

Human nature and cognitive–developmental niche construction

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Abstract Recent theories in cognitive science have begun to focus on the active role of organisms in shaping their own environment, and the role of these environmental resources for cognition. Approaches such as situated, embedded, ecological, distributed and particularly extended cognition look beyond ‘what is inside your head’ to the old Gibsonian question of ‘what your head is inside of’ and with which it forms a wider whole—its internal and external *cognitive niche*. Since these views have been treated as a radical departure from the received view of cognition, their proponents have looked for support to similar extended views within (the philosophy of) biology, most notably the theory of niche construction. This paper argues that there is an even closer and more fruitful parallel with developmental systems theory and developmental niche construction. These ask not ‘what is inside the genes you inherited’, but ‘what the inherited genes are inside of’ and with which they form a wider whole—their internal and external *ontogenetic niche*, understood as the set of epigenetic, social, ecological, epistemic and symbolic legacies inherited by the organism as necessary developmental resources. To the cognizing agent, the epistemic niche presents itself not just as a partially self-engineered *selective* niche, as the niche construction paradigm will have it, but even more so as a partially self-engineered *ontogenetic* niche, a problem-solving resource and scaffold for individual development and learning. This move should be beneficial for coming to grips with our own (including cognitive) nature: what is most distinctive about humans is their developmentally plastic brains immersed into a well-engineered, cumulatively constructed cognitive–developmental niche.

Keywords Ontogenetic niche · Developmental systems theory · extended mind · Cognitive niche construction · Human nature

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Introduction: from selective to developmental cognitive niche construction

The newer generations of cognitive science of the past few decades, such as situated, ecological, embedded and scaffolded cognition research, recognized and investigated the powerful role of environmental resources—including the body—for cognition. No account has questioned the interface between mind, body and environment more deeply than *the extended mind hypothesis*, formulated by Clark and Chalmers and developed further by Clark and others (Clark and Chalmers 1998; Clark 1997, 2003, 2008; Menary 2007; Rowlands 2009; Sterelny 2004; Wheeler 2005; Wilson 2004; Wilson and Clark 2009):

Maximally opposed to BRAINBOUND (Clark's label for methodological solipsism) is a view according to which thinking and cognizing may (at times) depend directly and noninstrumentally upon the ongoing work of the body and/or the extraorganismic environment. Call this model EXTENDED. ... The local mechanisms of mind, if this view is correct, are not at all in the head. Cognition leaks out into body and world. (Clark 2008, xxviii)

One extended cognition argument derives from Clark and Chalmers's 'spread of epistemic credit', modulated into Wheeler and Clark's argument of 'causal spread', which 'obtains when some phenomenon of interest turns out to depend, in some unexpected ways, on some causal factors external to the system previously/intuitively thought responsible' (Clark and Chalmers 1998, 8; Wheeler and Clark 1999, 106). This 'parity principle' is therefore a stance against the uncontested privileging of some causal factors over others on pure intuitive grounds; its main function is to provide a 'veil of ignorance' that can prevent 'biochauvinistic prejudice' in identifying the material vehicles of cognitive states and processes (Clark 2008, 77). This conceptualization of human agency contrasts sharply with the view of a human being defined by its locked-in physical, behavioral and cognitive abilities. Instead it sees

human minds and bodies (as) essentially open to episodes of deep and transformative restructuring in which new equipment (both physical and mental) can become quite literally incorporated into the thinking and acting systems that we identify as our minds and bodies. (Clark 2008, 31)

Within cognitive science with its long history of interpreting the mind as a disembodied symbol-processing machine, the extended mind hypothesis has been treated as quite a radical departure. Even from accounts that would like to integrate views of the mind as deeply embodied, embedded in and scaffolded by the environment into the traditional view (Adams and Aizawa 2001; Rupert 2009). Still, for Clark, these latter views are intimately related to EXTENDED and form an undividable package deal. They are unified in attempting to identify the role that environmental resources (including the body) play in cognitive systems. That is not to say that all cases in which some environmental factor interacts with the cognitive system should be treated as newly created systemic wholes. The hypothesis of extended cognition aims to develop criteria under which a causal coupling of inner and out elements creates 'sufficiently integrated cognitive wholes' in order for EXTENDED not only to be warranted, but also to provide a highly advantageous and heuristically compelling perspective (Clark 2008, 74).

Many creatures seem to have evolved to assert ‘ecological control ... to make the most of the reliable properties and dynamic potentialities of body and world’ (Clark 2008, 37). Embodied agents can save precious and expensive neural control by exploiting the dynamics of the agent’s interaction with the environment. But this control *extends* much further when agents ‘define, choose, modify and partly create their own niches’ (Laland et al. 2000, 131). It is no wonder that some authors have related the hypothesis of extended cognition to the niche construction perspective in biology. ‘Thinking is ... a kind of intellectual niche construction that appropriates and integrates material resources around one into pre-existing cognitive structures’ (Wilson and Clark 2009). And in the case of humans much niche construction is the ‘epistemic engineering’ of the informational character of agents’ environments (Sterelny 2003, 147). Through ‘cognitive niche construction ... animals build physical structures that transform problem spaces in ways that aid thinking and reasoning about some target domain or domains’ (Clark 2008, 62). Many animals, particularly mammals, not only change their own environments but either directly— if their behavior is contingent on the presence of offspring—or inadvertently—just as a byproduct of their own living and niche construction activities—*engineer the epistemic niche of their young and thereby scaffolding their development*. A large range of such behavior fall under the rubric of maternal or parental effects; mechanisms by which the parent’s phenotype or environment affect the phenotype of their offspring (Mateo 2009; Maestriperi and Mateo 2009a). These niches generally afford many of the experiences the young have to make. Clark refers particularly to this ‘downstream informational engineering’ when he stresses the importance of niche construction for human evolution and development. He sees an *analogy* between the cultural transmission of knowledge and practices on the one hand and physical niche construction on the other. While the latter produces selection-impacting feedback cycles in *evolutionary time*, the former alters the fitness landscape for *individual lifetime learning* (Sterelny 2003, 153; Clark 2008, 62, 66).

Interestingly, both Sterelny and Clark unknowingly come very close to a different theory of niche construction that developed independently from and in parallel with Odling-Smee’s account of selective niche construction and until now unbeknownst to the philosophy of biology community,¹ namely the idea of the ‘ontogenetic niche’ as the social and ecological legacies inherited by offspring (Odling-Smee 1988; West and King 1987). Both accounts share the underlying idea that organisms actively construct their environments and by this means provide another inheritance mechanism, but differ in their perspectives and research objectives. One is evolutionary, the other developmental (but with evolutionary implications, see “[The selective versus the developmental niche](#)”). In this paper, I want to follow the argument of Griffiths and Stotz (2000) that the recent emergence of work on situated, embodied, and extended cognition is strongly convergent with the perspective of ‘developmental systems theory’ (DST), and want to extend this argument towards ontogenetic niche construction. I believe that all *these perspectives combined will give some very valuable insights into the nature of biological–cognitive*

¹ It is that reason that DST has only recently embraced the developmental niche construction paradigm (Stotz 2008; Stotz and Allen 2011).

systems, the role of external ‘scaffolding’ and ‘extensions’ in development and cognition, and more generally, human nature.

More than one decade before Clark and Chalmers’s influential paper, DST was introduced as an attempt to resituate the organism in its environment in order to illuminate the interplay between development, heredity, and evolution. At the heart of DST lies the opposition against dichotomous views of development and evolution, which divide causal factors into genetic (‘nature’, biology) and environmental (‘nurture’, culture). This distinction assumes that genes alone are the units of inheritance, since other developmental resources lack this transgenerational causation of parent–offspring resemblance, one of the main conditions for natural selection to take place. DST argues for the explanatory parity (uncannily similar to Clark’s ‘nontrivial causal spread’ or ‘parity principle’) between genes and a whole range of other developmental resources in cases where both share the same causal role, such as reliable transmission to the next generation. This leads to the redefinition of the whole developmental (organism–environment) system as subject of development and evolution, replacing the organism embedded into but still separated from an external environment. In developmental systems necessary genetic resources are complemented by equally necessary and reliably reproduced epigenetic, bodily, social, ecological, epistemic and symbolic resources for development (Oyama 1985; Oyama et al. 2001; Griffiths and Gray 1994; Griffiths and Gray 2004).

Rupert, an outspoken critic of the extended mind, sees DST’s concept of extended organism–environment systems as a questionable biological basis for extended cognition. First, he uses Salmon’s ‘screening-off’ constraint to undermine DST’s argument of causal parity (‘nontrivial causal spread’) (Rupert 2009, 113). This constraint has been developed to purify explanations by disallowing (screening off) all events as potential explainers that do not increase the probability of the effect in question occurring (e.g. spurious correlations). However, real causal parity is established by the fact that the additional or alternative causes, including those external to the system, increase the probability of the effect (e.g. the existence of a genetic variant needs to be supplemented by the necessary cellular conditions such as transcriptional, editing, splicing and environmental signaling factors).

Second, Rupert identifies as the main problem for both extended perspectives how to individuate systems and discriminate between those external factors that merely contribute to from those that are really part of the developmental/cognitive system (Rupert 2009, pp. 114–118). Problematic from the start is his understanding of developmental (organism–environment) systems to be solely defined on the basis of the process of niche construction and its feedback on selection pressures. However, developmental systems are extended not just in virtue of constructing their environment, but in virtue of relying on their own reproduction and development by means of extended inherited resources (genes and extended ‘parental effects’) transmitted from the parental generation – hence in virtue of cumulative downstream developmental niche construction. Rupert utilises Sterelny and Griffiths’ distinction between cases of selection for traits of either extended biological systems or individual organisms by means of the ‘common-fate’ criterion—i.e. to what extent do the components or resources share a common reproductive fate (Sterelny and Griffiths 1999, pp. 161–77). Here, he either unknowingly or deliberately conflates the authors’ discussions of group selection with their treatment of extended

developmental systems. The common-fate criterion was designed to distinguish between individual and group selection (a kind of extended individual or superorganism in the eye of natural selection), which both can reproduce independently of each other as well as a group. This criterion should not be misused, as Rupert does, to distinguish between whole organism–environment systems on the one hand and singular developmental resources on the other. Only for the question of group selection does it make sense to compare the reproductive fate of components of superorganisms (which are potentially all independent individuals). If one were to apply the same criterion to extended systems as Rupert attempts to do, be they biological or cognitive, one would need to compare between the selective fate of different developmental resources that contribute to producing the individual, or between two differentially extended systems as a whole. To compare the reproductive fate between an individual (one reproducing system in its own right) and a single developmental/cognitive resource with obviously no self-reproductive capacity is simply quite inappropriate. This is exactly Rupert's move when he recalls Clark's example of an artist whose final drawing is creatively influenced by the use of a sketch pad (Clark 2003). He is trivially right that the person may still reproduce without the sketchpad, while the sketchpad does not. But so would an organism stripped of a whole range of non-vital developmental resources, including many genes, while the gene alone would wither. Would the latter case lead Rupert to conclude that these genes are not part of the system?

Rupert seems to generally misunderstand the process of natural selection; it occurs if slight fitness advantages measured in differential reproductive success within a population is conferred to individuals due to some variations in their inherited developmental resources causing phenotypic variations. What is at issue is the *rate of reproduction* not of the whole population but of certain variants within a population. One may compare the fitness between artists who do and do not use sketch pads or different variants of sketch pads, or between organisms that differ in the presence of a particular allele, or better hunting tools. If the sketchpad (or the allele or tools) increases the fitness of the whole system, then with the help of this system more copies of itself will be produced. Instead, Rupert insists:

Although the development of these tools [external language, nautical tools, etc.] *surely affected human's rate of reproduction*, human organisms are *reproductively independent* of all such resources; humans reproduced without them for millennia. (Rupert 2009, p.117, my emphasis)

It is hard to be independent of resources you are affected by.

DST has designed a criterion to distinguish between those factors that are and are not part of the developmental system. Key is the reliable, transgenerational availability of each resource, in other words, extended inheritance. While natural selection can only select for *heritable* variation in fitness it is blind to the causes of transgenerational stability and hence reliable similarity between parents and offspring. If extended cognitive resources are part of the cognitive–developmental niche, then the same criterion applies. This will be different for singular resources within an individual's lifetime. For these cases, Clark and his allies have designed a list of necessary and sufficient features, such as regular availability, reliability and durability, for resources to become part of the extended mind.

The developing organism inherits its ‘ontogenetic niche’, i.e. its ‘ecological and social legacies’, as reliably as it inherits its genome, even if the mechanisms of transmission may be remarkably different and often depend on the active (re-) construction of this niche for each generation. The process of ontogenetic niche construction is therefore designed to give exogenetic inheritance a formal name (West and King 1987). The ontogenetic niche as the link between two generations highlights ‘not only the ultimate dependence of the generations on one another, but their proximate dependence via mechanisms that promote orderly transitions in species-typical development for both adult and young’ (West et al. 1988, 47). This is particularly true if one sees development as a life-long process of life-history transitions. While the inheritance of the genetic sequence is permanent and static throughout the life course of the progeny, it passes through a succession of inherited niches that often require the active maintenance from both parents and offspring. These niches, however, are in a constant, complex interactive relationship with the genome through the epigenetic regulation of gene expression that scaffolds the reliable unlocking of the genetic potential.

So how should this help us in coming to grips with our own (including our cognitive) nature? The answer may be that what is most distinctive about humans is the reaction of extremely developmentally plastic brains to a total immersion and involvement into a well-engineered, cumulatively constructed cognitive–developmental niche (Clark 2008; Sterelny 2003)

In the light of current biological knowledge any scientifically credible conception of human nature must leave behind the folkbiological idea of an inner essence that makes us what we are. The psychological sciences need to take up this challenge and assimilate both their own findings and the results of the biosciences with a new and very different conception of human nature. This paper will explore such a conception.

Coming to grips with human nature, I will argue, means understanding development. Human nature does not lie in any set of ‘essential’ traits with certain ‘innate’ properties, but in the particular nature of the human *developmental process*. It is development that lifts us to Humankind, assisted by an extreme behavioral and developmental plasticity of the human brain. This non-essentialist, process view of human nature attempts to ground the notion of ‘nature’ in development ([Reliable development through developmental niche construction](#)), and the process of development in mechanisms of *extended* inheritance ([Extended inheritance](#)), to make explicit how a matrix of reliable developmental factors, organized by the developmental niche, shapes the developmental system of brain, body, and its—engineered—environment. The reproduction of the developmental system through successive lifecycles is the result of the robust yet flexible availability of a wide range of developmental resources that reliably transmit crucial information from parents to offspring. Through formulising the processes of extended inheritance, developmental niche construction renders development as an evolutionarily salient process in the origin, maintenance and distribution of new trait variants ([The selective versus the developmental niche](#)). Organisms have developed a range of strategies to manage aspects of their own or their offspring’s developmental environment to guide the developmental process. This active *developmental niche construction* provides dependability, but also adaptive flexibility, in the provision of these resources, the latter leading to phenotypic plasticity ([Phenotypic and developmental](#)

plasticity). This is particularly true for the human species, a master in niche constructing and extending its terrain into the cognitive, cultural and symbolic realm. In order to understand ‘human nature’, it therefore becomes imperative to acknowledge human *cognitive niche construction* extending the developmental niche ([Extended minds and cognitive–developmental niche construction](#)), that at times amount to real extended minds, and at other times is more equivalent to the external scaffolding that reliably nurtures our nature (Sterelny, this issue). Showcasing cognitive, cultural and symbolic niche construction as part of the overall process of ontogenetic niche construction helps us to overcome the old dichotomy between biological and cultural inheritance and evolution and see them not as analogous processes, as Clark, but as interlocking into a single extended process of human development and evolution ([Dual versus extended inheritance](#)). This will finally facilitate the reconstruction of the idea of human nature ([Human nature revisited](#)).

Reliable development through developmental niche construction

While human ontogenesis may be seen as a specific adaptation allowing for the intergenerational transmission of the accumulated skillful practices and knowledge of their social group, evolution came up with a wide range of strategies to construct the ‘ontogenetic niche’ to dependably guide and scaffold the developmental process of most species.

Jeff Alberts conceptualizes the development of the rat in terms of four consecutive ‘nurturant niches’ the pup passes through on the way to adulthood: the uterine niche, the dam’s body, the huddle in the natal nest, and the coterie (Alberts 2008). They all provide channels of sustenance for the developing organism, such as nutrients, warmth, insulation, and behavioral and social stimuli, and ‘nurture’ in the form of resources, stimulation, and affordances for development. The early ontogeny of species-typical rat behavior is directed mainly by olfactory, but also tactile, cues that are provided by the different ontogenetic niches. Olfactory cues on the dam’s nipples guides the pup’s attaching to and suckling from it. The pup’s developing sensoria need to learn this odor recognition of the nipple through chemical cues in the amniotic fluid provided by the earlier ‘uterine niche’. The spread of amniotic fluid over the dam’s body after birth bridges the pre- and postnatal niches of the pup. Filial huddling preferences in the natal niche are mediated by learned olfactory cues provided from the close proximity of the siblings during the suckling stage. This huddle or natal niche in turn induces species preferences, prerequisite for the functioning of the rat in the social context of the ‘coterie niche’, through thermotactile stimulation. Alberts notes:

Again we find a stereotyped, species-typical, developmentally-fixed behavior is learned, with all of the key components [...] existing as natural features of the ontogenetic niche. ... Specific features of these niches elicit specific reactions and responses in the developing offspring. (Alberts 2008, 300)

These niches afford the pups a range of other experiences. Micheal Meaney’s laboratory has in painstaking experiments in the past 15 years discovered that natural variation in maternal care, elicited by environmental experiences of the dam,

influence stress responses, exploratory and maternal care behavior in the offspring. The quality of the mother's licking and grooming behavior results in a cascade of neuro-endocrine and epigenetic mechanisms, e.g. the permanent down-regulation in the expression of the glucocorticoid receptor gene via the methylation of its promoters (Meaney 2001; Champagne and Curley 2009). Stressful mothers produce stressful mothers. Such transgenerational transmission of maternal behavior has also been studied in primates (Maestripieri 2009).

Meredith West and Andrew King were the first to fashion the concept of the ontogenetic niche in order to resituate the odd couple of 'nature' and 'nurture'. The niche does not equal nurture, even though it nurtures the developing organism, and it does not equal nature even though it is part of the organism's endowment. In many decades of painstaking research their research team could show that a nest parasite, the Brown-headed Cowbird, is not the paradigm example of a hardwired species, as normally assumed. Both males and females need to learn how to behave successfully as a cowbird. Males may spontaneously produce quite potent songs if reared under isolation. But it needs the responses from a female audience and the competition with other males in order to produce 'proper' cowbird songs that lead to successful mating.

Potency may be [genetically] inherited, but the 'right' to sing is not (...). In cowbirds the juvenile niche is a forum in which males learn the pragmatics of singing, which appears to be a performatory, if not sometimes martial, art. (West and King 1987, 52)

If there is a 'safety net' you cannot find it in a 'genetic program' but in the social structure of the flock. An individual cowbird's niche, defined by the cowbird's position within the flock, 'gates' what is 'bioavailable' to be culturally transmitted or learned throughout the lifespan. According to West and King the developmental system is designed to be as open as ecologically possible. To that effect evolution has trusted a developmental niche to transmit extragenetic information that is vital to the reproduction of a lifecycle (West and King 2008). 'It's the dependability of the niche in delivering certain resources to the young that makes it a legacy' (West et al. 1988, 46).

There are countless more examples of the way in which developmental niches afford the robust experiences necessary for normal development. They include food and habitat imprinting in insects through oviposition; maternal care and stimulation for neural development (sexual behavior and fear reaction in rats; learning disposition in chickens); territorial and habitat inheritance (nest sites, food resources, a hierarchy of relatives) in woodpeckers and jays; maternal rank inheritance in carnivores and primates; exploratory, social, reproductive, and mating behavior; to name just a few (Maestripieri and Mateo 2009a).

Extended inheritance

The ontogenetic niche has been defined as the set of ecological and social (and I would add epigenetic, epistemic, cultural and symbolic) legacies inherited by organisms, functioning to guide the expression of the genetic potential (West and King 1987). In contrast to genetic inheritance, exogenetic inheritance mechanisms allow for the reliable but flexible transmission of information *acquired* by the parent.

They provide several pathways, including learning, by which *effects of experience* on the parental generation can be transmitted to later generations (Lamm and Jablonka 2008). The developmental niche also enables the next generation to make necessary experiences, albeit not through mere exposure to certain stimulation; the right context of development gates what is available to be learned. The niche functions as an information centre that exposes the young to stimuli of future relevance and hence defines which experiences are bioavailable (West and King 2008).

The developmental niche can provide an alternative framework to the persistent yet unsatisfactory nature–nurture dichotomy since it goes beyond nativist and empiricist oversimplifications of ontogeny (Stotz 2008). It is a particularly helpful framework for understanding *behavioral* development since it highlights how learning processes are involved in the development of species-typical, not just individual, behavior. Exogenetic legacies demand continuous behavioral effort to maintain their value, hence ‘behavior must be transmitted as to how the legacies are to be maintained. Exogenetic legacies are inherited, but they are also learned’ (West et al. 1988, 50).

West and King advise: ‘Ask not what’s inside the genes you inherited, but what the genes you inherited are inside of’. These ‘genes inherit a rich and supportive environment, a fact few dispute but few discuss with any urgency’ (West and King 1987, 552). A look at the enormous complexity of gene expression of all higher organisms reveals a very flexible and reactive genome open to many intra- and extra-organismal influences. Not so much the particular gene you inherit is important but when, where and how this sequence is transcribed or translated by the complex network that regulates the time- and tissue-dependent expression of genes (Stotz 2006). The cytoplasmic chemical gradients, messenger RNAs and transcription factors that are inherited through the mother’s cytoplasm give this process a head start, but the mother’s control over her progenies’ environment does not stop there. After birth rearing practices, such as the differential licking of pups by rat mothers, continue to influence neurological development through gene expression levels (Moore 1984; Meaney 2001). The protein packaging and chemical modification of DNA (epigenetics) are open to environmental influences that can have long-lasting control over the offspring’s gene expression. Countless other *parental effects* beyond the parents’ genetic contribution to the gametes influence the phenotype of their offspring (Jablonka and Lamb 2005; Mousseau and Fox 1998; Maestriperi and Mateo 2009a).

The fidelity of transmission does not necessarily depend on the nature of the mechanisms of transmission. A suitable mechanism of scaffolding can lend the transmission its reliability (learning scaffolded by teaching, gene expression scaffolded by imprinting, etc.). It is important to note that different ‘channels’ of inheritance are not independent of each other but interact directly and indirectly in producing the specific conditions of development.

The selective versus the developmental niche

The niche construction paradigm developed by Laland et al. (2000) advocates the creation of new feedback cycles in which the activity of population introduces new selection pressures and alters the fitness landscape of this population. The selective

aspect of niche construction links the organism to its environment in a more active way than traditionally perceived. The developmental viewpoint, however, goes beyond the contextual aspect of the niche by conceptualizing the niche as *part of the developmental system*. Foremost a developmental concept, through its effect of transgenerational stability the ontogenetic niche achieves evolutionary relevance by providing additional foci for selection, such as cultural traits, to act on.

The utter reliability of the ontogenetic niches and the affordances that exist in each are inherited as surely as are genes. An offspring's behavioral interactions with the dam or with its siblings in the nest can be framed as active 'niche construction' (Alberts 2008, 301).

[F]orm ... is not received by the organism at the point of conception, but is generated within the dynamic functioning of developmental systems. And through contributing to the environmental conditions of development for successor generations, organisms—including human beings—actively participate in their own evolution. (Ingold 1995, 187)

Both the selective and ontogenetic niche describe additional inheritance mechanisms. However, only developmental niche construction offers the evolutionarily more relevant vertical intergenerational relationship that causes offspring to resemble their parent. Arguably, developmental niche construction contributes to a variety of evolutionary questions by providing explanation of: (a) the origin of a trait by introducing new epigenetic or behavioral resources for variation and innovation and describing how developmental processes can produce novel phenotypes, (b) the spread of a trait by showing in detail how organisms or their parental generation co-construct a selective environment, and (c) the maintenance of a trait through processes of transgenerational stability of variation through extended inheritance.

Developmental niche construction in humans

The developmental niche concept has not yet been applied to human development, but the large range of maternal and paternal effects in mammals and others forms of extended inheritance mechanisms apply equally to humans, and arguably to an even larger extent through the vastly increased importance of social and cultural transmission of developmental resources during the extended juvenile period in humans. To a large extent they affect cognitive growth, skills, and social behavior which is caused by cognitive niche construction ([Cognitive niche construction and the nurturing of human nature](#)). In recent years, however, research has revealed some mainly parental effects that exert some major influences on health and disease in humans.

According to the fetal programming hypothesis, the human fetus reacts with vascular, metabolic and endocrine adaptations to circumstances in its environment. It suspects that nutritional or hormonal factors in the intrauterine environment induce epigenetic mechanisms, which profoundly affect the trajectory of prenatal development (Nathanielsz and Thornburg 2003). Recently, Peter Gluckman and his coworkers have argued such programming should be explained as *developmental plasticity* that allow organisms including humans to adapt to a suite of different environments with the most suitable phenotypic variant (Gluckman et al. 2007).

Beyond a flood of epidemiological studies and research on animal systems, molecular evidence emerged in the last few years that underpins the proposed causal relationship between the periconceptual, prenatal and perinatal environment (e.g. maternal nutritional state or stress) and permanent changes in adult morphology, physiology and behavior (e.g. diseases such as obesity and metabolic syndrome or depression). It has been proposed that the observed plasticity in human (and nonhuman) developmental trajectories is to a large part achieved through the altered expression of key regulatory genes that regulate cell number and differentiation early in development, which can permanently reset the levels of activity of many homeostatic mechanisms. These epigenetic processes are induced by environmental cues mediated by the placenta (Gluckman et al. 2007).

Today, we understand epigenetics as heritable changes in phenotype that are not caused by changes in the DNA sequence. Their underlying mechanisms include a wide range of cellular processes, but modern accounts often limit them to the molecular modification of the DNA itself or posttranslational modifications of the proteins that package the DNA. The long-term ‘epigenetic programming’ induces stable changes in cellular phenotype by means of targeted activation and silencing of genes. This results in the irreversible differentiation of cells from their totipotent state as stem cells to differentiated somatic cells of different tissue types. The term ‘genetic imprinting’ describes the parent-of-origin-specific expression of many developmentally relevant genes in the descendants. It has been shown that particularly maternally imprinted genes are targeted in fetal programming through the omission of epigenetic marks in certain tissues. Normally not imprinted genes, however, can also be the target of selective activation or silencing (O’Malley and Stotz 2011).

One hypothesis explains such long-term effects as ‘Predictive Adaptive Responses’ (PARs) to environmental cues which shift the developmental pathways to modify the phenotype in expectation of a particular later environment. These PARs may only manifest their adaptive effect later in life. The advantage of such a plastic strategy crucially depends on the accuracy of the forecast of the postnatal environment. A thrifty phenotype with a high ratio of fat cells versus muscle cells, a highly efficient metabolism designed to make the most of a meal, and a changed appetite and exercise regulation may have clear advantages in an environment with poor nutritional supply, but would likely lead to highly increased weight gain and an increased risk of associated diseases in an environment with an overabundance of high-fat food. Such a scenario has been dubbed the ‘Environmental Mismatch Hypothesis’, which encompasses most recent accounts of epigenetic explanation of obesity and related disease risks (Gluckman and Hanson 2006).

Phenotypic and developmental plasticity

While the existence of adaptations is notoriously difficult to prove, several researchers have argued forcefully for the adaptiveness of PARs (and phenotypic plasticity in general):

A trend to obesity, insulin resistance and endothelial dysfunction can be induced by high-fat diets, low-protein diets, maternal global undernutrition,

and maternal glucocorticoid exposure at differing times in gestation in sheep, rats, mice and guinea pigs. That different cues converge on a common outcome reflecting an integrated response of the fetus to a perceived threatening postnatal environment suggests that the induced phenotype has value for the fitness of the offspring ... resulting in improved growth, survival, or reproduction. (Gluckman et al. 2007, 16)

Kim Sterelny also argues in favor for the adaptiveness of plasticity and constructed a scenario in which such plasticity may have evolved in humans. While niche construction may buffer against environmental instability, it can also accentuate it through the rapid succession of selective environments. Many species have survived in heterogeneous environments with the production of alternative phenotypes as an adaptation to such variability. Such evolution of *phenotypic plasticity* may have happened in the human lineage particularly in response to their niche construction activities. Generally, we have to distinguish between two kinds of plasticity which interact with and potentiate each other: Humans are *developmentally* plastic in the sense that they adapt to different environments with contingent but stable phenotypes (PARs are an example of this kind of plasticity); our large brain also affords us immense *behavioral* plasticity throughout the life cycle. In addition, brains also show great neural plasticity by creating different cognitive architectures in response to variable developmental resources (Sterelny 2003, 152, 162ff).

Human brains are developmentally plastic, so transforming hominid *developmental* environments transformed hominid brains themselves. As hominids made their own world, they indirectly made themselves. (Sterelny 2003, 173, italics K.S.)

Summary

The ontogenetic niche presents a twofold link, first between the young and adult form by scaffolding its development, and second between generations: ‘Members of both generations must act to realize their investment as parents or inheritances as offspring. The niche is thus a way of life and is the study of behavioral ecology’ (West et al. 1988, pp. 46–47). Ontogenetic niche construction functions as a *distributed ecological control system for development that makes the most of, and actively produces, robust, reliable sources of relevant order in the bodily and worldly environment* (paraphrasing Clark 2008, 5f, 14).

All inheritance equates with the dependable, transgenerational transmission of crucial information, but extended inheritance leads to ‘transgenerationally extended plasticity’ or ‘cross-generational phenotypic plasticity’ in the form of developmentally induced heritable epigenetic variations (Lamm and Jablonka 2008, 305; Maestripieri and Mateo 2009b, 2). Thus coming to terms with an animal’s nature means transcending features of similarity, universality and fixity in order to integrate diversity, plasticity and adaptability (Linguist et al. 2011).

Cognitive niche construction and the nurturing of human nature

In “Introduction: from selective to developmental cognitive niche construction”, I claimed that development lifts us to humankind. Specifically, I want to argue here that the emergence of humankind depended on the origin of ‘childhood’ as one particularly important *developmental niche of humankind*. Due to the incompatibility of pelvic width and head size, humans are born 12 months prematurely, and as ‘extra-uterine fetuses’ retain an extraordinary fetal neural growth rate of 250,000 neurons/min for their first year (Portmann 1941). This affords the unique opportunity of a more direct interaction with a very rich environment, which ‘should provide a new level of plasticity, one that *adds experience to endowment*; for the nervous system ... can develop according to environmental needs’ (Gilbert 2002, 133, my emphasis). This differential growth rate of the human brain may have necessitated the invention of childhood and adolescence as new stages of the life cycle that bridges the infant and juvenile stages both common to all social species of birds and mammals (Furth 1987; Sinha 1989; Stotz 1996; Bogin 1997). The delayed physical and psychic maturation with simultaneous highly versatile learning powers and a marked sense of curiosity results in an intensive inclusion of ‘acquired’ components of behavior. Such juvenile development in all species depends critically on living in a social group, but only human juveniles are scaffolded by special tuition, teaching and instruction to acquire the necessary repertoire of skills. We acquire skills not possessed by other primates, and often not even shared by all humans; humans create experts (Herrmann et al. 2007). These powerful forms of developmental plasticity may have emerged as adaptations to deal with a rapid variation in selective environments brought about by rampant human niche construction. A substantial part of it is epistemic engineering that modifies the informational and cognitive character of our environment and that of our descendants.

Extended minds and cognitive–developmental niche construction

According to Andy Clark, the cognitive niche functions as a supersized, distributed ecological control system for cognizing that makes ‘the most of robust, reliable sources of relevant order in the bodily or worldly environment of the controller ... in terms of the flow and transformation of energy, information, control, and where applicable, representations’ (Clark 2008, 5f, 14). Organisms, particularly humans, employ these relevant sources of order in ways to reduce and simplify the complexity of the environment and any appropriate action to achieve certain goals. They replace the necessity to meticulously manage and plan any task at hand by exploiting regularities in the agent’s motor, sensory and neural systems and the physical and social environment. With the aid of this external scaffolding, they can accomplish tasks beyond the capacity of the ‘naked brain’.

Both Clark and Sterelny have interpreted cognitive niche construction as part of the overall evolutionary force of niche construction. But given what we have seen so far, to the canny cognizer the epistemic niche present itself not just as a problem space (as a partially self-made adaptive or selective niche) but equally, if not more,

as developmental scaffolding to acquire cognitive powers and day-to-day problem-solving resources (both in terms of modified informational environment and informational processing equipment).

For example, let us look at the development of intentionality: Humans are born into intentional surrounding as part of a lineage which has co-evolved with environments in which intentionality and representation exist externally in other subjects, objects, and their context-of-use (Sinha 1989; Ingold 1995). The development of intentionality in human babies is assisted by the intentional behavior of the mother, but even more so by the intentional ascriptions of the baby's behavior by the mother (Hendriks-Jansen 1996). This research is convergent with the comparative psychology of wild and enculturated apes, where the latter master an intentional understanding of actions and other social skills beyond their wild conspecifics. Tomasello and his coworkers ascribe the origin of this set of skills mainly to the fact that these apes have been *treated as intentional beings* (Tomasello and Call 2004).

A cognitive niche is partially created by the appearance of artifacts as representations of social norms. Sterelny uses human cumulative niche construction activities, with a special focus on the creation of learning environments, as an alternative explanatory scenario against evolutionary psychology's massively modular view of the monomorphic human mind. Cumulative epistemic engineering provides a 'wealth of the stimulus argument' against nativist speculations of the origin of large suites of human psychological traits (e.g. Theory of Mind, folk biology and folk psychology) and instead argues for a 'massively self-engineered' view of our minds (Sterelny 2003, 223, 178). It is not just that epistemic engineering supports apprentice learning in a structured learning environment, in addition cultural and symbolic representations on top of a narrative tradition facilitate concept formation, the acquisition of cultural knowledge, and perceptual adaptations which scaffold the extraction of data from a sea of experiences (Sterelny 2003, 203). A cognitively plastic human child is immersed in a rich cognitive-cultural niche that scaffolds the development of typically human cognitive abilities not just superficially via association but with architectural consequences. In a similar vein Griffiths and Stotz aimed to break the link between the evolutionary perspective on the mind and nativism:

It is possible to wholeheartedly endorse the idea that the mind is a product of evolution without accepting the claim that the mind is constrained to develop or to reason in certain, limited ways. The key to separating these two claims is to recognise that what individuals inherit from their ancestors is not a mind, but the ability to develop a mind. The fertilised egg contains neither a 'language acquisition device' nor a knowledge of the basic tenets of folk psychology. These features come into existence as the mind grows. (Griffiths and Stotz 2000, 31)

Theories of embodied, embedded and extended cognition and cognitive niche construction suggest that the individual representational system is part of a larger representational environment that extends far beyond the skin and relies on actively building physical structures that transform problem spaces in ways that enhance problem solving, and even creates new forms of cognition. I do not think that the extended mind or niche construction picture is false but that for the purpose of this

paper the developmental niche construction paradigm provides the right framework for understanding human (cognitive) nature. Situated cognition takes place within complex social structures that ‘scaffold’ the individual by means of artificial, linguistic and institutional devices. When applied to cognitive development these approaches suggest that culture makes humans as much as the reverse. Human beings have had a culture since before they were human. Since the human ontogenetic niche is culturally co-constructed, human nature is not the biological basis for culture but the partial product of it. Humans are the result of developmental systems that contain as crucial components cultural and symbolic resources. Contemporary humans differ from their ‘anatomically modern’ predecessor because they owe a good part of their capacity to develop cognitive powers to the successful replication of earlier developmental systems, which included a range of distinct cognitive, social and cultural resources.

Dual versus extended inheritance

It might be tempting to construe the human construction of a cognitive niche as a special form of cultural inheritance running parallel to, independent of, and analogous to genetic inheritance. Here, the concept of the developmental niche helps to situate cognitive niche construction, and cultural inheritance in general, into an overall process of transgenerational stability and reliability of the development of successive generations within a lineage. It is a truism that traits result from the interaction of genes and environment, but it is nevertheless quite common to ascribe a whole suite of phenotypic characters, both physiological and behavioral, to ‘mainly’ genetic or ‘innate’ causes, be it eye color, walking, or linguistic competence. But no trait exists at conception; all are acquired during development. It is equally common to relegate the environmental contribution to traits to contingency, since only DNA is inherited. However, DNA is not born nakedly into the world to produce the next generation, it is carefully placed into a nurturing niche that supervises its correct expression: DNA within its chromatin state; chromosomes within an egg; an egg within an uterus; the newborn into the maternal care of the mother; the infant into the nurturing social group; the human person into a cultural and symbolic background. ‘The biology of human development is a product of the interaction of biological and cultural evolution at the site of ontogenesis’ (Sinha 1988, 104). Along with DNA the emerging organism *inherits a world*. According to Ingold:

these capacities [e.g. walking and cycling] cannot be opposed as, respectively, biologically innate and culturally acquired. They are, in every case, embodied skills, incorporated into the human organism through a process of development. Thus the differences we call cultural are themselves biological. ... What each generation contributes to the next, then are ... the specific conditions of development under which successors, growing up in a social world, acquire their own embodied skills and dispositions. (Ingold 1995, 187, 207)

A separation between genetic and cultural factors in completely independent spheres relies on an artificial, or at least a vastly overstated distinction, seeing as they just represent two kinds of interacting developmental resources among others such as epigenetic, maternal and ecological factors, which are reliably reproduced in each

generation to reconstruct a new lifecycle. This is not to say that there are no differences in kind between different developmental resources in reliability, variability, kind of information transfer, and other aspects, only that they act interdependently and interactively in producing the specific conditions of development (see “[Extended inheritance](#)”). So while cultural information is embedded in a material culture, it is still generated and reconstituted through appropriation in virtue of the involvement of the developing human beings in their diverse environment.

The differences of developmental experience are incorporated anatomically so as to make each of us an organism of a different kind. ... There is, in truth, no species-specific, essential form of humanity, no way of saying what an ‘anatomically modern human’ *is* apart from the manifold ways in which humans actually *become*. These variations of developmental circumstance, not of genetic inheritance, make us organisms of different kinds. (Ingold 1995: 207, 212)

In no species is it truer that environmental engineering becomes self-engineering (Sterelny 2003; Clark 2008). Human nature must inevitably be a product of its cognitive–developmental niche that includes a great deal of cultural and symbolic scaffolding.

Human nature revisited

Part of the rationale of the traditional idea of human nature was to isolate features that do not depend on culture. These ‘biological’ features represented our ‘true’ nature—the naked ape stripped of its cultural clothes. But just as isolating the cowbird from its social flock environment, a bee from her hive, or any single gut microbe from our gut turned out to be misguided if not entirely impossible, we cannot isolate anatomically modern humans from their real-world instantiation. Isolation experiments never produced the bare, innate core of an organism but rather a malfunctioning cripple. Take away its niche and you remove the address and identity of an organism. All organisms have evolved as part of a developmental system heavily dependent on a more or less rich ontogenetic niche; any difference within the parts of its composition—i.e. its informational resources – would lead to changes of the developmental system as a whole.

As Merlin Donald describes it, humans are peripatetic self-assemblers, self-invented to the core (Donald 2000a). We humans construct our cultural and cognitive niche in ways that can actually *remodel* the operational structure of the cognitive system.

Culture is the store-house of crucial replicative information for certain aspects of our collective cognitive matrix, without which we cannot reproduce the cognitive systems by which we now function as a species. The memory repositories of culture allow our species to transmit across generations the codes, habits, institutional structures, and symbolic memory systems that are needed to operate a significant portion of the processes of modern cognition in human culture. (Donald 2000a, 20)

The focus on the human-being-in-its-developmental-niche dispenses with the need of a definition of humankind based on universal and genetically specified

abstractions. It should help us to embrace plasticity, human self-engineering, and an openness to the world. The ‘nature’ of the organism becomes the natural outcome nurtured through the open-ended process of development that is not genetically predetermined but reliably and flexibly guided by the process of developmental niche construction.

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