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Changes in the average of mankind in the historic period have come about more by expansion of some types and decrease and absorption of others than by uniform evolutionary advance. During the recent period, no doubt, the phases of intergroup competition and crossbreeding have tended to overbalance the process of local differentiation, but it is probable that in the hundreds of thousands of years of prehistory, human evolution was determined by a balance between these factors. (Wright 1932)

From Conventions to Institutional Norms

Most mammals are social, although significant variation in social complexity is observed across species (Clutton-Brock 2016). Studies of social behavior have addressed primates more than any other mammalian order (Silk and Kappeler 2017), revealing a diverse set of mechanisms mediating social relationships. In chimpanzees, for example, hand clasps and other traditions have been classified as conventions, or sets of arbitrary and socially transmitted rules regulating behavior in some but not all populations (Whiten et al. 1999). However, although conventions seem to suggest that certain behaviors are desirable or expected among chimpanzees, there is no convincing evidence that violations of such behaviors generate frequent emotional reactions or active punishment by bystanders (Bicchieri 2006). In contrast to conventions, behaviors such as aggression toward infants are often met by strong negative reactions and even defensive coalitions of unrelated chimpanzees (Newton-Fisher 2006), implying the possible existence of 'proto-norms' or parameters of appropriate social behavior (von Rohr, Burkart, and van Schaik 2011).

By contrast, social norms in human groups regulate social life much more extensively than conventions and proto-norms in chimpanzees. Social norms often imply universal or collective rules prescribing the behaviors of all group members and general agreement on the punishment of violators even by observers not directly affected (Fehr and Fishbacher 2004b). Prescriptive norms generally accepted in groups are often described as institutions, which are conspicuous in structured states and large-scale societies. However, they can also be identified in extant hunter-gatherer groups adopting a subsistence system typical of humans prior to the advent of agriculture.

¹ This chapter is drawn from the following book:

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From this perspective, institutions range from strict rules for food sharing and gender equality in extant hunter-gatherers (Dyble et al. 2016; Kaplan et al. 2000) to general kinship systems found across human societies. As a unique human feature, institutionalized norms must therefore have first evolved in ancestral hunter-gatherers.

In this chapter we attempt to explain the transition from ape-like social regulation in earlier hominins to the more complex normative behavior found in human societies including extant hunter-gatherers. We argue that the transition was a consequence of the evolution of a unique foraging niche including hypercooperation, roughly defined as intensive cooperation toward both related and unrelated individuals (Burkart et al. 2014). Hypercooperation is seen as an ancestral human feature observed both in extant hunter-gatherers (Kaplan et al. 2000) and contemporary societies, where it extends to anonymous individuals (Fehr and Fischbacher 2004a; Moffett 2019). Due to hypercooperation, human societies have often been described as a new form of social entity structured by a new form of biological information (Maynard Smith and Szathmary 1995) or as a 'collective brain' (Muthukrishna and Henrich 2016) exhibiting unique collective intelligence (Woolley et al. 2010) and problem-solving abilities (Wilson, Timmel, and Miller 2004). Such fundamental transition in sociality, with its associated biological and structural features, only occurred in some ancestor of *Homo sapiens* and might have required the evolution of social norms and institutions to regulate the human collective brain (Migliano and Vinicius 2021).

Given the evidence of cultural transmission and its pervasiveness across human societies, the evolution of social norms and institutions may be better understood within the broader context of human cumulative cultural evolution. Hill (2009) classified human cumulative culture into three domains: technology (socially transmitted information related to exploitation of the material world), social norms (information regulating social organization), and symbolic systems (moral regulation of social rules). The three domains are connected, with social norms regulating the transmission of technology and distribution of its products and symbolic systems (including institutions such as kinship and marriage) regulating human social behavior. In the following, we examine the evolution of the social niche in earlier hunter-gatherer humans, its relationship with human cumulative culture, and how human social norms and institutions may have evolved as a dimension of culture regulating human collective brains. Specifically, we propose that social norms and institutions evolved early in hunter-gatherer groups to regulate distribution of benefits derived from technology, division of labor and role specialization, and between-group trade as ancestral hunter-gatherers gradually expanded their social networks and created large metapopulations in Africa (Migliano and Vinicius 2021; Padilla-Iglesias et al. 2022; Scerri et al. 2018).

Current Views on the Evolution of Human Social norms and Institutions

Hill's classification highlights the role of social norms in the regulation of human hypercooperation (Fehr and Fischbacher 2004a, b; Fehr and Schurtenberger 2018). The related concepts of parochial altruism (Bernhard, Fischbacher, and Fehr 2006; Choi and Bowles 2007) and cultural group selection (Boyd and Richerson 2009; Richerson et al. 2016; Soltis, Boyd, and Richerson 1995) have become particularly influential in accounting for how and why social norms evolved as a dimension of cumulative culture. They have in common the idea that unique patterns of within-group cooperation in humans are mostly the selective outcome of between-group competition and hypercooperation and later large-scale sociality have evolved due to the operation of norms ascribing individuals with a shared social identity. The combination of ingroup cooperation for more cohesive social units, and the spread of successful groups with their norms and institutions (Handley and Mathew 2020). The long-term operation of cycles of competition and selection of culturally defined groups would explain the eventual emergence in *Homo sapiens* of more complex institutions underlying religions and central governments in large-scale societies.

Although parochial altruism and cultural group selection provide a coherent account of various features of human sociality, the models face a few challenges. For example, some authors have concluded that hypercooperation must be a recent human phenomenon, derived from the emergence of large-scale societies exhibiting warfare, formal obligations toward established leadership or states, and religions based on punishing gods (Purzycki et al. 2016). Since such features emerged late in human evolution in complex hunter-gatherers and became more frequent in the Neolithic period, by implication small-scale societies, and especially extant hunter-gatherers with no formal concept of state or church, should exhibit relatively lower levels of within-group cooperation. Accordingly, some experimental studies have proposed that Westernized societies show much higher levels of prosociality, and more trustworthy individuals concerned with the common good, than extant hunter-gatherer groups (Henrich 2020). By contrast, other studies have proposed a more inclusive view that acknowledges hypersocial behavior as a human universal (Burkart et al. 2014; Fehr, Fischbacher, and Gächter 2002), and hence an ancestral human, trait. It should be noticed that, according to the parochial altruism view, the ancestrality of hypercooperation also implies that between-group conflict or even warfare must have already been frequent in the common human ancestor. For example, Choi and Bowles (2007) have explicitly argued that cultural group selection and conflict in remote ancestors is the best explanation for human cooperation in past and present hunter-gatherers.

However, evidence of warfare at the origin of *Homo sapiens* or from the archaeological and fossil record of past hunter-gatherers remains scarce. A recent analysis showed that if warfare in Australian hunter-gatherers was as frequent as required by Choi and Bowles (2007), expected

levels of genetic differentiation between groups would be seven times higher than observed (Dyble 2021). Thus, relatively low levels of genetic differentiation between extant hunter-gatherer groups seem to rule out warfare as a major long-term mechanism promoting within-group cooperation. By contrast, in the recent evolutionary past, events of conflict and warfare have been identified in Nataruk at 14–12 kya (Lahr et al. 2016), Jebel Sahaba at 13.4 kya (Crevecoeur et al. 2021), and more recent groups such as the complex hunter-gatherer groups in North America from 5 kya (Schwitalla et al. 2014). Therefore, conflict and warfare seem to have been more recent in *Homo sapiens* than implied by the theory of parochial altruism and possibly limited to more territorial groups occupying monopolizable areas such as lake shores, where the presence of large fauna was more predictable. Finally, inter-group competition and large-scale warfare seem to be equally rare events among extant hunter-gatherer groups (Fry and Söderberg 2013), casting additional doubts on parochial altruism as the explanation for the origin of hypercooperation in humans.

Another issue relates to the evolution of large-scale cooperation, defined as events or activities involving the simultaneous participation of many individuals or whole communities (Boyd and Richerson 2022). Examples of large-scale cooperation in extant hunter-gatherers, such as net hunting in /Xam San recruiting up to 70 people (Manhire et al. 1985), are surprisingly rare, and evidence from the archaeological record, including warfare, is relatively recent (Boyd and Richerson 2022). By contrast, examples of hypercooperation typically involving many fewer individuals at any given time, such as cooperative breeding and hunting within groups, are virtually universal among extant hunter-gatherers (Kaplan et al. 2000). Therefore, on the basis of current evidence, small-scale cooperation seems to be a better candidate for a human ancestral trait than large-scale activities within groups. Nonetheless, the archaeological record provides convincing evidence of between-group cooperative activities in earlier Homo sapiens populations, such as long-distance trade dating back to over 180 kya (Blegen 2017). This possible combination of small-scale within-group cooperation and extended cooperation among distant groups in earlier hunter-gatherers is in stark contrast to the scenario emerging later in the Neolithic period, characterized by large-scale cooperation, between-group conflict, and state formation (Powers and Lehmann 2013; Stanish and Levine 2011). In summary, hostile group-level interactions may have contributed to hypercooperation in complex or large-scale societies in the recent human past. However, between-group conflict does not seem to be a convincing explanation for the deep origins of hypercooperation, long-range trade between groups, and associated ancestral social norms and institutions.

We are therefore left with a dilemma. While evidence of hypercooperation from huntergatherer groups to historical populations supports the idea of its universality and ancestrality, there is not enough evidence that hypercooperation can be explained by group-level competition, largescale organization, or central institutions. The implication is that selective pressures behind human hypercooperation may have already been present in the foraging niche of earlier hunter-gatherers, before the Neolithic transition, before the first dispersals of *Homo sapiens* out of Africa, before the split between the Southern African Ju'/hoansi and other hunter-gatherers at around 120 kya, and therefore at the origins of modern humans (Migliano and Vinicius 2021). In summary, an alternative explanation may be necessary to reconcile the early origins of hypercooperation in hunter-gatherers, the role of norms and institutions in human groups, and the relative scarcity of between-group competition.

Human Hypercooperation: Social Norms and the Regulation of Collective Brains

Until recently, it was widely believed that hunter-gatherers lived in small bands and only cooperated with known or related individuals (Steward 1968). This misconception added to the puzzle regarding when and why social institutions became necessary to regulate and coordinate human cooperation. In fact, if cooperation in hunter-gatherers living in small-scale groups could be solely explained by mechanisms such as kin selection and indirect reciprocity found in other mammals, it would follow that hypercooperation must be a later phenomenon following the emergence of large-scale societies and their institutions.

However, extant hunter-gatherers exhibited high levels of cooperation within groups as described above. They also exhibited a fluid social structure extending beyond kinship networks and covering multiple camps over large geographic areas (Migliano et al. 2017; Migliano et al. 2020). A study of 32 hunter-gatherer groups showed that camps consisted mostly of unrelated individuals (Hill et al. 2011), with high inter-camp mobility and fluid camp composition implying potential interactions with hundreds and sometimes thousands of individuals over a lifetime (Hill et al. 2014). A recent study (Bird et al. 2019) proposed that high interconnectivity among Australian hunter-gatherer bands produces real hunter-gatherer 'states' with no central authority but covering hundreds of kilometers and multiple languages. In Central Africa, forest spirit rituals regulate the use of forests across multiple interconnected hunter-gatherer camps and even ethnicities (Lewis 2019). We have recently shown that evidence of connectivity between geographically distinct hunter-gatherer groups goes deeper in time, with significant levels of genetic exchange between Western and Eastern African groups for at least 120,000 years (Padilla-Iglesias et al. 2022).

The evidence of cooperation with unrelated individuals and large social networks in hunter-gatherers suggests that social institutions may have played a long-term role in regulating and coordinating cooperative behaviors in humans. We therefore propose that the first social norms and institutions exclusive to humans originally evolved to coordinate cooperation within groups and were later extended to regulate between-group connectivity and trade in early modern humans (Migliano and Vinicius 2021). More explicitly, we propose that social norms and institutions evolved cumulatively, first as cultural rules for sharing knowledge or resources within groups, such as food sharing or knowledge sharing (social integration within groups), and later as rules for cultural or economic exchange across interconnected groups, including rules mediating between-group trade (market integration between groups). The evolution of human societies into collective brains would result in structural properties characterizing major evolutionary transitions (Maynard Smith and Szathmary 1995), such as (i) specialization among functional types, (ii) modularity or differentiation across functional subgroups, and (iii) integration or functional interdependence among modules. Human groups would have increasingly benefited from a combination of skill differentiation and interdependent specialists, only possible due to increasing returns from culturally transmitted lithic and non-lithic technologies, resulting in increased collective intelligence (Wooley et al. 2010), uniquely complex cumulative culture (Migliano et al. 2020), and the requirement of between-group exchanges to avoid cultural loss (Henrich 2004).

How Material Culture Produced Collective Brains and Institutions

From the above it follows that social norms and institutions evolved in stepwise fashion in Homo sapiens, and possibly earlier, as consequences of selection for increased efficiency of transmission and recombination of material culture. The sophistication of and dependence on paleolithic technology is known to have gradually increased from australopithecines to Homo sapiens (Kuhn 2020; Migliano and Vinicius 2021). From at least 3.2 mya, early hominins already relied on lithic technologies to a significantly larger extent than African apes and used stone tools for butchering or extractive foraging of meat as a high-value resource (Carvalho et al. 2019; Harmand et al. 2015). Despite the intrinsic difficulty of reconstructing early hominin behavior, archaeological, comparative, and experimental evidence seem to suggest that Oldowan from around 2.6 mya (Braun et al. 2019) and more likely Acheulean lithic industries from 1.6 mya (Semaw et al. 2020) required cultural or horizontal transmission, possibly assisted by gestural language evolving as a specific tool-making teaching aid (Cataldo, Migliano, and Vinicius 2018; Morgan et al. 2015). The requirement of cultural transmission and teaching would provide compelling evidence that hominin technology, even at the stage of complexity observed in the first lithic industries, consisted of a body of knowledge that could not be recreated by a single individual and had to be socially learned from or taught by other group members (Dean et al. 2014).

The fact that a decreasing fraction of culture could be transmitted and stored by single individuals had an important consequence. As cultural accumulation proceeded, hominin material culture gradually evolved from a private and monopolizable good, as observed in other apes where cultural transmission occurs mostly if not exclusively within matrilines (Wrangham et al. 2016) and where most of a small cultural repertoire can be learned by a single individual (Bandini and

Tennie 2017; Boesch 2012), into a horizontally transmitted common or public good accessible through cooperative interactions. For example, while medicinal plant knowledge among a sample of about 200 Bayaka hunter-gatherers encompassed approximately 35 species in total, average knowledge did not exceed 20 plants, and no individual possessed knowledge of the full set (Salali et al. 2016). We may equally interpret the complex culture represented by durable artifacts from the Middle Stone Age onward as the cumulative product of a cooperative community of innovators, teachers, and selective learners collectively contributing to the curation of a large pool of techniques.

We therefore favor a scenario where social norms and institutions may have originally evolved as cultural mechanisms regulating the sharing of technology, the dimension of cumulative culture directly affecting components of individual fitness through its effects on foraging, survival, and reproduction. The increasing individual benefits of technology may have been enough to provide the selective context for the evolution of social norms and, at a later stage, the evolution of institutions and symbolic systems regulating social norms themselves. Together, the three dimensions of cumulative culture proposed by Hill (2009) may explain the existence of social roles and skill complementarity in collective human brains.

A Brief History of Cumulative Culture and Social Integration from African Apes to *Homo* sapiens

If human social institutions gradually evolved as mechanisms to regulate the creation, teaching, and sharing of complex cumulative culture within collective brains, they cannot be a recent outcome of post-Neolithic population expansions. They should instead be the outcome of a deep history of cultural evolution differentiating hominins from other African apes. Despite examples of cultural accumulation, information transfer, and even incipient teaching (Musgrave et al. 2020), no tools beyond combinations of three parts or sequential stages have yet been observed in chimpanzees or bonobos (Boesch 2012). Resources such as nuts and honey resulting from tool-assisted foraging are most often described as fallback foods making a small contribution to ape diets (Marshall and Wrangham 2007). In addition, hunting of red colobus or Diana monkeys has never been associated with tool use. Overall, this suggests potentially low benefits from common cultural goods in chimpanzees and bonobos. Unsurprisingly, despite the existence of cultural traditions mediating social interactions in non-human apes, no signs of pervasive conventions or proto-norms specifically regulating general access to tools have been identified so far.

By contrast, the archaeological and fossil record suggests that australopithecines already consumed larger amounts of meat than any extant African ape (Balter et al. 2012; Tennie, O'Malley, and Gilby 2014), with *Homo erectus* showing increased consumption of meat and underground storage organs (Anton, Potts, and Aiello 2014). Exploitation of high-quality savannah

resources in australopithecines and *Homo* may have started with the scavenging of large carcasses, as demonstrated by increased use of C4 resources in *Australopithecus afarensis* (3.4–2.9 ma) and *Kenyanthropus platyops* (3.3 ma), possibly requiring percussive use of stone tools for bone marrow exploration (Carvalho et al. 2019; Wynn et al. 2013) and butchering from 3.4 ma (Braun et al. 2019; Harmand et al. 2015; McPherron et al. 2010,). After the emergence of *Homo erectus*, evidence for greater reliance on group scavenging (Hatala et al. 2016) is provided by a further increase in the consumption of meat and aquatic resources near lake shores, higher C4/C3 isotope ratios, and larger home ranges (Cerling et al. 2013; Patterson et al. 2019) and foraging groups, if we trust evidence from footprints (Roach et al. 2016) and comparisons with other primates in open environments (Willems and van Schaik 2017). In summary, the association between increased meat consumption and tool use indicates dependence on socially transmitted technology in earlier hominins to a degree not observed in extant African apes.

Later, the fossil and archaeological record of early Homo sapiens in Africa points to more frequent between-group interactions, and possibly more extensive market integration, with convincing evidence of continental-scale networks, trade and exchange of materials, and migration among differentiated populations. Two examples seem to provide clues to within- and betweengroup norms regulating material and cultural exchanges. First, from 200 kya the transport of obsidian (a high-quality raw material used in the production of stone tools) covered distances of up to 160 km in East Africa, beyond the home range of extant hunter-gatherers (Blegen 2017). This may suggest that raw materials were circulating across trade networks and distinct groups. Further evidence comes from long-distance transport of pigments used for artefact and personal decoration up to 50 km as early as 320 kya (Brooks et al. 2018), pointing to a possibly ancient origin of group identity markers in the absence of widespread inter-group conflict. Second, ochre-processing workshops at 100 kya (Henshilwood et al. 2011) demonstrate the recombination of various techniques created at distinct times and locations, including pigment and point production at 320 kya (Brooks et al. 2018), charcoal and fire at 780 kya (Gowlett 2016), and shell fishing at 164 kya (Marean et al. 2007). Workshops may indicate that widely distributed human populations were exchanging technical information rather than independently recreating techniques and locally sourcing materials. Together, the evidence from early hominins to early *Homo sapiens* points to a gradual increase in levels of social integration, possibly starting with cultural transmission mostly at the scale of matrilines and cooperation among related individuals in ape-like ancestors and followed by the emergence of larger foraging groups exploiting more valuable resources in Homo erectus and eventually by integration at market level among differentiated and interdependent groups in Homo sapiens.

Social Integration and Collective Regulation

Ethnographic evidence has shown that cooperation and social integration within huntergatherer groups are often regulated by social norms (Glowacki and Lew-Levy 2022; Henrich and Boyd 2008). For example, Central African Aka forager children are punished by parents for not assisting in childcare (Boyette 2019). Batek children from Malaysia are also punished by parents for aggressive behavior (Endicott and Endicott 2014). Social norms can also be acquired from unrelated peers and in playgroups where children from different families simulate adult social behaviors such as cooperative foraging, food sharing, and sex division of labor (Lew-Levy et al. 2020; Wiessner 2005).

Due to fluid sociality and constant mobility, extant hunter-gatherers often face problems misleadingly associated with the recent evolution of large-scale societies, such as difficulty in tracking reputations and measuring reciprocity in interactions with hundreds and possibly even thousands of individuals met over a lifetime (Hill et al. 2014). Since direct identification of violators and rule enforcement are often difficult to achieve, we observe the operation of some social institutions that seem to serve to enforce rules at a collective scale. For example, the BaYaka *mòsámbò* (Lewis 2014) and central African Aka *sámbò* (Thomas and Arom 1991) institutions are based on elders making public speeches in order to solve public problems in a persuasive rather than coercive way. The Ju/'hoansi also perform a ritual where three to eight adults voluntarily speak to a public audience and solve collective issues (Konner 2015). Among the Agta from the Philippines, storytelling plays a role in spreading norms of cooperation and equality in more general and abstract terms across individuals, demonstrated by an association across camps between the number of skilled storytellers and increased cooperation (Smith et al. 2017).

Division of Labor and Cultural Specialization

Division of labor is an often-neglected aspect of social organization in extant huntergatherers (Bednar 2022). For example, medicinal knowledge is a fundamental aspect of huntergatherer cumulative culture and social life (Salali et al. 2016), and central African hunter-gatherers exhibit a diversity of healers specializing in infant and general health, family issues, sorcery, jealousy, exorcism, and negotiation with threatening forest entities, among others (Bombjaková 2018). Other specialist roles performed by designated individuals include public speakers, spirit guardians, song composers, and ritual runners (Lewis 2019). Another example is that while hunting is a general male task, elephant hunters were limited to a few individuals (Lewis 2019). Finally, ethnographies of central African hunter-gatherers have identified a few elderly men in charge of communicating with external members, demonstrating the importance of inter-group relations (Bombjaková 2018). We also find evidence of interdependence among individuals with complementary skills in addition to production of complex cultural traits by recombination, such as the mixing of medicinal plants into cocktails and transmission of knowledge through specialized social network channels (Salali et al. 2016). We therefore observe a level of social differentiation beyond the combination of strategies found in other species, such as the coexistence of cooperators and free-riders (Lewis et at. 2014) or producers and scroungers (Harten et al. 2018), which may become stable under certain circumstances. Moreover, while producers do not depend on scroungers and cooperators do not depend on free-riders, social roles in hunter-gatherers seem to be interdependent and generate mutual benefits. Although explicit rules about social roles are hard to identify in the ethnographic record, an informal social contract seems to assure that individuals may become specialists and hence dependent on others.

From Social to Market Integration

Specialization and integration at the group level in trading markets also occur in huntergatherers, taking the shape of regional differentiation of labor and economic roles (Bhui, Chudek, and Henrich 2019). An example of a regulatory system operating between groups is the Hadza lukuchuko gambling game that results in the circulation of rare goods over hundreds of kilometers (Marlowe 2010). The Ju/'hoansi hxaro is another well-studied gifting system based on a strict set of rules regarding establishment of friendships, rights, and obligations among individuals across various residential camps in the Kalahari Desert (Wiessner 1998). A network of Baka and Aka hunter-gatherers extending across Cameron, Gabon, and Congo Brazzaville, as well as across language groups (Furniss and Joiris 2011), allows groups to exchange musical and costume elements used in spirit plays, copying rituals and songs while preserving their own repertoires (Bonhomme, De Ruyter, and Moussavou 2012; Lewis 2015). Importantly, the fact that ostrich eggshell beads dating back to 33 kya closely resemble those described in studies of hxaro suggests that current exchange systems may be direct descendants of long-range trade networks in operation since the Middle and Late Stone Age (Stewart et al. 2020). This would provide another argument for an early origin of norms and institutions regulating between-group interactions in humans and for their close link to benefits associated with material culture.

The examples above demonstrate that between-group integration was already a key feature of hunter-gatherer social structuring before the origin of and subsequent contact with farming populations. Economic games conducted in small-scale societies have revealed a consistent correlation between cooperation and market integration in hunter-gatherers, horticulturalists, and farmers (Henrich et al. 2005). However, the association in hunter-gatherers has often been attributed to a reactive or passive transition from cooperation mostly with kin to a broader range of economic and social interactions with neighboring farming or industrial societies. An alternative

explanation is that an increase in market size resulting from contact may increase rewards from further specialization and interdependence and may therefore be actively pursued by huntergatherer groups. An example is the trade that often takes place when hunter-gatherers and farmers overlap in territory, with the former specializing in forest products in exchange for crops. From this perspective, hunter-gatherers are not introduced into the market economy, but instead extend their markets beyond the frontiers of their own ethnic groups and original economic systems. This could explain the phenomenon of 'embeddedness' (Schweizer 1997), whereby small-scale populations including hunter-gatherers adapt and take advantage of opportunities to integrate into larger economic and social networks with their neighbors. This suggests that cultural rules regulating differentiation among interdependent individuals, multiple trades, and economic niches may have gradually evolved within and between human social groups. Therefore, market integration may have been an ancestral process central to hunter-gatherer societies and later extended after the spread of agriculture.

Surviving Market Institutions in Complex Hunter-Gatherers and Post-Neolithic Populations

Human populations grew larger and more sedentary in complex hunter-gatherers and post-Neolithic groups. Arguably, territorial defense and conflict may have brought about further regulation of within-group cooperation and collective action (Carballo, Roscoe, and Feinman 2014), with parochial altruism and between-group competition becoming significant factors behind institutional change. However, it is reasonable to assume that regulation of the collective brain or market integration may have continued to play a role in between-group cooperation, in spite of increased between-group conflict. Examples are represented in this volume by the *Potlatch* ritual in complex hunter-gatherers from the Northwest coast of North America, where people competed through gift giving for cooperation or status, resulting in the distribution of goods across multiple groups (Smith, Mattison, and DiNapoli 2022), a system also present at a smaller scale in BaYaka hunter-gatherers (Chaudhary et al. 2016). Wiessner (2022) has described how the Enga from the Papua New Guinea highlands establish Yae Tee partnerships based on the circulation of gifts, preventing between-group conflict and preserving the trade of diverse products over large areas. Another example of institutions integrating markets is the *kula* ring ritual in the Trobriand Islands, also based on a gift system that prevents the economic and social isolation of communities separated by large geographical distances (Malinowski 1922). Thus, institutions regulating social behavior and cooperation may have first appeared in ancestral Homo sapiens and later diversified with the emergence of complex hunter-gatherer and farming populations.

Conclusion: Social Norms, Cumulative Culture, and the Evolution of Collective Brains

From a macroevolutionary perspective, Maynard Smith and Szathmary (1995) defined major transitions as a set of eight evolutionary processes of unique importance due to two features. First, they engendered new systems of biological information or inheritance (for example, the origin of information-storing DNA molecules and the genetic code). Second, they involved the origin of new types of biological structure through the grouping of previously independent units (for example, the emergence of multicellular organisms from preexisting unicellular species). They described the evolution of human societies from ape-like ancestors as the last major evolutionary transition, corresponding to a new form of social unit structured by language.

However, it is arguable that the role of a new inheritance system binding human societies together was played by human cumulative culture in all its dimensions. Cumulative culture comprises multiple technologies, including communication (language), material culture (tools, medicinal knowledge, environmental knowledge, cosmology), and social regulation (norms, institutions, associated belief and symbolic systems). Since cumulative cultural processes gradually engendered technical repertoires beyond the capacity of single individuals, material culture evolved from a private to the most valuable common good available to earlier humans. Social norms and institutions may have thus evolved as mechanisms organizing individual contributions to and participation in this common good. This perspective highlights the increasing rewards from inclusion into larger cultural and economic markets in ancestral hunter-gatherers and how specialisztion and interdependence may have created more integrated collective brains. Finally, in addition to the widely discussed process of cultural ratcheting, our perspective draws attention to the fact that extended networks in hunter-gatherers have also produced a 'social ratchet' where specialization within populations becomes an irreversible evolutionary outcome.

Reconstructing the origin and evolution of culturally transmitted norms and institutions in the hominin lineage since our split from a common ancestry with African apes is a daunting task. However, by investigating the social structures of extant simple hunter-gatherers, as well as the evidence of extensive social networks and long-distance trade in early modern humans, we believe that regulation of social interactions, trade, and technological exchanges may have been present at least since the origin of *Homo sapiens* over 300 kya (Bergström et al. 2021; Mounier and Lahr 2019). We therefore speculate that the regulation of collective brains and exchange of knowledge through norms and institutions may have been present in the first hunter-gatherers, later taking new forms in complex hunter-gatherers and post-Neolithic societies, and finally in historic and Westernized societies. Hence, the processes currently identifiable in current hunter-gatherers as social and market integration may also have been a key social feature in earlier hominins. This perspective does not deny that between-group conflict in the manner envisaged by parochial altruism and cultural group selection has become a more influential factor in relatively recent times. We therefore mirror the view proposed by Sewall Wright (1932), who emphasized the

importance of between-group interconnectivity as a catalyzing force for most of human evolution. We conclude that human norms and moral systems can be seen as social technology tools responsible for the coordination of functions of collective brains and as such were the product of stepwise cumulative cultural evolution.

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