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Fire in the Plio-Pleistocene: the functions of hominin fire use, and the mechanistic, developmental and evolutionary consequences

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Summary - *Fire is a powerful natural force that can change landscapes extremely quickly. Hominins have harnessed this resource for their own purposes, with mechanistic and developmental physiological consequences. In addition, the use of fire has niche constructive effects, altering selective environments for genetic and cultural evolution. We review the record for hominin fire use in the Plio-Pleistocene, before considering the various functions for its use, and the resultant mechanistic and developmental consequences. We also adopt the niche construction framework to consider how the use of fire can modify selective environments, and thus have evolutionary consequences at genetic and cultural levels. The light that fire produces may influence photoperiodicity and alter hormonally-controlled bodily rhythms. Fire used for cooking could have extended the range of foods hominins were able to consume, and reduced digestion costs. This may have contributed to the expansion of the hominin brain and facial anatomy, influenced by a higher quality cooked diet. Fire may also have allowed dispersal into northern areas with much cooler climates than the hominin African origin, posing novel problems that affected diet and social behaviours.*

Keywords - *Fire, Photoperiodicity, Hominin dispersal, Social evolution, Cooking, Niche construction.*

Introduction

The use and control of fire is considered one of the most significant innovations in the evolution of modern human behaviour. Harnessing the warmth and light provided by burning fires has wide-ranging implications for our ancestors' lifestyles, from opening up new avenues for food preparation via cooking, to providing safety from predators, and extending the visible part of the day during which tasks could be safety conducted. The implications may be physiological and morphological as well as behavioural; for example, changes in the dietary resources that can be exploited will have an effect on the digestive process of energy extraction and the masticatory architecture responsible for processing the food. Toxins found in campfire smoke, which may accumulate in the placenta during pregnancy, have even been suggested to account for the lack of placentophagy in humans, a homoplastic trait unique only to extant camelids and ourselves (Young *et al.*, 2012).

Fire is a naturally occurring process, having long played a key role in ecosystem composition and maintenance on a global scale (Scott, 2000; Bond *et al.,* 2005; Thevenon *et al.*, 2010; Pausas & Keeley, 2009). It can be responsible for clearing old growth and encouraging new, dispersing seeds and maintaining open patches in otherwise closed habitats (Kerr *et al*. 1999; Bond & Keely, 2005). The savanna mosaics and dry forests of Africa where early hominins evolved, characterised by an increasing amount of flammable C4 grasslands provided the perfect conditions for natural wildfires (Menault, 1983; Gichohi *et al.*, 1996; Bobe, 2006; Pausas & Keeley, 2009). Palaeosedimentary records trace the existence of these natural fires through charred grass cuticles in Africa from the Late Miocene onwards, corresponding to the emergence of both C4 grasslands and the hominin lineage (Morely & Richards, 1993; Jacobs, 2004).

It is reasonable to surmise that early hominins would have come into contact with fire as often as the other mammals in their Pliocene and Pleistocene communities. This familiarity would certainly be the necessary precondition for any emergent behaviour in which fire is approached and its possible uses eventually ascertained. Anecdotal observational evidence suggests that this basic familiarity may be accompanied by the ability to infer the movement of natural fires and alter behaviour accordingly in extant chimpanzees, our closest living relatives, in Fongoli, Senegal (Preutz & LaDuke, 2010). If living apes are indeed good models for reconstructing the behavioural repertoire of our earliest ancestors, there is no reason to believe that hominins would have been anything but familiar with and able to adapt to the movement of natural fires. However, this behaviour evolved over the past 6-8 million years to encompass not simply a conscious awareness of natural fires, but the cognitive capability to learn what its light and heat could be useful for and the knowledge of how fires could be maintained over time when they occurred naturally.

A major phase shift seems to have occurred after 1 million years ago, when archaeological evidence indicating that hominins developed the ability to ignite their own fires begins to mount (e.g. Goren-Inbar *et al.,* 2004; Berna *et al.,* 2012). Hominins thus became a part of the natural fire regime, representing an additional source of ignition (i.e to lighting strikes, etc; Archibald, *et al.,* 2012). At this point, the ability of hominins to shape their own environments through the use of fire increased significantly. It is thought that the peak of human-driven burning in Africa occurred between 4,000 and 40,000 years ago (Archibald *et al.*, 2012), but both its historical and current utility in many societies, who transform landscapes for agricultural and other purposes, is undeniable.

Our review sets out the record for hominin fire use in the Plio-Pleistocene, before considering mechanistic and developmental responses, in addition to evolutionary consequences of fire use. The latter considers both changes in biological and cultural evolutionary trajectories, which can be conceptualised together using a niche construction framework. Niche construction refers to the modification that organisms make to their environments (Odling-Smee *et al.*, 2003) and offers a convenient way of tracing the complex causal interactions between evolving genetic and cultural variation over hominin history. Key aspects of this framework include explicit accounting for the effects of ontogenetic processes, including hormonal change and social learning, on the selective environment, and also the ecological inheritance of modified environments across generations (see Fig. 1).

A unique feature of hominin evolution is likely to have been the high degree of cultural niche construction, for instance, as human species altered and constructed their own environments through cumulative cultural evolution of technology and social normative systems (Richerson *et al.,* 2010). This process caused rapid qualitative change in the selective environments of both human genes, as well as affecting cultural evolutionary dynamics (Odling-Smee *et al.,* 2003; Laland *et al.,* 2010). As an illustration of this relationship between human behaviour and biological change, we speculate that the use of fire for cooking, which kills many of the harmful pathogens present in raw meat[1], potentially relaxed genetic selection for resistance to meat-borne pathogens. Similarly, the use of fire and clothing counteracts exposure to variation in environmental temperature, dampening

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[1] Although focussing on the relationship between meat-eating and longevity in humans, Finch & Stanford (2010) provide a useful summary of the pathogens found in animal organs which may have been encountered by early hominins exploiting animal resources.

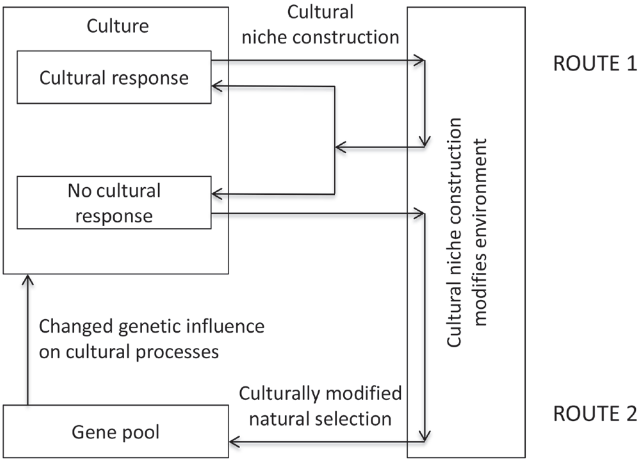

Fig.1 - Cultural niche construction can alter the selective environment to affect cultural evolution (route 1) or, in the absence of a cultural response, to affect genetic evolution (route 2). The resultant genetic evolutionary change can feed back to affect further cultural change. Figure redrawn from Odling-Smee* et al. *(2003).

selection for genes favoured for hot or cold climates (Laland *et al.,* 2010). Figure 1, redrawn from Odling-Smee *et al.* (2003), illustrates that cultural niche construction, such as the use of fire facilitating the migration to cold climates, may result in cultural evolution (route 1), such as the use of warm clothing. To some degree however, the cultural evolution of technology may not counteract exposure to the cold, resulting in the opportunity for genetic evolution over a longer time scale (route 2), such as the reduction in limb length as posited by Allen's rule (1877).

Early record of hominin fire use

Past fires may be evidenced by layers or lenses of ash, charcoal and the charred remains of vegetation or bone. The determination of hominin-controlled or hominin-ignited fires versus those which have occurred without their involvement (for instance, lightning or volcanic activity) relies on being able to calculate the temperature at which a fire has burned, the effect it had on localised sediments and the type and extent of chemical changes that have occurred in bone exposed to heat. Intentionally controlled fires tend to burn longer and at higher temperatures, the effects of which are particularly noticeable at sites that have been used on multiple occasions, such as hearths (e.g. Bellomo, 1993; Preece *et al.,* 2006; Goren-Inbar *et al.*, 2004). Problematically, there is little that can be done to identify naturally occurring fires that may have been utilised by hominins as and when they occurred prior to their ability to control it even for a short period of time. For example, tree stump fires occur naturally and leave little trace but may have been used opportunistically as cooking fires (Bellomo, 1994). This early stage in our relationship with fire is therefore nearly impossible to reconstruct and remains highly speculative.

Wonderwerk Cave in South Africa has a long history into the investigation of hominin controlled fire use (Fig. 2). Evidence of fire can be seen throughout most of the sequence, but of greatest interest to the evolution of fire use are the burnt bones and plants present throughout the entirety of the Acheulean occupied Stratum 10, which has recently been dated to 1 mya (Berna *et al.,* 2012). The consistent pattern of burnt remains is suggestive of intentional and continued fire use; in one excavated unit, 80% of the bone sample displayed discolouration typical of burning. Fourier transform infrared microspectroscopy analysis of the remains concludes that fires reached no higher than 700°C, consistent with light plant vegetation, such as leaves and grasses, as fuel. Numerous researchers (see Beaumont, 2011 for a review and references therein) had previously postulated that ash and an extremely high frequency of small charred bone remains in the excavated areas of Major Unit 9b, signified fire use by approximately 1.7 mya, even estimating that the 1 m^3 volume of ash was formed through the burning of at least 3,000 night-long fires, each requiring 5kg of woody fuel. The distribution of ash within the unit is also argued to be consistent with a home base type of living situation, supporting the idea of a band of hominins living and communicating together inside the cave. Although the presence of associated Acheulean deposits in Stratum 10 makes it reasonable to conclude a relationship between the burning and hominin occupation, the earlier estimated date of 1.7 mya for this level is likely to have been incorrect. Earlier Oldowan strata do date to this time, but evidence for the presence of fire there is inconclusive (Chazan *et al.*, 2008). Member 3 of Swartkrans Cave, further north in the Cradle of Humankind cluster of sites, has also been suggested as the earliest instance of southern African controlled fire at 1.5 mya by developed Oldowan hominins (Brain, 1993; Sillen & Hoering, 1993; Brain & Sillen, 1988). A relatively small proportion of flint artefacts do appear to have reached reasonably high temperatures, but the context of this material is unclear (Brain, 1993). Many find it difficult to accept an association between the burnt remains and hominins, the most abundant species from Member 3 being the robust australopithecine *Paranthropus robustus* (Pickering, 2001).

The earliest, although highly contested, evidence of hominin fire use in East Africa dates to 1.6 mya at Koobi Fora, Kenya, on the eastern shores of Lake Turkana. Here some of the most frequently cited early oxidised sediment studies and spatial analyses were applied specifically to substantiate the presence of hominin-induced fire (Bellomo, 1991, 1993, 1994; Bellomo & Kean, 1994). Numerous lithic artefacts were uncovered during early phases of research at the site (Harris, 1978) and subsequently two oxidised features of unknown origin were identified in one of the main excavated areas. Although there is no evidence that the lithic tools from either oxidised feature were intentionally burned, their distributions around one of the features indicates some association, assumed to be behavioural rather than taphonomic (Bellomo, 1994). The lack of both charred tools and boney remains indicates that the fires had no role in preparing lithic resources for manufacture or food processing for consumption. However, sedimentation studies infer that a campfire had been lit and maintained over a period of several days and the spatial analyses suggest that the fire served as a focal point around which tools were created (Bellomo, 1994). They represent the distinctive Karari Industry, an early Acheulean tool type restricted to the Koobi Fora region between 1.65 and 1.39 mya (Brown, 1994) and thought to be associated with the arrival of the hominin species now referred to as *Homo ergaster*.

Additional early East African evidence is even more scant than at Koobi Fora. It includes some evidence of burnt clay further south at Chesowanja, near Lake Baringo, which is said to be caused by longer-term burns than a natural fire would allow (Gowlett *et al.*, 1981) and the Ethiopian site of Gadeb and other isolated Middle Awash localities (Barbetti *et al.*, 1980; Clark & Harris, 1985) where burnt rocks have been reported. These sites collectively do not make the most convincing case, but some have argued that they represent an early phase of a technological transition associated with the Acheulean hominin, *Homo ergaster* (e.g. Clark & Harris, 1985; Clark, 1987).

It is not until well into the Pleistocene that evidence for the use of fire by hominins becomes more widely accepted. The earliest of these sites is Gesher Benot Ya'aqov in Israel, a lake margin site dated to 790 kya (Goren-Inbar *et al.,* 2000: Goren-Inbar *et al.,* 2002, 2004; Alperson-Afil & Goren-Inbar,

Fig. 2 - A map of Plio-Pleistocene sites in Africa, Asia and Europe where evidence for hominin use of fire is known in each region. Only sites mentioned in this review are shown. Dates are taken from the following sources: Gowlett* et al.*, 1981; Clark & Harris, 1985; Brain, 1993; Bellomo & Kean 1994; Mercier* et al.*, 2004; Rolland, 2004; Thieme, 2005; Mania & Mania, 2005; Preece* et al.*, 2006; Arzarello* et al.*, 2007; Karkanas* et al.*, 2007; Carbonell* et al.*, 2008; Richter* et al.*, 2008; Alperson-Afil & Goren-Inbar, 2010; Berna* et al.*, 2012; Peris* et al.*, 2012.

2006; Alperson-Afil *et al.*, 2007; Alperson-Afil & Goren-Inbar, 2010). Thermoluminescence analysis indicates that wood and flint artefacts were burnt continuously during the 100,000 year occupation, and the distribution of the lithics further suggests burning in specific areas, as would be the case in a hearth-like arrangement (Alperson-Afil & Goren-Inbar, 2010; Alperson-Afil *et al.*, 2007). It is unlikely that natural fires are responsible for the thermal damage or spatial patterns of artefacts found at the site; the frequency of burnt organic materials, including presumed food items, are not high enough to be attributed to natural wildfire and the repetitive nature of fire over such a long time period further infers that hominins were able to ignite and maintain it themselves without harvesting flames from natural sources (Goren-Inbar *et al.,* 2004; Alperson-Afil, 2008; Alperson-Afil & Goren-Inbar, 2010). The hominin species responsible for the fires at this site in this time period remains unknown, but other evidence suggests that the Acheulean tool-making inhabitants of the area hunted, processed meat, gathered plant foods, extracted bone marrow, quarried multiple lithic resources, created tools and kindled fire effectively (Goren-Inbar *et al.,* 2000, 2002). Others argue that fire was not a significant aspect of Levantine hominin lifeways until approximately 400-200 kya, as evidenced by wood ash and numerous associated burnt mammal remains Qesem Cave (e.g. Karkanas *et al.*, 2007)

If the date from Qesem Cave is accepted as evidence that hominins did not control fire in the corridor between Africa and Asia until around 400 kya, this behaviour must have evolved independently in Asia if fire use at Zhoukoudian, China, at 780-680 kya is correct (Rolland, 2004). Evidence at Zhoukoudian includes charred mammal bones and burnt hackberry shells, lithics and eggshell flakes. The processing of these materials is likely to have been performed by *Homo erectus*, the remains of which have also been uncovered in the same layers (Rolland, 2004). Some mammal remains appear to have been burnt as fresh bone and other remains bear tool-induced cut marks, suggestive of scavenging aided by fire (Boaz *et al.,* 2004). However, fire within these caves cannot be conclusively attributed to hominin activity. Although hominin occupation is likely, many of the bones, both hominin and non-hominin mammal, bear traces of carnivore tooth marks; this and other evidence points to occupation by large carnivores during this time (Boaz *et al.,* 2000). There is also no trace of ash or charcoal at the site suggesting natural causes are at the root of the fire (Weiner *et al.,* 1998).

In Europe the evidence for fire is clearer, though it confuses the story of hominin occupation in Europe. *Homo* made it to Europe 1.2 - 1.1 mya (Carbonell *et al.,* 2008), if not much earlier in limited numbers (if the dates are correct from Pirro Nord in Italy) by 1.7 mya (Arzarello *et al.,* 2007). However, fire control evidence is dated to only 400 kya (e.g. Preece *et al.,* 2006, 2007; Richter *et al.,* 2008) (see Fig. 2). The much more recent date for fire control compared to the initial hominin occupation suggests that early populations survived in Europe without the use of fire for an extended period of time (Roebroeks & Villa, 2011). For example, at Beeches Pit in Suffolk, UK, evidence dated to 400 kya includes burnt flints, charred and calcified bones and burnt sediments (Preece *et al.,* 2006). The distribution of artefacts suggests a hearth-like arrangement in which the fire was the centre around which focused activities such as tool making would occur. Elsewhere in northern Europe, at Menez-Dregan in France, evidence has been found of controlled fire dated to 200 kya in layers 5c and e, and potentially evidence from 400 kya in layer 9 (Mercier *et al.,* 2004). In Germany, evidence of domesticated fire dated to 400 kya has been found at Schöningen (Thieme, 2005) and also at Bilzingsleben around 370 kya (Mania & Mania, 2005). More recent evidence at Bolomor Cave, Spain has been dated to 230 kya (Peris *et al.,* 2012). The evidence of hearths here shows that the fires were not of long duration, and were not repeated at exactly the same points. The time between each fire varied and the characteristics of the area suggest they were used for subsistence. This is currently the earliest evidence of controlled fire in Southern Europe.

Function and consequences of fire use

There are a myriad of ways in which the use and eventual control of fire may have impacted upon hominin biology and culture. We consider below the most relevant, direct effects and evidence in support of them.

Photoperiodicity

Here we focus on the developmental effects of light on photoperiodicity and consider Burton's (2009) assertion that firelight, by extending daylight hours, may have physiological consequences for daily and annual cycles. We consider such claims worthy of mention although with caution and in the spirit of interesting conjecture, until preliminary evidence is substantiated.

Photoperiodicity is the response of organisms to the length of exposure to daylight and allows organisms to synchronise seasonal and daily activities according to the duration of daylight hours as a function of the earth's rotation. This has important implications for timing certain behaviours, such as reproduction, to the most appropriate part of the year (Kuller, 2002). For example, it is particularly advantageous to ensure there will be enough food available at metabolically expensive periods of reproduction, whether that is gestation or lactation, to increase the chance of offspring survival. This is especially important for seasonal breeders, including many primates such as the lesser mouse lemur, whose breeding season occurs only after the shortest day of the year. As daylight hours increase, females come into oestrus, male testicles increase in size, and offspring are eventually born in the rainy seasons of their native Madagascar when food is most abundant (Glatstone, 1979). Indeed, dietary restrictions are generally considered to be the ultimate reason for the seasonal regulation of birthing cycles in primates (Doran, 1997), with photoperiod being the proximate explanation (Lindburgh, 1987; Wehr, 2001; Tsantarliotou & Taitzoglou, 2012). However, even non-seasonal breeders show a peak in conceptions coinciding with food abundance for either gestation or lactation (Brockman, 2005; Tsantarliotou & Taitzoglou, 2012) and limited experimental evidence suggests this is also the case in humans and other apes, with chimpanzees known to resume postpartum cycles during the dry season in preparation for conceptions and birth later in the year when food scarcity has decreased with the onset of the more abundant, wet season (Wallis, 1995, 1997; Wehr, 2001). Studies of humans are clouded by multiple confounding factors including cultural differences and attitudes towards reproduction, but it is known that some females vary in their seasonal reproductive responses much more than others, and that this may be a heritable characteristic (Wehr, 2001).

Light is important in cueing daily activity patterns and circadian clocks. In humans, the suprachiasmatic nucleus in the hypothalamus controls daily oscillations (Stehle *et al.,* 2003) such as red blood cell turnover, heart rate, sleep/wake cycles and hormone levels. While the 24 hour cycle is “built in” to many animals (Gorman & Lee, 2002), sunrise and sunset act as reference points for these cycles and shifts in these reference points may cause concomitant shifts in daily rhythms. In humans and apes, photoreceptor cells in the eye are responsible for sensing light and converting it into chemical substances, such as the pigment melanopsin, which acts on the pineal gland in the brain (Sancar, 2000, 2004; Cashmore, 2003). Melatonin, the only known hormone to be secreted by the pineal gland, is heavily influenced by the amount light detected by the eyes. Light suppresses its production, so that the peak is typically two hours after nightfall (Brainard *et al.,* 2001; Goldman, 2001).

Melatonin has a number of effects throughout the body[2], one of which is on the pituitary gland, which controls all other endocrine glands in the body; it therefore has an effect on all aspects of homeostasis that are controlled by hormones, and particularly reproduction through an extremely complex hormonal cascade. Melatonin influences a number of points within the cascade, all of which have implications for the onset of puberty. Studies have found that exposure to differing levels of melatonin can induce puberty in seasonal breeders such as rhesus monkeys, whose onset is known to be triggered by short day length (Wilson & Gordon, 1989; Wilson *et al.,* 1988). Prepubertal rhesus monkeys injected with melatonin, which has the effect of lengthening the natural night-time rise in melatonin, reach puberty earlier than those not receiving the injections (Wilson & Gordon, 1989a). In humans, longer daylight hours can reduce the age of menarche (Dossus *et al.,* 2013).

Melatonin also induces sleep (Cajochen *et al.,* 2003) and a lack of it can result in sleeping disorder or a change in sleeping pattern (e.g. Ried & Zee, 2005; Dumont & Beaulieu, 2007). Along with a change in sleeping pattern, changes in light exposure and melatonin levels can have negative effects. For example, a change in the timing of the biological clock, as a result of changes in melatonin levels that does not correspond to daily activities, is known to be the main cause of circadian sleep disorders (Reid & Zee, 2005). Seasonal affective disorder (SAD) has also been related to light exposure, with higher than normal melatonin levels believed to be a contributory factor (Rosenthal *et al.,* 1984; Wehr *et al.,* 2001).

Burton (2009) considered the possible impact of fire on hominin physiology and development by speculating on the possible impact of reduced

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[2] Although not the focus of this review, there is increasing medical evidence that bed-time supplements of melatonin can lower the blood pressure of nocturnal hypertension patients, reducing their risk of numerous cardiovascular problems. The exact mechanism for this has not been determined, but the role of melatonin in regulating more than sleep cycles during the night is becoming clear (see, for example, Grossman *et al.,* 2006, 2011)

melatonin production caused by exposure to firelight in modern humans, which may have shifted the body clock. Blue light (446-477nm) has the greatest effect on human circadian rhythms (Lockley *et al.,* 2003), with only 1.5 hours of exposure being enough to shift the body clock by 3 hours (though the intensity of light is also important). Blue light is found at the base of a flame, and only 1.3 lux of light is required to affect melatonin levels in humans (Raloff, 1998). But is the light from a fire enough to have caused a physiological effect in hominins? Burton's (2009) preliminary experimentation suggests that the lux entering the eye in various positions and distances from a campfire would range from 3-50 lux, though only if the gaze was trained towards the base of the campfire. She speculates that even at the lower end of the range, firelight may have had an effect on melatonin levels, since as little as 5 lux can suppress production (Lockley *et al.,* 2003). Thus, although empirical support demonstrating that fire-induced hormonal effects occurred in our evolutionary past is lacking, it would appear feasible that the effects of firelight on melatonin could have contributed to a phase shift in sleep patterns in addition to the timing of puberty. A recent study also demonstrated in humans that exposure to light suppressed uterine contractions during night-time labour, with melatonin decreases implicated in the delay of parturition (Olcese *et al.,* 2013).

While fire may have hormonally-mediated photoperiodic effects, it is not clear that the proposed photoperiodic changes have evolved under natural selection, rather than simply being a plastic developmental response to modification of the environment. However, there is mounting evidence from small mammals, such as hamsters, and a variety of insect species that strongly suggests photoperiod timing is passed to the next generation during foetal development through maternal melatonin secretion patterns (Goldman, 2003), but this has not yet been demonstrated in humans (Wehr, 2001). In addition to this heritable component, photoperiodic changes may well have provided hominins with a novel temporal niche affecting the cultural evolution of traditional hours for activities such as sleeping, or facilitated the evolution of norms for social interaction and information exchange around the camp fire.

Social evolution

The warmth and light of a camp fire would provide a natural focal point for social gathering in safety from predators (Rolland, 2004). As Stiner *et al.* (2010, p. 230) say, "sheltered spaces are intensely social spaces" and, as such, may have created new selective conditions for both the genetic and cultural evolution underpinning hominin sociality.

The social brain hypothesis is particularly relevant, suggesting that hominin brain size evolved as a result of demanding social environments, such as large group size. In order to keep track of all the members of a group and manage relationships within it, an individual would require a larger brain to process information concerning identity, reputation and allegiances (Dunbar, 1998). There are a number of cognitive implications that maintaining a fire has on the brain related to both group sharing and the specific provisioning of the fire (we refer the reader to an extensive review by Twomey (2013) for details). A fire would be too demanding for a single individual to care for and protect alone, so the maintenance of a flame requires within-group co-operation or significant power differential and enforcement. If a public good, no one individual would own or use the fire, while many would have access to it and work to keep it alight. This form of cooperation may require understanding of a shared goal, the capacity to arrange the division of labour and cooperative planning to ensure continuation of the flame, for example collecting fuel or protecting the flame (Tomasello, 2009; Twomey, 2013). As Twomey notes (2013, p. 114), these capacities may rely on cognitive facilities such as "informational theory of mind, joint attention, collective intentionality and intersubjective communication".

Also important would be the communications between groups, because inevitably flames go out from time to time. Evidence such as that from Beeches Pit, Suffolk, UK (Fig. 2), suggests that even at 400 kya, fire could not be intentionally kindled and therefore needed to be maintained over long periods of time (Preece *et al.,* 2006). If so, fire may have been collected from neighbours once a group's own source had gone out, thus affecting the development of between-group social networks (Gamble, 1999). The longer term ties between groups would have required a large memory store to be able to remember individuals within another group. It would have also required the ability to put value to items if receiving the source of a flame was achieved by trade. Together, these cognitive challenges may have contributed to the major increase in brain size observed at 400-200 kya (Shultz *et al.,* 2012), consistent with the timing for the regular, habitual use of fire.

Dispersal

Northward dispersal of hominins into cooler, more temperate climates, and survival during glacial periods in Europe, are both likely to have intensified the selective advantage of fire use (Gamble, 1999; Gowlett, 2006). Gowlett (2006) suggests that when northern areas were occupied, the utilisation of fire must have been necessary, for example, in thawing food (Brace 1999) or maintaining warmth while sleeping (Wrangham & Carmody, 2010).

However, the archaeological record does not clarify whether the timing of dispersal into Eurasia from Africa, or to colder, more seasonal parts of Europe and Asia by existing populations occurred before or after fire was actively used by these migrant hominins. Although the Levantine sites of Gesher Benot Ya'aqov (Goren-Inbar *et al.,* 2004) and Qesem Cave (e.g. Karkanas *et al.*, 2007) show that fire was likely used along the most obvious migratory route between Africa and the rest of the Old World during the Middle Pleistocene, dates from the earliest fire-related sites in Asia (i.e. Zhoukoudian 780-680 kya; Rolland, 2004), and Europe (approximately 400 kya; e.g. Preece *et al.,* 2006, 2007; Richter *et al.,* 2008) do not accord with the idea that fire simply accompanied the first waves of hominins leaving Africa and was maintained as a tradition. There is no evidence, for example, of fire use at 1.8 mya at Dmanisi, Georgia, which is likely to represent one of the first populations that migrated from Africa (Gabunia *et al.*, 2000). The late arrival of fire use in Europe and the apparently simultaneous emergence of this behaviour in Asia and the Levant relative to the arrival of hominins suggest three possible scenarios: 1) fire did not accompany the first migratory populations and this behaviour evolved in Europe and Asia *in situ* at different times or 2) fire accompanied the first migratory populations but the skill was either forgotten or practiced so ephemerally that it left no observable trace or 3) fire accompanied the first migratory populations but they are not represented in the Levantine record despite having moved through the area or because they took another route. None of these scenarios can be substantiated at present, although it has been postulated that the mis-match between the distribution and timing of the evidence in comparison to the presence of hominins is likely to indicate that the use of fire did in fact develop independently in multiple locales (e.g. Roebroeks & Villa, 2011). Thus, it is possible that sustained living in northerly climates contributed to the cultural evolution of controlled fire use rather than knowledge of fire facilitating initial movement into these latitudes. If that is the case, and hominins were able to innovate the use of fire for heat protection against the cold, a form of counteractive niche construction, it may have allowed them to continue surviving in the areas they had already occupied.

The ecological data from Europe makes it particularly difficult to reconcile the lack of fire with hominin success in this region. Europe experienced repeated glaciations during the Pleistocene, resulting in climate fluctuations and concomitant changes in ecosystems. But, it is possible that early hominin populations first arrived and thrived in northern Europe during an interglacial period with a relatively mild climate, so that fire was not a necessity (Gowlett, 2001). Once a glaciation event began to reduce the temperature and cover northern Europe with an ice sheet, these cold temperatures of glacial periods, regularly below 0°C, would have posed significant problems for hominins in maintaining body temperature and collecting food and other resources. Selective pressures to develop fire control may have acted on these early populations. This homeostatic use of fire is a form of counteractive niche construction, by buffering against selection pressure imposed by exposure to cold temperatures (Odling Smee *et al.*, 2003). However, the warmth of fire would have only partially reduced exposure to the external environment, thus by contributing to the persistence of populations living in northern climes, fire use is likely to have affected genetic and cultural evolutionary adaptations to cold climes. For example, the cultural practise of wearing clothes may have been influenced by the necessity to keep warm and certainly there are tools in the archaeological record that were likely to have been utilised in the preparation of hides (i.e. scrapers), which are thought to have been used by Neanderthals and earlier taxa by approximately 780 kya in Europe (Carbonell *et al.*, 1999). However, evidence for the hides themselves is obviously lacking. Genetic evidence for the initial emergence of modern human clothing lice further suggests that the use of clothing was an established behaviour by 170 kya, correlating to the onset of an ice age in Europe (Toups *et al.*, 2011). This suggests that the technology necessary for the creation of items that would protect against the increasingly colder temperatures may have contributed to the success of modern humans when they migrated out of Africa. The "modern" cultural behaviours attributed to *Homo sapiens,* including the production of better adapted and more complex clothing as evidenced by tools that would facilitate their production (i.e. needles), are commonly understood to have contributed to the success of this species over Neanderthals once their populations were established in Europe and following their prolonged sympatric existence of two to five thousand years in some areas (Higham *et al.*, 2014).

Cooking

Heat is a significant product of fire that may have had an evolutionary effect on hominins through its use in cooking, which will have enhanced the digestion and palatability of animal foods, resulting in a higher energy and quality diet, and mitigated the effects of the toxic and digestion-inhibiting substances found in many plants and tubers (Wrangham & Carmody, 2010). Overall, the effect would likely be a broadening of the dietary niche exploited by the populations that engaged in fire-assisted processing of resources, consequently changing selection pressures acting on the hominin digestive and masticatory systems.

Diverse and primarily vegetation-based diets are well-documented in early hominins via isotopic studies, microwear patterns and craniodental correlates (see Teaford & Ungar, 2001 for a review). Incorporating cooked plants into the hominin dietary repertoire, even after the point when animal resources joined the menu, may have allowed a much broader range of plant species to be utilised (Leopold & Ardrey, 1972; Alperson–Afil & Goren-Inbar, 2006; Gowlett, 2006) or, conversely, it might have increased reliance on a smaller range of plant foods.

Secondary compounds in plants, which include digestion inhibitors and toxins, are found in varying doses in many plants (Stahl, 1984). The issue with these compounds is not in their presence per se, but in the dosage consumed, larger doses causing more damage to the body or digestive process. Glander (1982) suggests that hominin dietary diversity offsets problems with secondary compounds by effectively diluting the amount consumed such that they only had small or entirely unnoticeable effects. Yet, cooking does often mitigate the effect of these compounds, opening up the possibility that larger amounts of plants containing them could be consumed than when raw, without suffering any negative consequences. Inhibitors act on digestion to reduce the amount of nutrients that can be adsorbed, while toxins have effects elsewhere in the body. Digestion inhibitors often impact on enzyme action. For example, trypsin inhibitors reduce the action of this protein-digesting enzyme and are found in many plant foods (Liener & Kakade, 1980). The protein structure of inhibitors is mitigated by heat, which disrupts their tertiary structure, making them inactive (e.g. Privalov & Khechinashvili, 1974). Toxins such as cyanogenic glycosides, glucosinolates, lathyrogens, gossypol and antivitamins act on other parts of the body, sometimes once they have been hydrolysed, to cause problems in the nervous system, liver, kidneys and, if the dose is large enough, they can lead to death. The effects of these compounds are also often mitigated if the food item is cooked (Stahl, 1984).

The possible effects of reduced ingestion of secondary compounds through cooking could have influenced the digestive system by relaxing the selection for dealing with such substances (Wrangham, 1984). For example, the advantages related to heightened sensitivity to xenobiotics in plants, or a more efficient detoxification system, would have been relaxed as fire reduced the need for systems to deal with these compounds (Wrangham & Carmody, 2010). However, these possible adaptive responses to reduced toxin ingestion have not, to our knowledge, been studied from this evolutionary perspective.

Along with mitigating secondary compounds, cooking may also "pre-digest" food (Milton, 2000), increasing digestibility and therefore allowing more energy to be extracted for growth and reproduction (Aiello & Key, 2002; Carmody & Wrangham, 2009). This has been demonstrated in non-human mammals. For instance, Nestares *et al.* (1996) found that rats gained more weight on a diet of cooked versus raw chick peas, and similarly Carmody *et al*. (2010) observed the same phenomenon in mice eating cooked food compared to those eating raw food. Plant foods, though containing high levels of energy dense polysaccharides, are often relatively difficult to digest when raw. Cellulose, a polysacaride making up cell walls, is highly tough and fibrous, so is not easily broken down by digestive enzymes and may prevent enzyme access to other nutritious compounds such as proteins. Humans are only able to metabolise 0.6 - 2.1% of the raw cellulose they consume (Southgate, 1973), because of the relatively short digestive tract and lack of adaptive cellulose-digesting gut flora which assist with this process in other mammal species. As a result, plants are costly to digest, with cellulose making up 33% of plant matter and only a small amount of net energy gained from their consumption. Many of the non-human primate species used to model hominin behaviour preferentially eat fruit and underground storage organs that contain less cellulose (Milton, 1980), suggesting the early hominin diet may have been restricted in a similar way. Cooking plants containing cellulose makes them much easier to digest, as heat solubilises cellulose and breaks down its physical structure (Lucas, 2011), allowing more energy to be absorbed from the plant.

The energy value of cooked meat in comparison to raw meat is less clear than that for plants. It has been suggested that cooking it increases the energy that can be gained by denaturing proteins, making them easier to digest (Carmody & Wrangham, 2009). Proteins, which comprise a significant amount of animal matter in comparison to plants, are metabolically expensive to digest, so cooking may increase the net energy that can be gained, by reducing overall digestion costs, an effect observed in captive snakes under controlled conditions (Bobeck *et al.,* 2007). Cooking also reduces the structural integrity of meat by denaturing the proteins that make up collagen, which forms muscle fibres, thus making meat not only easier to digest but much easier to chew, so less time and energy is required for mastication, similar to the effect of cooking some plant foods (Carmody *et al.,* 2011b). Cooking may also kill pathogens in meat, reducing the immune reaction costs of ingestion. Cumulatively, all of these effects may allow more energy to be diverted to the body for functions other than digestion or immune reaction.

There are, however, aspects of cooking meat which may reduce its energetic value. For example, fat is lost through dripping as it becomes liquid when heated (Bender, 1992). Since fat provides more calories per gram than protein, its loss may significantly reduce the overall energetic value of meat. The method of cooking in this regard is important though, with roasting causing the greatest loss (Bender, 1992). The Maillard reaction, in which amino acids combine with sugars to create a complex indigestible structure, may also reduce the energy content of meat when cooked (Maillard, 1916; Seiquer *et al.*, 2006). An experiment in mice did find that cooked meat improved energy gain when compared to raw meat (Carmody *et al.,* 2011a) but whether this effect is seen consistently in humans, and for what methods of cooking, needs to be evaluated in order to establish the possible effect of cooked meat on hominin evolution. Currently the literature abounds with food science studies evaluating this in modern, processed goods for purposes of improving the products or establishing links with diseases such as cancer (e.g. Sinha *et al.*, 1995; Dal Bosco *et al.*, 2001; Serrano *et al.*, 2007), with little effort directed towards wild resources or those simulating the animal resources that hominins procured (but see Wandsnider, 1997; Speth, 2000).

It is possible that the extra energy that could be gained from cooked food may have had an effect on hominin morphological and physiological evolution. Aiello & Wheeler (1995) suggest in their "Expensive Tissue Hypothesis" that the brain expansion seen in *H. ergaster* around 1.5 mya, and then again in Middle Pleistocene *Homo* around 0.5 mya, could only have occurred with the reduction of another metabolically expensive tissue, which they propose is the gut. They concluded the reduction of the gut would have been necessary to reduce the energy it required overall, thus freeing up energy that could be directed towards the brain. This theory suggests such a reduction could only occur with the introduction of higher quality diet, possibly in the form of carnivory or later, cooking.

In a more recent approach to this hypothesis (Navarrete *et al.,* 2011), no correlation between digestive tract and brain size or between digestive tract and any other "expensive" organ across mammals was found. However, brain size was demonstrated to negatively correlate with adipose deposits (see Navarette *et al.,* 2011, Fig. 2, p. 92); the trade-off between brain size and the amount of adipose tissue is hypothesised because adipose is heavy and therefore expensive to carry and maintain. By comparison to other primates, humans in fact carry a significantly greater amount of adipose, especially during infancy, and less muscle, yet also have highly encephalised brains (Vasey & Walker, 2001; Leonard *et al.*, 2007; Snodgrass *et al.,* 2009). Energy savings would be required for this relationship to have evolved. Amongst a suite of proposed behaviours and adaptions, locomotion is implicated. Bipedalism is a more metabolically efficient means of moving than other typical primate modes such as arboreal quadrupedalism, suggesting that humans can support larger fat deposits because it is less expensive to carry. The energy that adipose stores provided was likely to be one of the conditions that allowed the hominin brain to become so large at a relatively lower metabolic cost than in other species.

This renewed view of the "Expensive Tissue Hypothesis" does not, however, entirely rule out the importance of fire-induced dietary change. Encephalisation to the extent seen in the already bipedal early *Homo* would also have required an increase in energy input, which may have been provided through the consumption of cooked food at this stage and again later during the Middle Pleistocene when evidence for the control of fire and animal resource processing is more consistent and further brain enlargement occurred (Ben-Dor *et al.,* 2011; Navarrete *et al.,* 2011). Increased cognitive buffering and the ability to plan, cooperate and avoid starvation, are also likely to have unlocked the extra energy input required to fuel hominin brain expansion (Kaplan *et al.,* 2000; Navarrete *et al.*, 2011). Similarly, cooperative breeding, which is linked to food sharing, could have increased the amount of energy hominins consumed whilst also reducing the individual cost of gathering food (Burkart *et al.,* 2009). Thus, the cultural transmission of fire may have contributed to the genetic selective environment for brain size and cognition, which then provided the capacity for further invention to counteract variation in the nutritional environment.

In addition to physiological and soft tissue responses, cooking may have affected the selective environment for cranial and dental morphology, contributing to the reduced post canine dentition of *Homo erectus* (Wood & Aiello, 1998), and comparatively small facial size of later hominin species. Cooked food is much easier to chew than raw, reducing masticatory strain and selection for large molar teeth (Lieberman *et al.,* 2004). *H. sapiens* features, such as increased salivary amylase to digest starches in the mouth, reduced volume in the oral cavity, and a reduction in jaw-muscle myosin (as less force is required to chew softened food, see McCollum *et al*., 2006 for a brief summary of studies investigating the genetic mechanism behind this), may also have been influenced by consuming softened cooked food (Lucas *et al.,* 2006). Wrangham & Conklin-Brittain (2003) use such morphological correlates to date the advent of cooking to 1.9 mya and when *H. ergaster* may have eaten "the first hot meal" (Wrangham *et al.,* 1999). However, the opposing view sees hominin cranio-dental morphology at the time as being influenced more greatly by the advent of carnivory through scavenging raw animal resources of carcasses, a major step change in and of itself. In this scenario the second rapid phase of encephalisation seen in Middle Pleistocene *Homo* is due to cooking, indicating a later date for the evolution of this behaviour and correlating more closely with the archaeological record for controlled and consistent use of fire (e.g. Aiello & Wheeler, 1995).

Conclusions

We think it unlikely that there was a critical factor which "sparked" the unique trajectory of hominin evolution towards modern human morphology, behaviour and culture. However, it is clear that the harnessing of commonly experienced natural fires and the social transmission of fire creation and maintenance technology had the potential to play an important role in both cultural and genetic evolutionary dynamics within the Plio-Pleistocene hominin lineage. Determining when this occurred relies on an understanding of the residual effects of fire in the archaeological record, but we must also contend with the likelihood that the earliest phases of fire use were too ephemeral to leave clearly detectable traces. Although earlier examples are debated in the African record, evidence for the consistent use of fire emerges in the Middle Pleistocene at hominin sites such as Gesher Benot Ya'aqov in the Middle East. It spreads eventually and probably during successive events to Asia, Europe and Africa. Zhoukoudian in China provides the most compelling evidence for the independent evolution of fire use behaviour outside of the Middle East during this early stage. Fire is visible in Europe somewhat later in time and long after the initial arrival of *Homo*, raising questions about its necessity in hominin survival.

There are numerous ways in which the use of fire may have impacted upon hominin evolution, with light and heat being the two primary "drivers". As we have reviewed, light allows the active part of the day to continue into the night and heat is used to process animal and non-animal resources. Both light and heat may facilitate the exploration of and migration into cooler, northerly regions and are clearly contributors to the social function that fire has in bringing groups together for security and socialisation, as well as keeping predators at bay. The consequences stimulated by such fire-related behaviours are commonly hypothesised to be biological/physiological, such as in the light that enters the eye and the subsequent hormonal cascade which may have impacted upon sleep cycles and reproductive timing, or the consumption of cooked foods providing increased energy diverted towards encephalisation and concomitant evolution of craniodental morphology relating to the mastication of new foodstuffs. We have also emphasised the possible cultural evolutionary effects of fire use and co-evolutionary scenarios such as the way that individuals were brought together into potentially larger groups interacting with each other around a central fire source and the relationship between this social scenario and increasing brain size and cognitive complexity.

The hominin fossil and archaeological records provide sources of information regarding evidence for fire use in the Plio-Pleistocene and the evolutionary consequences of this behaviour. Future work should seek to develop a biogeographical picture of the evolution of fire use, as well as an explanation for the long gaps in time that occur in between the first few observable traces of fire and its widespread, intentional use (be this a consequence of genuinely limited use in the initial stages or taphonomy). Additionally, research should focus on setting the use of fire in a palaeoecological context to test hypotheses of dispersal and niche construction. Many of the more nuanced physiological effects may be difficult to detect in the past and pursuing a line of enquiry that includes determining how firelight and heat impact on extant mammals, especially non-human primates and modern humans in different ecological and cultural settings, will assist in substantiating some of the current hypotheses and determining the extent which the effects had a significant influence on the evolution of the global, social species that we are today.

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