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Cooperative feeding and breeding, and the evolution of executive control

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Abstract Dubreuil (2010b, this journal) argues that modern-like cognitive abilities for inhibitory control and goal maintenance most likely evolved in *Homo heidelbergensis*, much before the evolution of oft-cited modern traits, such as symbolism and art. Dubreuil's argument proceeds in two steps. First, he identifies two behavioral traits that are supposed to be indicative of the presence of a capacity for inhibition and goal maintenance: cooperative feeding and cooperative breeding. Next, he tries to show that these behavioral traits most likely emerged in *Homo heidelbergensis*. In this paper, I show that neither of these steps are warranted in light of current scientific evidence, and thus, that the evolutionary background of human executive functions, such as inhibition and goal maintenance, remains obscure. Nonetheless, I suggest that cooperative breeding might mark a crucial step in the evolution of our species: its early emergence in *Homo erectus* might have favored a social intelligence that was required to get modernity really off the ground in *Homo sapiens*.

1 Introduction

There is a growing trend against the model known as the “Human Revolution”, according to which modern behaviors (such as art and symbolism) emerged suddenly some 50,000 years ago, an event supposedly signaling a dramatic cognitive advance, most likely triggered by a reorganization of the human brain (see, most notably, McBrearty and Brooks, 2000, and the collection of essays in Mellars et al., 2007). Against the model, scholars in various disciplines nowadays try to offer an account portraying the evolution of human culture and of human higher cognitive abilities as gradual, rather than abrupt.

Following this trend, Dubreuil (2010b, this journal) provides an argument meant to show that two fairly modern behaviors (i.e. human cooperation in matters of feeding and breeding), supposedly indicative of two fairly high-level cognitive capacities (i.e. inhibitory control and goal maintenance), can be traced back to *Homo heidelbergensis* (700,000 - 300,000 years ago).¹ If his

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¹ A similar argument is found in Dubreuil's book *Human evolution and the origins of hierarchies* (2010a). There, however, the focus is more on joint attention and norm following than on executive control; and on how these abilities account for the evolution of cooperative feeding and breeding in humans. Here I will focus on executive control for two reasons: first, because Dubreuil's discussion of joint attention and norm following has already been criticized by Driscoll (forthcoming; see more below); and second, given that executive control is a necessary, but *not* sufficient condition for norm following, any problem for Dubreuil's views concerning executive control is *de facto* a problem for his views concerning norm following. In light of this, I will refer to Dubreuil's book only when useful.

argument is sound, Dubreuil indeed has a case against the “Human Revolution”, since some forms of higher-level cognition (c.q. inhibition and goal maintenance) would have been around some 250,000 - 650,000 years *before* the supposed great leap forward.

However, in the next few sections I show that Dubreuil’s argument fails. I do so in two steps. First, I explain that cooperative feeding and cooperative breeding are poor indicators of inhibition and goal maintenance (Section 2 & 3). So even if one could date the emergence of these two cooperative behaviors (which Dubreuil fails to do, see the second point), that wouldn’t suffice as evidence for the emergence of the two higher cognitive traits.

Second, I show that Dubreuil likely misdates the occurrence of human cooperative feeding and cooperative breeding (Section 4). Science’s best conjecture is that these behaviors arose in *Homo erectus*, ca. 1 million years before *Homo heidelbergensis*.

Both points of course do not imply that the idea of the “Human Revolution” is true. They do show, however, that Dubreuil’s argument doesn’t provide (extra) reason to abandon it. Still, I think that cooperative breeding *can* be used as evidence against the “Human Revolution”, and in the final section (Section 5) I suggest how.

2 Cooperative feeding and executive control

According to Dubreuil (2010b), two cooperative foraging strategies stand out as evidencing increased executive control in the *Homo* lineage: hunting in group and extensive food sharing. In both, Dubreuil believes, cooperation is secured by agents’ ability to stick to the cooperative arrangement (i.e. goal maintenance) and the ability to resist the temptation of acting self-interestedly (i.e. inhibition).

This seems an intuitively plausible interpretation. Prospective cooperators have an incentive to consume the public good, without contributing to it. In case of food sharing, the temptation is to receive food, but not to give away. To secure cooperation, then, agents must keep in mind the goal and benefits of long-term sharing relationships (e.g., pooling risks yields a more regular energy intake), and inhibit the current desire to eat a bit more now, at the expense of eating less later.

In case of hunting the temptation is to drop out early from the hunting coalition (thereby putting others at a greater risk), yet get hold of a piece of meat. Again, joint hunting is stable and effective, only if individual hunters stick to the shared goal, and inhibit impulses to step aside and put themselves in safety (rather than to do their fair share of stone-throwing and clubbing).

Yet, there are two reasons for thinking that both cooperative behaviors are poor indicators of inhibition and goal maintenance. The first is that cooperative hunting and food sharing is widely present in our closest relative the chimpanzee, which lacks advanced, human-like mechanisms for inhibition and goal maintenance. The second reason is that much simpler cognitive mechanisms may explain cooperative hunting and food sharing. Let me address these issues each in turn.

2.1 Hunting and meat sharing in chimpanzees

Dubreuil acknowledges that joint hunting and meat sharing is present in apes, yet thinks these practices are not as pervasive as in humans. The advent of cooking and large-game hunting (presumably in *Homo heidelbergensis*) has made cooperation in matters of meat necessary and default, and—so Dubreuil thinks—required mechanisms for inhibition and goal maintenance (i.e. in humans, but not apes).

The first problem with this line of reasoning is that the human diet is probably not as meat-based as Dubreuil suggests. In colder climates, meat may perhaps account for a large fraction of energy intake, in the tropics and the subtropics, many traditional hunter-gatherers forage primarily for plant foods, and meat is only a very small part of the overall diet—indeed, just like in our closest relative the chimpanzee (Stanford, 2001). Interestingly, Dubreuil (2010b, p. 60; 2010a, p. 70) makes the very same observation, yet shies away from the fairly obvious consequence: that the necessity of sharing may be as large/small for chimps as it is for humans.

But even if one grants that humans cooperate more pervasively, there is a second, more fundamental problem. The *pervasiveness* of a practice doesn't count as extra evidence for the reality of the mechanisms supposedly subserving it. For an existential proof, a species-wide observation of the practice suffices—whether or not the practice is more pervasively present than in another species. For instance, the fact that subtropical human foragers hunt not as frequently as their colleagues in cooler climates, doesn't imply they don't have the requisite mechanisms for inhibition and goal maintenance. Rather, subtropical foragers are not as frequent hunters, most likely because plant foods are more abundantly and reliably available in subtropical habitats. The crucial fact is that they are able to and do in fact hunt, not how often they do. In a similar vein, then, the robust, species-wide observation of joint hunting in chimpanzees (see e.g., the overview of Muller and Mitani, 2005), though less pervasively as in humans, should suffice to demonstrate chimpanzees' capacity for inhibition and goal maintenance (or any other capacity deemed necessary for joint hunting)—unless Dubreuil can show that human and chimpanzee hunting are *qualitatively* (rather than quantitatively) different, and additionally, a much harder nut to crack, that that qualitative difference is attributable to a difference in capacities for executive control.²

Now, in his detailed comparison of hunting practices of traditional hunter-gatherers and chimpanzees, Stanford (2001) finds seven such qualitative differences. But only one of these directly links to cooperation: whereas cooperation in chimpanzees just involves increased numerical strength, cooperation in human hunters is actively coordinated through vocal and/or gestural communication. Inasmuch as prehistoric hunters can be modeled on contemporary traditional hunters, it would be more natural to argue that human cooperative hunting depends on improved communicative abilities, rather than on better executive control (inhibition, goal maintenance).

Stanford also observes a difference that indirectly links to cooperation. Humans bring back their (excess) returns to share with individuals not present at the kill; chimpanzees, in contrast, eat and share meat from hand to mouth on the spot. Whether this difference attests to a difference in executive control cannot be taken for granted, though, for differences in locomotion (bipedal vs. quadrupedal) provide a much more parsimonious explanation for the lack of meat transportation in chimps, and consequently for their smaller networks of exchange.

Incidentally, Dubreuil (2010a, p. 71) observes that chimpanzees are not as fond of sharing as humans. Yet again, it remains to be shown that this difference is due to a difference in executive functions. Plausibly, in order to be able to share, sharing-averse individuals need *more* inhibitory control than individuals endowed with a spontaneous prosocial psychology.

Finally, meat sharing in chimpanzees can be reconstructed in terms of inhibition and goal maintenance just as easily as meat sharing in humans. According to a first common explanation of chimp meat sharing, meat is shared with others to build and strengthen social bonds (de Waal, 1998); according to a second, males share meat with females, and hope to get sex in return (Stanford et al., 1994; Stanford, 1996). Here is the reconstruction: on both accounts, current appetite is suppressed for a future goal (strategic and reproductive, respectively).

To be sure, I don't deny that contemporary humans outperform chimpanzees in matters of executive control, since there is ample evidence that they do (for an overview, Vaesen, forthcoming). Still, the idea that cooperative feeding can be used as an evolutionary marker of this cognitive divergence, as Dubreuil suggests, does not stand firm in light of the above.³

² Another possibility is to argue that human and chimpanzee hunting are qualitatively similar, but are produced by different mechanisms (in humans, through executive control, in chimpanzees, through something else). This is a reasonable suggestion (which will be discussed more fully in Section 2.2). Yet, it will not help Dubreuil. If cooperative feeding may be realized by mechanisms other than executive control, its discriminating power is too low to qualify as an evolutionary indicator of executive control.

³ Even if chimpanzees did not involve in cooperative feeding practices at all, cooperative feeding would be a good indicator of the emergence of inhibition and goal maintenance in humans, only if chimpanzees didn't involve in any other cooperative behaviors requiring inhibition and goal maintenance. Chimpanzees, however, are known to cooperate on many non-food issues (e.g., social grooming, territorial defense, attacking enemies); and these behaviors may all be reconstructed (just like hunting and food sharing) in terms of inhibition and goal maintenance.

2.2 Alternative cognitive explanations of hunting and food sharing

While it may be convenient to reconstruct cooperative feeding practices in terms of inhibition and goal maintenance, it is a mistake to think that only such sophisticated future-oriented attitudes offer a plausible explanation. Cognitively undemanding backward-looking mechanisms may perform as good—and, even better.

For example, chimpanzees commonly involve in reciprocal relationships (e.g., in matters of food sharing, social grooming, agonistic support, territorial defense) notwithstanding their poor inhibitory control, and notwithstanding their inability to foresee future events. The most plausible explanation for chimp reciprocation, then, is that it is motivated by *past* altruism received, rather than by the expectation of *future* rewards (Schino and Aureli, 2009, see also, de Waal, 2000). According to Schino and Aureli, a simple mechanism of “emotional bookkeeping” suffices here: chimpanzees make decisions on whether to act altruistically towards a partner based on emotions associated with previous encounters with that partner. Emotions, not reasoned projections, guide social interactions.

Another primate example concerns marmoset and tamarin monkeys. These cooperatively breeding species are known to spontaneously share foodstuffs with their own offspring and the offspring of others, to act prosocially even with unrelated others (for tamarins: see Hauser et al., 2003; for marmosets: see Burkart et al., 2007), and to cooperate when harvesting and processing large fruits (Garber, 1997). In general, marmosets and tamarins engage in cooperative feeding more spontaneously and generously than chimpanzees. Given that marmosets and tamarins are relatively small-brained, and given that they do *not* outperform their independently breeding sister taxa (e.g., squirrel monkeys) with respect to inhibitory control and working memory (Burkart et al., 2009; Burkart and van Schaik, 2010), there is good reason to think that their cooperative feeding practices do not trade on high-level cognitive abilities. The most plausible explanation for marmoset and tamarin cooperation is a simple and spontaneous prosocial psychology.

Such cognitively undemanding prosocial machinery arguably guides much of reciprocal altruism even in modern humans (Schino and Aureli, 2010). An emotion as gratitude, for instance, is a potent motivator for subsequent altruism. In light of this, and in light of marmoset/tamarin prosociality, affect-based explanations for cooperative feeding in *Homo heidelbergensis* seem at least as plausible as explanations in terms of executive control.

In sum, the multiple realizability of cooperative feeding is bad news for Dubreuil. Cooperative feeding is too coarse-grained to mark unequivocally the emergence of increased abilities for inhibition and goal maintenance. So even if one could accurately date its occurrence in the early human lineage, that wouldn’t show that humans got cognitively more sophisticated at that point. And, unfortunately, the same kind of argument holds for cooperative breeding—a topic I turn to now.

3 Cooperative breeding and executive control

In cooperative breeding systems, some individuals actively engage in caring and provisioning infants that are not their own. Clearly, humans are cooperative breeders in this sense. For example, a large fraction of the 13 million calories that are needed to rear a modern human from birth to maturity (approx. age 15–16) is provided not by the mother, but by other caregivers, both kin and non-kin (Hrdy, 2009). The delayed maturity characteristic of humans, and the unusually short intervals between births, makes indispensable the aid of fathers, older siblings, aunts, uncles and even unrelated others. Thus, Dubreuil is right that human cooperative child-care implies huge transfers of resources. But again, it is a mistake to think that such transfers can be secured ‘only once individuals [are] able to represent and ascribe value to long-term cooperative goals [i.e. goal maintenance], as well as to resist the temptation of defection on a daily basis [i.e. inhibition].’ (Dubreuil, 2010, p. 62)

To start, it is questionable whether cooperative breeding drives on long-term cooperation at all. Dubreuil thinks it is: adults invest so much in children, because children ‘are generally expected to provide support for parents in their old age, as well as to help build economic and

political alliances' (Dubreuil, 2010a, p. 75). In other words, the benefits children receive now are paid back only several years later.

For care by kin, however, no such extra return on investment is needed; parents and other kin have a genetic interest in helping related infants. In case of non-kin breeding assistance, investments by helpers can usually be explained in terms of *short-term* benefits. According to a review by Bergmüller et al. (2007), helpers may help raise non-related infants to gain parenting experience; to avoid expulsion from the territory of the breeders they are assisting; to avoid expulsion from the group; to benefit from group augmentation effects (e.g. safety in numbers effects); or to advertise their genetic quality and thereby gain social prestige and perhaps increase future mating opportunities. The authors also mention the theoretical possibility of non-kin long-term cooperation *sensu* Dubreuil; but note that conclusive evidence for it is currently lacking.

Importantly, even if benefits for kin and non-kin caregivers are situated in the future, that doesn't imply that care is *motivated* by future gain. Future gain may operate at the level of ultimate causes, without figuring at the proximate (i.e. motivational) level. de Waal (2008) gives the example of the honeybee that stings an intruder. That altruistic behavior has been selected for its long-term fitness consequences, yet is motivated by anger, rather than by predictions of future events.

The same applies to cooperative breeding in marmosets and tamarins. These monkeys typically live in family groups composed of a breeding pair, its dependent offspring and helpers (Burkart and van Schaik, 2010). Helpers include older siblings, members of the extended family, and unrelated others, some of which get reproductively inactive to serve the reproductively active pair (Digby et al., 2007). Help encompasses infant carrying, food sharing, babysitting, and even allonursing.⁴ There is a strong correlation between the availability of male and female alloparental caregivers and infant survival rates (Hrdy, 2009). In sum, in tamarin and marmoset groups, substantial transfers of resources take place. Yet, as mentioned above, these monkeys are fairly modest-brained, and have no increased abilities for inhibition and working memory. So at the proximate level, tamarin and marmoset other-regarding behavior is likely *not* motivated by expectations of future reciprocation, but rather by simple and spontaneous helping impulses. If Dubreuil thinks this is different for humans, for *Homo heidelbergensis* in particular, he definitely needs to tell us why.

What about Dubreuil's suggestion (2010a, p. 81) that cooperative breeding requires increased inhibitory control to allow individuals to conform to sexual norms? These sexual norms (e.g., norms of monogamy), Dubreuil argues, see to it that males living in multimale groups can assess paternity with relative confidence, which decreases the risk that they invest in infants which are not their own. Dubreuil thus sees high paternal certainty as a necessary condition for the evolution of paternal care; and conformance to sexual norms as the most salient way of increasing paternal certainty. Both assumptions are problematic. First, low paternal certainty is consistent with high male-infant care. Saddle-back tamarins, moustached tamarins, lion tamarins, black-capped capuchins, olive baboons, chacma baboons, barbary macaques, stumptail macaques, Japanese macaques all live in multimale polyandrous groups, thus face high paternal uncertainty, yet all exhibit high male investment (Smuts and Gubernick, 1992). These investments are likely motivated by the benefits Bergmüller discerns (see above). Second, social norms are a fairly expensive way of increasing paternal certainty. Much less-demanding solutions include concealed ovulation (even if just exapted for that purpose), a natural aversion to casual sex in females, mechanisms of pair-bonding and of female-female competition, or a combination of these (see e.g., Geary, 2000).

To sum up the previous sections: cooperative feeding and breeding are poor indicators of inhibition and goal maintenance.⁵ They are not particular to humans, and moreover may be

⁴ Cooperative childcare in marmosets and tamarins is a response not so much to long childhoods as to a remarkable fecundity: twins and triplets are common, and females often produce two litters per year (Garber, 1997).

⁵ In my opinion, much better indicators are long distance trade (150-200kya), the colonization of Sahul (45kya) and, as Coolidge and Wynn (2005) point out, technologies like traps and deadfalls (which obviously do not preserve well in the archaeological record).

realized by fairly undemanding cognitive traits. In addition, it is doubtful that Dubreuil dates cooperative feeding and breeding in humans correctly—the next section explains why.

4 When did cooperative feeding and breeding arise?

Let me start with Dubreuil’s timing of cooperative breeding. Cooperative breeding scholars commonly estimate that cooperative breeding arose with *Homo erectus*, ca. 1.8 Ma—rather than with *Homo heidelbergensis* (700kya), as Dubreuil has it.

van Schaik and Burkart (2010) summarize several convincing lines of argument. First, cooperative breeding is favored where successful dispersal is difficult, and infant helping positively affects survival rates. The idea is that novel habitats ask for novel foraging strategies; juveniles whose earlier strategies do no longer work must be assisted, so as to bridge the food scarcity in between colonization and their development of the appropriate skills. *Homo erectus*, now, colonized two novel habitats—i.e. savanna habitats and habitats outside Africa—and as such, faced unpredictability with respect to food availability twice. Moreover, following an argument of Hawkes & O’Connell and colleagues, shifts toward cooler and drier climates around 1.8 mya decreased the availability of easy-to-process foods. Infants would have had to rely more on foods harvested and pre-processed by others, most notably, their grandmothers (O’Connell et al., 1999; Hawkes et al., 2000).

Second, body size of *Homo erectus* was much larger than that of earlier hominins. One reasonable solution to the increased reproductive burden for females was cooperative breeding, with energetic inputs being provisioned to infants by mothers *and* allomothers.

In a similar vein, third, hominin brain size clearly exceeded that of the great ape range for the first time in *Homo erectus* (Schoenemann, 2006). Energetic inputs provided by others may have enabled this marked increase. This is consistent with the idea that larger brains ask for longer maturation times, which external aid would again have made possible.

The timing of cooperative breeding in *Homo erectus* has ramifications for the timing of cooperative feeding too, since cooperative breeding implies cooperative feeding almost per definition (Driscoll, forthcoming). Sharing food with (un)related infants is the paradigmatic example of cooperative childcare. True, cooperative breeding doesn’t imply large game hunting; and that practice perhaps appeared indeed with *Homo heidelbergensis*.

5 Down with the revolution?

Dubreuil’s argument was supposed to show that human cooperation and culture did not evolve in one step (ca. 50kya, with the advent of symbolism and culture), but developed gradually, with modern-like abilities for inhibition and goal maintenance already appearing with *Homo heidelbergensis*. I have shown that Dubreuil’s argument is unsatisfactory: cooperative feeding and breeding do not need to mark enhanced abilities for inhibition and goal maintenance, and cooperative feeding and breeding most likely arose long before *Homo heidelbergensis*.

Nonetheless, I think there is still room to deploy cooperative breeding (in particular) against the idea of the “Human Revolution”. This has to do with the finding that cooperative breeding primates, presumably given their strong reliance on others, outperform their independently breeding sister taxa in socio-cognitive tasks (but not in non-social cognitive tasks, like those mentioned by Dubreuil, 2010b).⁶ That is, in their systematic review of the literature, Burkart and van Schaik (2010, see also, Burkart et al., 2009) explain that cooperatively breeding tamarins and marmosets are better than their independently breeding sister taxa with respect to: social learning, vocal communication, teaching-like behaviors, gaze understanding, cooperative problem solving (but not with respect to: general cognitive ability, working memory of actions, innovation rates, tool-use rates, patience, and inhibitory control). Burkart et al. (2009) argue that such social intelligence is as much a necessary ingredient for human cooperation and culture

⁶ Dubreuil (2010a) tries a similar idea: cooperative breeding marks enhanced capacities for joint attention and norm following

as the general intelligence commonly invoked. They suggest that when both intelligences were combined (from *Homo erectus* onward), the divergence between humans and apes really gets going. In other words, an increase in general intelligence, as usually implied in the model of the “Human Revolution”, could be powerful only given a set of previous innovations, including (refinements to) a suite of socio-cognitive skills that accompanied (refinements to) cooperative breeding practices. Modernity might have taken off with *Homo erectus*, rather than with *Homo sapiens*.

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