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Evidence for chronic omega-3 fatty acids and ascorbic acid deficiency in Palaeolithic hominins in Europe at the emergence of cannibalism

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ABSTRACT

At the Middle-Upper Palaeolithic (M/UP) transition in Western Europe, hominins depended mostly on terrestrial mammals for subsistence, being pointed out that reliance on reindeer (*Rangifer tarandus*) would have promoted declines in human population densities during that period. Food-composition tables have been compiled for hominins at the M/UP transition, listing protein, fat, energy, different omega-3 fatty acids and ascorbic acid concentrations. These data were used to compute the regular relations between fatty and lean tissues of the main hunted food-animals to meet hominin energy needs. Then, with daily protein intake considered critical, the optimal contribution of the different omega-3 fatty acids from different hunted species to hominin diets were computed. Several faunal assemblages from different human sites at different M/UP periods were used to assess the overall daily intake of the various omega-3 fatty acid classes. The results of the calculations made in this work are quite clear; hominins at the M/UP transition had a deficit of both omega-3 fatty acids and ascorbic acid. Data on human organs summarized here are also conclusive: these contain such nutrients in amounts much higher than reached in the corresponding mammal organs consumed, and thus could have been alternative sources of those nutrients for Palaeolithic hominins. Therefore, nutritional cannibalism detected at such times could have had the function of alleviating these deficits. The evolutionary advantages gained by the consumption of the various omega-3 fatty acids of human origin are also discussed.

1. Introduction

Assessing the nutritional status during the Palaeolithic is of great interest because detecting diseases associated with different diets in the past offers an understanding and improvement of the nutrition of current humans. The term "essential nutrients" refers to those that the human body must derive from foods (Hockett and Haws, 2003). Today, many studies examine the availability of essential fatty acids (EFAs) for humans in the Palaeolithic because, among other reasons, anthropological and epidemiological works have indicated that during the Palaeolithic the human diet had an omega-6 (n-6) to omega-3 (n-3) EFA ratio ~1, while today in Western diets the ratio is ~16:1, which may be responsible for the pathogenesis of many diseases (Simopoulos, 2006). Conversely, studies on the occurrence and availability of ascorbic acid in the Palaeolithic are scarce.

FAs, the fat components in addition to glycerol, can be classified into two main types: saturated and unsaturated, depending on whether or not they have double bonds in their structure. Monounsaturated fats have one double bond, while polyunsaturated fats have more than one double bond. For the latter, the n-3- omega-reference system indicates the number of carbons, the number of double bonds, and the position of the double bond closest to the omega carbon, counting from the omega carbon (which is numbered 1 for this purpose). Monounsaturated FAs (MUFAs) are mainly n-9 FAs, for instance oleic acid (OA, 18:1n-9), while polyunsaturated FAs (PUFAs) belong to two families: n-6 and n-3 (Fig. 1). Two C18 PUFA, linoleic acid (LA, 18:2n-6) and α-linolenic acid (ALA, 18:3n-3), are considered EFAs because they cannot be synthesised by humans, and therefore they must be included in the diet. Conversely, the C20-22 very-long-chain PUFAs (VLCPUFAs) can be biosynthesised by the consecutive action of several enzymes from their respective dietary EFA precursors: arachidonic acid (ARA, 20:4n-6) from LA, and eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3) from ALA (Guil-Guerrero, 2007).

Used as an energy source, n-6 and n-3 PUFA also influence cell

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Abbreviations

ALA	α-linolenic acid (18:3n-3)
AFFSA	French Food Safety Agency
ARA	arachidonic acid (20:4n-6)
DHA	docosahexaenoic acid (22:6n-3)
DPA	docosapentaenoic acid (22:5n-3)
EFA	essential FA
EFSA	European Food Safety Authority
EPA	eicosapentaenoic acid (20:5n-3)
FA	fatty acid
LA	linoleic acid (18:2n-6)
LCPUFA	long-chain PUFA
M/UP	Middle- Upper Palaeolithic
NISP	number of identified specimens
MNI	minimum number of individuals
MUFA	monounsaturated FA
OA	oleic acid (18:1n-9)
PUFA	polyunsaturated FA
S/DF	subcutaneous and depot fats (fatty tissues)
VLCPUFA	very-LCPUFA

and tissue metabolism, function, and responsiveness to hormonal and other signals (Calder, 2015). Intracellular activities of FAs include: the regulation of membrane structure and function (Calder, 2012); regulation of intracellular signalling pathways, transcription factor activity, and gene expression (Georgiadi and Kersten, 2012); and regulation of the production of bioactive lipid mediators (Calviello et al., 2013). Such activities depend on AA, EPA, and DHA. These have important roles in immune regulation and inflammation (Miles and Calder, 2012). Through these effects, VLCPUFA influence cardiovascular diseases and a wide range of other illnesses, such as metabolic diseases (e.g. type 2 diabetes), inflammatory disorders, and cancer (Calder, 2012). Moreover, VLCPUFA are involved in the healthy performance of several physiological functions, for instance blood pressure and blood clotting, and the proper development and functioning of the brain and nervous system. A crucial fact is that DHA is scanty outside the central nervous system, representing a high proportion only in the lipids in the retina and grey matter of the brain (Guil-Guerrero, 2007; Wainwright, 2002).

Today, ample evidence indicates that the bioconversion of ALA to EPA and DHA is very low, although the exact extent is subject to controversy, being the capacity to generate DHA from ALA higher in women than in men. Based on previous studies, Harris (2012) estimated an average bioconversion of ALA to EPA and DHA of 3.7 and 0.8%, respectively, whereas for n-6 PUFA-enriched diets the bioconversion is reduced by 40–50% (Guil-Guerrero, 2007). Such conversions are rate-limited by hepatic Δ6-desaturase, which rapidly declines with age (Bradbury, 2011). In men, this decline has been demonstrated to be between three-to six-fold lower in older than in younger individuals (Burdge et al., 2003). Thus, the maintenance of the EPA and DHA status in older individuals may depend primarily upon dietary intakes of preformed EPA and DHA (Burdge and Calder, 2005). On the other hand, for women, some differences have been reported in the activity of this enzyme among ethnic groups (Gray et al., 2013). Due to low efficiency in the conversion in the n-3 route, it is recommended that EPA and DHA be derived from additional sources, and thus they are considered “conditionally essential” nutrients (Bradbury, 2011).

All mammalian species have high DHA and ARA levels in their brain (Crawford and Sinclair, 1976) and thus their intake restriction will determine limitations to brain development. Such a restriction could have dramatic consequences for *Homo* spp., because of the large brain size, in contrast to previous hominins, such as *Australopithecus* spp., which had a low encephalization rate (Crawford et al., 1999).

In contrast with n-3 EFAs, the significance of ascorbic acid (Vitamin C) in Palaeolithic diets has hardly been studied, although there are indications for consumption deficiency, which could have led to significant pathologies (Ortner and Ericksen, 1997). Ascorbic acid is an essential nutrient for humans, participating in collagen synthesis, and has antioxidant functions as a scavenger of free radicals. It also seems to protect tissues from harmful oxidative products and maintains certain enzymes in their required reduced forms (Padh, 1990). Vitamin C deficiency shows symptoms such as bruising, arthralgias, or joint swelling, and common signs are pedal oedema, bruising, or mucosal changes, myalgias, and general fatigue (Olmedo et al., 2006).

The M/UP transition is a period that refers to the age of the most recent Neanderthal fossils and the earliest modern human remains in Europe, and the inferred overlap between the Châtelperronian and the Aurignacian (Bocherens et al., 2014). This period is vital to understand diverse constraints on the current human society, from religious worship and artistic expression to administrative structures (Roebroeks, 2008). In Western Europe, the M/UP transition included a widespread adoption of blade-based toolkits, the emergence of artistic behaviour, and a shift towards modern human anatomical features. Data from this period reveal a significant climatic deterioration, which was associated with a reduction in mammalian species diversity (Morin, 2008). Today there is clear evidence for the strong dependence on animal foods by M/UP hominins in Europe. Both lithic and faunal assemblages and stable isotope analysis provides a direct measure of human diets in the past and supports the hunting hypothesis for M/UP populations (Richards et al., 2000, 2000b, 2008; Garcia-Guixé et al., 2009; Craig et al., 2010; Drucker and Henry-Gambier, 2005; Bocherens et al., 2005; Grayson and Delpech, 2002; Wißing et al., 2015). The isotopic evidence indicates that this scenario is true in all cases for Neanderthals, which were top-level carnivores whereas, by contrast, early modern humans (≈40,000 to ≈27,000 y BP) showed a wider range of $\delta^{15}N$ values, and evidence from some individuals point to the consumption of aquatic (marine and freshwater) resources (Richards and Trinkaus, 2009). However, a shift in $\delta^{15}N$ at the base of the terrestrial foodweb could have been responsible for such a pattern, with a preserved foodweb structure without any significant change in the diet composition before and after the M/UP transition (Bocherens et al., 2014).

At the M/UP transition, when subsistence in Europe heavily depended on animal foods, the question arises as to whether animal-food resources could provide those hunters certain essential nutrients necessary to maintain a good health status, and whether M/UP hominins could have exploited n-3 PUFA and ascorbic acid resources in addition to those from hunting. This study attempts to resolve these issues.

2. Material and methods

The relevant literature was searched for articles dealing with FAs and ascorbic acid composition of mammals living at the M/UP transition, as well as other articles on the content of these nutrients in human organs. Also, the literature on M/UP assemblages was scrutinized, and articles about the emergence of cannibalism around the world, as well as others concerning Inuit nutrition. Data were acquired from databases such as Google Scholar, Scopus, and other similar resources.