hypothesis	Neonate brain mass and through this adult brain mass links to maternal energy invested in her young (such as gestation length, yolk, lactation).	(Isler and Van Schaik, 2009b; Martin, 1989; Martin, 1996; Martin, 2007)
Expensive Brain Hypothesis	Reallocation of the body's energy budget by reducing the energy consumption of the gut or alternatively skeletal muscle by reducing their relative mass in the body to provide extra energy for brain enlargement.	(Isler and van Schaik, 2009a) (Aiello and Wheeler, 1995) (Isler and van Schaik, 2006; Leonard et al., 2003)
Brain Malnutrition Risk Hypothesis	Increase in brain size makes juveniles vulnerable to unexpected energy shortages increasing risk of infant mortality. This risk is minimized if maternal energy investment is increased.	(Deaner et al., 2003)

Neuromaturation Malnutrition Ceiling Hypothesis	Increase in brain size advantages the prolonging of energy expensive neuromaturation to maximize the acquisition of the adult cognitions made possible by expanded brains. This prolongation plus the increase in brain size, however, puts such juvenile brain at risk of energy shortages (due to the combination of brain high size relative to the juvenile body and the extra costs of neuromaturation). This requires extra energy provision to juveniles. If this does not occur there is no advantage—and so a block— upon the selection of larger brains.	
The Juvenile Neuromaturation Energy-Adult Cognition/Cooperation Loop (or HEBE Ring)	The neuromaturation malnutrition risk was overcome in human evolution through an energy loop by which extra cognitions, as a result of prolonged neuromaturation, produced adults better able to acquire increased energy foods, and engage more cooperatively in pooling such foods to provision juveniles so supporting their costly and extended neurodevelopment.	

Energy constraints upon juveniles risks limiting the development of cognitive capabilities and their organization in those animal species that combine a high EQ with a brain that is also absolutely large. This is because large brains have more minicolumns (Casanova and Tillquist, 2008), more surface area (Im et al., 2008) and more cortical areas—by roughly the square root of its neuron number (Changizi and Shimojo, 2005). As a result, large brains have more potential cognitive benefits to gain in neuromaturation from refining the functions of such areas and reorganizing the connectivity optimally between them, in what are called small world network attributes (Bullmore and Sporns, 2009; Bullmore et al., 2009; Watts and Strogatz, 1998). However, the brain of a highly encephalized animal, whether adult or juvenile, will also be highly energy expensive. Thus, the neuromaturational realization of the cognitive capabilities of an animal species (such as *Homo*) that is both highly encephalized and

possessed of a large brain will critically depend upon that species' ability as a juvenile to find ways to reliably acquire or be supplied with energy. This is not the case with those species that are highly encephalized but with brains that are relatively small (such as Spider Monkeys brain: 24 g, body: 660 g, brain body percentage 3.6% (Hulshoff Pol et al., 2006)) since such small brains have less to gain from extended neuromaturation. Nor is it the case with those animals that have large brains but are lowly encephalized (such as elephants and whales) since their brains utilize only a very small fraction of their total body energy expenditure—an elephant may weigh 3216 kg and have a brain of 5.22 kg and a brain body percentage of 0.016%.

8.2. Implications for human neurobiology

8.2.1. Encephalization is limited by a neuromaturation ceiling

If a brain gets large and also highly encephalized in relation to its body, its neuromaturation will create an energy conflict between restricted juvenile energy intake and its potential to acquire better cognition. This conflict will restrict the evolution of large brained and highly encephalized animals by putting a ceiling on their bioenergetic viability. This makes the evolution of increased encephalization dependent, not only upon increased energy for brain formation (an already recognized factor), but also more critically upon the existence of increased energy support during juvenility for its protracted and developmentally elaborate maturation. Without this, animals with greater brain size will not gain the full advantage offered by their increased number of neural networks for creating smarter cognitive abilities that act to offset the higher energy maintenance costs in adults of their larger brains. This will limit their selection.

8.2.2. Enhanced cognition links to prolonged expensive neuromaturation through juvenile energy intake

Synapse and myelination neuromaturation, in their length of duration and spatial-temporal elaboration, has a close relationship with the complexity of cognitive capabilities including communication that humans acquire. This is due to such neuromaturation allowing for the more effective refinement of neural networks, and for the enhanced integration and differentiation of their cross brain connectivity that shapes their small world attributes and so the "intelligence" of their information processing capacities. But such neuromaturation is highly expensive due to synapse exuberance. Immature myelination also increases its energy costs. This will act to restrict the evolution of such extended neuromaturation. However, if such energy supplies arise, the evolutionary opportunity occurs for a prolongation in the neuromaturation period together with the evolution of extra and more complex developmental stages, and due to this, the capacity of juveniles to learn more sophisticated cognitions. The adult provisioning of juveniles in human does this, and depends on indirect reciprocity, a form of cooperation dependent upon descriptive communication and reputation assessment. Thus neuromaturation that aids the development of descriptive communication is important since it can feedback upon itself. From an evolutionary perspective, therefore a theoretically intimate relationship exists between the energy provision to immature brains, and neuromaturation. This creates adult brains that have the cognitions needed for indirect reciprocity.

8.2.3. An energy loop exists between extended neuromaturation and human cognition

Human juveniles receive a greatly enhanced energy supply compared to those of

nonhuman animals (high-energy foods and food pooling behavior). Also, human adults show novel cognitive capacities linked to neural network refinement and the integration/differentiation of their network connectivity. This suggests that increases in energy provision made possible by cognition through enhancing human cooperation might have changed human neuromaturation. This would have happened if such increased energy provision to juveniles by allowing the selection of increasingly extended and spatially elaborate staged period of neuromaturation that while more costly also enhanced the ability a juvenile's ability to acquire more complex cognitions. One key cognition would have been descriptive communication and so the eventual possibility of language. The ability to produce and perceptive descriptive communication does not only depends upon neuromaturation but also underlies the existence of indirect reciprocity that results in human food pooling. As such descriptive communication feedbacks to support the costly neuromaturation that gives rise to its own existence

8.3. Limits upon the above detailing of the HEBE ring

No discussion is made of culture even though adult human cooperation and cognition is intimately linked to the symbolic and other content which it learns and which in biological terms makes its information processing particularly novel. In particular, the human capacity (shown particularly by pre-contemporary humans) for extended kinship networks beyond the nuclear family in this review is not detailed. This links to the human capacity for symbolic based kinship (complex kinship systems; kinship related rituals, such as marriage bonding parents and their in-law families) and so is a product of human neuromaturation. As such it is a further factor in reflecting the unique development of humans while also feeding back upon the provisioning of food resources to juveniles. However, though the anthropology of such networks is well developed, its role in energy support is not. The focus here is upon indirect reciprocity where such evidence is available and the issues of human exceptionally can be discussed. The HEBE ring allows for the existence of supplementary supporting connections.

Another omission is language even though the relevance of language to neuromaturation is discussed, no review is made of its origins. Nor is the more general issue of the selection of the enhanced communication that might be reasonably expected to have arisen as a precursor to the skilled communication now called "language" found in present humans. The origins of language are highly controversial. The role of language in human cooperation, however, can be detailed without venturing into speculative discussion of its specific origins or the nature of its precursor forms.

8.4. Chick and egg dilemma of the ring

How could the cycle arise if all its components needed already to exist for it function? Without prolonged expensive neuromaturation, the cognitive abilities needed for cooperation cannot exist. But without them the egalitarian food provisioning of juveniles cannot happen, and without this, prolonged expensive neuromaturation cannot be supported. The proposed loop would seem to beg the self-regression question of how its own existence might have arisen. It faces a chick and egg question.

This is not a problem: the contingencies of the ring exist in regard to the human brain due to its combination of large size, high encephalization and high neuron density. But the human brain arose from a less large one: such evolutionarily early and smaller

brains would have been supported by intergenerational bioenergetics loops with different components. It is known for example that early *H. erectus* had both a small brain and a much shorter developmental period to the *H. sapiens sapiens*. The constraints upon the development of *H. erectus* would therefore not have involved the same constraints that exist with the present human species and so could be met by different circumstances of juvenile energy support.

The origins of the HEBE ring lie in the nature of these circumstances and how they changed into those of the HEBE ring as described here. This is a separate issue to the ones raise here about the existence of the HEBE ring: it is possible to establish the existence of the HEBE ring and the necessary contingencies between its components without any theory as to the nature of earlier intergeneration bioenergetics loops and their change into that of modern humans. The present paper is concerned only with establishing the existence of the HEBE ring.

It should be noted that all the components of the HEBE ring are ones that allow of precursor stages from which they might have arisen. Juveniles with less great energy demands might be better able to support their own energy nutrition (a third of juvenile hunter-gatherer energy intake is in fact provided by them.) Egalitarian cooperative breeding could arise ranked forms through intermediary stages. While hunter-gatherers pool large food items, much smaller gatherer food items are not: change therefore is possible through a shift to a greater share in the proportion of large food items. By establishing the biology in humans of the HEBE ring, these issues which need to be discussed elsewhere can be explored in regard to the paleoanthropologically established constraints upon earlier ancestral hominid species.

8.5. Conclusion

The evolution of greater brain size/higher encephalization and energy has received much theoretical attention not only in paleoanthropology (Isler and Van Schaik, 2009b; Leonard et al., 2003; Parker, 1990; Robson and Kaplan, 2003; Sherwood et al., 2008) but also in life history theory (Parker, 1990), and by biologically orientated economists (Robson and Kaplan, 2003).

Brain size and encephalization is important and this, as much as prolonged juvenility, would have been aided in *Homo* by the increased energy availability to mothers for pregnancy and lactation made possible by food pooling. However, the formation of large brained and highly encephalized infants carries a second and biologically more important bioenergetic cost that needs theoretically to be considered: the greater need of juveniles for high energy intake to enable the neuromaturation that fully exploits their expanded brain's capacity for developing complex cognitions. This cost relates not only to the greater energy demands of creating large brains but also the greater need for a prolonged and energy expensive period of neuromaturation. Compared to this, the energy investment by the mother (pregnancy and lactation) in brain formation is relatively minor. Biologically it is a problematic cost in that it occurs with greatest need to juveniles when they are least able on their own to acquire food energy. It has already been noted that large brained juveniles are at risk due for increased morality unless provided with extra energy (Deaner et al., 2003). This raises the theoretical problem as to how human juveniles evolved to acquire this difficult-but-critical-to-get energy.

Anthropologists have observed that humans, when in the state comparable to that in which they evolved—as hunter-gatherers—unlike other Hominidae, show the

behavior of pooling food with juveniles. This behavior is also in need of explanation. The existence of food pooling can be directly linked to cognitions needed for indirect reciprocity that result from prolonged neuromaturation. The existence of provisioning to juveniles and prolonged neuromaturation therefore can be conjectured to be tied to each other through indirect reciprocity as complimentary energy supply and energy need aspects of evolved human biology.

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