

The emergence of emotionally modern humans: implications for language and learning

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Contents

Abstract	3
1. Setting the Plio-Pleistocene stage	4
2. The hominin infant's to-do list	11
(a) First order of business: appeal to mother	11
(b) Attract others	12
(c) Vocal control and more flexible vocalizing	16
(d) Incorporate others' preferences	20
(e) Add psychological dimensions to <i>Kindchenschema</i>	23
3. New dimensions to social learning	25
(a) Expanded avenues	25
(b) Emotionally modern and mentalizing mentees	26
(c) Concern for reputation and learning	28
4. Conclusion	32

Abstract

According to the Cooperative Breeding Hypothesis, apes with the life-history attributes of those in the line leading to the genus *Homo* could not have evolved unless male and female allomothers had begun to help mothers care for and provision offspring. As proposed elsewhere, the unusual way hominins reared their young generated novel phenotypes subsequently subjected to Darwinian social selection favouring those young apes best at monitoring the intentions, mental states and preferences of others and most motivated to attract and appeal to caretakers. Not only were youngsters acquiring information in social contexts different from those of other apes, but they would also have been emotionally and neurophysiologically different from them in ways that are relevant to how humans learn. Contingently delivered rewards to dependents who attracted and ingratiated themselves with allomothers shaped their behaviours and vocalizations and transformed the way developing youngsters learned from others and internalized their preferences.

This article is part of the theme issue ‘Life history and learning: how childhood, caregiving and old age shape cognition and culture in humans and other animals’.

1. Setting the Plio-Pleistocene stage

Apes with the life-history attributes of *Homo sapiens* could not have evolved unless male and female allomothers had helped mothers care for and provision offspring. We refer to this as the ‘Cooperative Breeding Hypothesis’¹². Across the animal world, breeding systems characterized by group members other than parents (alloparents) helping parents to care for and provision offspring have evolved many times in social insects, in 9% of 10 000 species of birds³, and in perhaps 3% of 4500 species of mammals. The prevalence of allomaternal care tends to be higher among social carnivores⁴, and higher still among primates, where females or males other than the mother care for and *at least minimally provision* offspring in more than 30% of species⁵⁶. Extensive alloparental in addition to parental provisioning, however, is only found among humans and in a distantly related subfamily of New World monkeys, the Callitrichidae, containing marmosets and tamarins.

Various circumstances conducive to the evolution of cooperative breeding pertained among hominins in Plio-Pleistocene Africa⁷. These included: cohesive social groups containing close relatives; production of increasingly costly, slower maturing young; increasing reliance on hunting and extractive foraging such that immatures began to

¹ Hrdy SB. 2009 *Mothers and others: the evolutionary origins of mutual understanding*. Cambridge, MA: Belknap Press. **Google Scholar**

² Hrdy SB. 2016 Development plus social selection in the emergence of ‘emotionally modern’ humans. In *Childhood: origins, evolution and implications* (eds Meehan CL, Crittenden AN), pp. 11-44. Albuquerque, NM: School for Advanced Research and University of New Mexico Press. **Google Scholar**

³ Cockburn A. 2006 Prevalence of different modes of parental care in birds. *Proc. R. Soc. B* **273**, 1375-1383. (doi:10.1098/rspb.2005.3458) **Link, Web of Science, Google Scholar**

⁴ Clutton-Brock TH. 2016 *Mammal societies*. Chichester, UK: John Wiley & Sons. **Google Scholar**

⁵ Isler K, van Schaik CP. 2012 Allomaternal care, life history and brain size evolution in mammals. *J. Hum. Evol.* **63**, 52-63. (doi:10.1016/j.jhevol.2012.03.009) **Crossref, PubMed, Web of Science, Google Scholar**

⁶ Perry S. 2020 Behavioural variation and learning across the lifespan in wild white-faced capuchin monkeys. *Phil. Trans. R. Soc. B* **375**, 20190494. (doi:10.1098/rstb.2019.0494) **Link, Web of Science, Google Scholar**

⁷ Meindl RS, Chaney ME, Lovejoy CO. 2018 Early hominids may have been a weed species. *Proc. Natl Acad. Sci. USA* **115**, 1244-1249. (doi:10.1073/pnas.1719669115) **Crossref, PubMed, Web of Science, Google Scholar**

depend on adults to acquire or process food for them and to facilitate their learning appropriate skills⁸⁹¹⁰¹¹¹²¹³¹⁴; and importantly, ecological instability¹⁵¹⁶.

Unpredictable rainfall against a background of increasing aridity almost certainly figured in the emergence of shared provisioning among early hominins¹⁷¹⁸¹⁹²⁰²¹. In spite of recurring periods of food shortage accompanied by high child mortality, hominin mothers in the line of bipedal apes leading to *H. sapiens* were producing slower maturing, increasingly large-brained, energetically more costly offspring, yet also beginning to produce infants after shorter intervals. How? Along with others, we hypothesize that by 2 Ma with *Homo erectus*, hominin mothers increasingly relied on assistance from other group members to supplement offspring who even after weaning remained years

⁸ Hrdy SB. 2009 *Mothers and others: the evolutionary origins of mutual understanding*. Cambridge, MA: Belknap Press. **Google Scholar**

⁹ Clutton-Brock TH. 2016 *Mammal societies*. Chichester, UK: John Wiley & Sons. **Google Scholar**

¹⁰ Emlen S. 1991 Evolution of cooperative breeding in birds and mammals. In *Behavioral ecology*, 3rd edn (eds Krebs J, Davies NB), pp. 301-337. Oxford, UK: Blackwell Scientific. **Google Scholar**

¹¹ Hawkes K. 2020 Cognitive consequences of our grandmothering life history: cultural learning begins in infancy. *Phil. Trans. R. Soc. B* **375**, 20190501. (doi:10.1098/rstb.2019.0501) **Link, Web of Science, Google Scholar**

¹² Jaeggi A, van Schaik CP. 2011 The evolution of food-sharing in primates. *Behav. Ecol. Sociobiol.* **65**, 2125-2140. (doi:10.1007/s00265-011-1221-3) **Crossref, Web of Science, Google Scholar**

¹³ Langen TA. 2000 Prolonged offspring dependence and cooperative breeding in birds. *Behav. Ecol.* **11**, 367-377. (doi:10.1093/beheco/11.4.367) **Crossref, Web of Science, Google Scholar**

¹⁴ O'Connell JF, Hawkes K, Lupo KD, Blurton Jones KG. 2002 Male strategies and Plio-Pleistocene archaeology. *J. Hum. Evol.* **43**, 461-485. (doi:10.1006/jhev.2002.0604) **Crossref, Web of Science, Google Scholar**

¹⁵ Burkart JM, van Schaik CP, Griesser M. 2017 Looking for unity in diversity: human cooperative childcare in comparative perspective. *Proc. R. Soc. B* **284**, 20171184. (doi:10.1098/rspb.2017.1184) **Link, Web of Science, Google Scholar**

¹⁶ Jetz W, Rubenstein D. 2011 Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* **21**, 72-78. (doi:10.1016/j.cub.2010.11.075) **Crossref, PubMed, Web of Science, Google Scholar**

¹⁷ O'Connell JF, Hawkes K, Lupo KD, Blurton Jones KG. 2002 Male strategies and Plio-Pleistocene archaeology. *J. Hum. Evol.* **43**, 461-485. (doi:10.1006/jhev.2002.0604) **Crossref, Web of Science, Google Scholar**

¹⁸ Antón S, Potts R, Aiello LC. 2014 Evolution of early Homo: an integrated ecological perspective. *Science* **345**, 1236828. (doi:10.1126/science.1236828) **Crossref, PubMed, Web of Science, Google Scholar**

¹⁹ Magill C, Ashley GM, Freeman K. 2013 Ecosystem variability and early human habitats in eastern Africa. *Proc. Natl Acad. Sci. USA* **110**, 1167-1174. (doi:10.1073/pnas.1206276110) **Crossref, PubMed, Web of Science, Google Scholar**

²⁰ Morgan TJH, Suchow JW, Griffiths TL. 2020 Experimental evolutionary simulations of learning, memory and life history. *Phil. Trans. R. Soc. B* **375**, 20190504. (doi:10.1098/rstb.2019.0504) **Link, Web of Science, Google Scholar**

²¹ Richerson PJ, Boyd R. 2020 The human life history is adapted to exploit the adaptive advantages of culture. *Phil. Trans. R. Soc. B* **375**, 20190498. (doi:10.1098/rstb.2019.0498) **Link, Web of Science, Google Scholar**

from nutritional independence²²²³²⁴²⁵²⁶²⁷. Earlier weaning meant mothers could resume cycling, conceive again and reproduce faster. This is a conservative interpretation. Others propose the emergence of allomaternal assistance as early as *Australopithecus*²⁸ or *Ardipithecus*²⁹.

Over time, stacking of closely spaced dependent offspring would further intensify reliance on allomaternal provisioning. By the Pleistocene, we suspect that hominins were adopting even more flexible residence patterns than those found in the other great apes³⁰, with ‘multi-local’ residence patterns beginning to resemble those typical of twentieth century hunter-gatherers³¹³². Greater female autonomy of movement and the emergence of pair-bonds (why they emerged being a topic still debated) would increase chances that probable fathers and matrilineal kin resided nearby³³.

Greater postpartum tolerance on the part of ordinarily possessive ape mothers co-evolved with growing, albeit still facultative, neurophysiological responsiveness on the

²² Hawkes K. 2020 Cognitive consequences of our grandmothering life history: cultural learning begins in infancy. *Phil. Trans. R. Soc. B* **375**, 20190501. (doi:10.1098/rstb.2019.0501) **Link, Web of Science, Google Scholar**

²³ Burkart JM, Hrdy SB, van Schaik CP. 2009 Cooperative breeding and human cognitive evolution. *Evol. Anthropol.* **18**, 175-186. (doi:10.1002/evan.20222) **Crossref, Web of Science, Google Scholar**

²⁴ Hawkes K, O’Connell JF, Blurton Jones NG, Alvarez H, Charnov EL. 1998 Grandmothering, menopause and the evolution of human life histories. *Proc. Natl Acad. Sci. USA* **95**, 1336-1339. (doi:10.1073/pnas.95.3.1336) **Crossref, PubMed, Web of Science, Google Scholar**

²⁵ Hrdy SB. 1999 *Mother nature*. New York, NY: Pantheon. **Google Scholar**

²⁶ Konner M. 2010 *The evolution of childhood: relationships, emotion, mind*. Cambridge, MA: Belknap Press. **Google Scholar**

²⁷ Meehan C, Crittenden A (eds). 2016 *Childhood: origins, evolution and implications*. Albuquerque, NM: School for Advanced Research and University of New Mexico Press. **Google Scholar**

²⁸ De Silva JM. 2011 A shift toward birthing relatively large infants early in human evolution. *Proc. Natl Acad. Sci. USA* **108**, 1022-1027. (doi:10.1073/pnas.1003865108) **Crossref, PubMed, Web of Science, Google Scholar**

²⁹ Raghanti M-A, Edler MK, Stephenson AR, Munger EL, Jacobs B, Hof PR, Sherwood CC, Holloway RL, Lovejoy CO. 2018 A neurochemical hypothesis for the origin of hominids. *Proc. Natl Acad. Sci. USA* **115**, e1108-e1116. (doi:10.1073/pnas.1719666115) **Crossref, PubMed, Web of Science, Google Scholar**

³⁰ Koenig A, Borries C. 2012 Hominoid dispersal patterns and human evolution. *Evol. Anthropol.* **21**, 108-112. (doi:10.1002/evan.21300) **Crossref, PubMed, Web of Science, Google Scholar**

³¹ Hill K et al. 2011 Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* **331**, 1286-1289. (doi:10.1126/science.1199071) **Crossref, PubMed, Web of Science, Google Scholar**

³² Marlowe F. 2010 *The Hadza hunter-gatherers of Tanzania*. Berkeley, CA: University of California Press. **Google Scholar**

³³ Behar D et al.. 2008 The dawn of matrilineal diversity. *Am. J. Hum. Genet.* **82**, 1130-1140. (doi:10.1016/j.ajhg.2008.04.002) **Crossref, PubMed, Web of Science, Google Scholar**

part of fathers and other allomothers increasingly motivated to care for immatures³⁴³⁵³⁶. The more dependent upon allomaternal assistance primate mothers are, the more sensitive they become to cues of social support, especially postpartum³⁷³⁸. Compared with the reflexive protectiveness and possessiveness typical of all but the most stressed or inexperienced great ape mothers, who carry comatose or even dead infants for days, postpartum commitment of these hominins would likely have been more conditional. Across traditional societies, mothers are known to abandon at birth infants considered defective as well as adjust parental investment in line with social and ecological circumstances³⁹, ch. 12 and 13]⁴⁰⁴¹.

Infants who could no longer count on being the sole priority of a single-mindedly dedicated mother had to elicit and maintain maternal commitment while also attracting, and increasingly ingratiating themselves with, others. Rewarded when they succeeded, over the course of development infants learned to express otherwise latent sociocognitive potentials. As we use the term, ‘ingratiating behaviours’ refer to anything an infant does to increase his or her chances of being chosen as the object of beneficent attention (including provisioning), where offspring best at ingratiating themselves with others would be most likely to survive. Over the course of development, these youngsters learned to monitor and be interested in the intentions, thoughts and feelings of others, and even internalize their preferences. Over generations, youngsters best at doing so would be more likely to survive, resulting in populations of apes emotionally very different from their ancestors ([figure 1]).

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³⁴ Raghanti M-A, Edler MK, Stephenson AR, Munger EL, Jacobs B, Hof PR, Sherwood CC, Holloway RL, Lovejoy CO. 2018 A neurochemical hypothesis for the origin of hominids. *Proc. Natl Acad. Sci. USA* **115**, e1108-e1116. (doi:10.1073/pnas.1719666115) **Crossref, PubMed, Web of Science, Google Scholar**

³⁵ Abraham E, Hendler T, Shapira-Lichter I, Kanat-Maymon Y, Zagoory-Sharon O, Feldman R. 2014 Father’s brain is sensitive to childcare experiences. *Proc. Natl Acad. Sci. USA* **111**, 9792-9797. (doi:10.1073/pnas.1402569111) **Crossref, PubMed, Web of Science, Google Scholar**

³⁶ Numan M. 2015 *Neurobiology of social behavior: toward an understanding of the prosocial and antisocial brain*. Amsterdam, The Netherlands: Elsevier/Academic Press. **Google Scholar**

³⁷ Hrdy SB. 1999 *Mother nature*. New York, NY: Pantheon. **Google Scholar**

³⁸ Hrdy SB. 2016 Variable postpartum responsiveness among humans and other primates with ‘cooperative breeding’: a comparative and evolutionary perspective. *Horm. Behav.* **77**, 272-283. (doi:10.1016/j.yhbeh.2015.10.016) **Crossref, PubMed, Web of Science, Google Scholar**

³⁹ Hrdy SB. 1999 *Mother nature*. New York, NY: Pantheon. **Google Scholar**

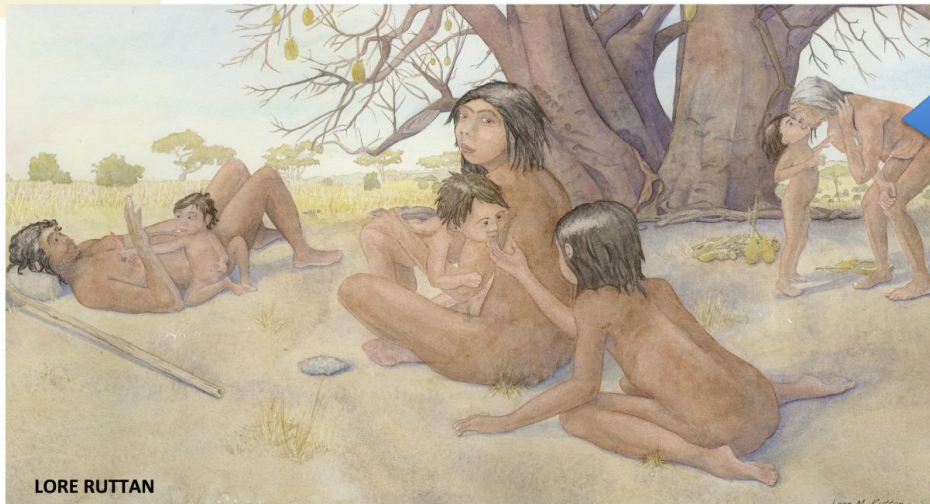
⁴⁰ Konner M. 1972 Aspects of the foraging ecology of a foraging people. In *Ethological studies of child behavior* (ed. Blurton-Jones N), pp. 285-304. Cambridge, UK: Cambridge University Press. **Google Scholar**

⁴¹ Scrimshaw S. 1984 Infanticide in human populations: social and individual concerns. In *Infanticide: comparative and evolutionary perspectives* (eds Hausfater G, Hrdy SB), pp. 419-462. New York, NY: Aldine de Gruyter. **Google Scholar**

MOTHERS and OTHERS THOUGHT EXPERIMENT



What would happen if you took clever, manipulative, tool-using apes possessing rudimentary theory of mind and reared them in a novel context where infants had to rely on facultatively provided care and provisioning from mothers and allomothers...



...while developing immatures learn to be more other-regarding, resulting in novel ape phenotypes? Over generations, directional social selection would favour those best equipped to ingratiate themselves with others.

Figure 1. This thought experiment traces dual ontogenetic and evolutionary processes set in motion when mothers in the line leading to the genus *Homo* began to rely on alloparental care and provisioning to rear increasingly costly, sometimes more closely spaced, offspring. Intermittent behavioural conditioning would encourage youngsters to repeat and refine facial expressions, attitudes and vocalizations most likely to appeal to potential caretakers. This would lead to the expression of otherwise latent potentials and the formation of novel neural networks. Over generations, these quite novel ape phenotypes would be exposed to directional social selection favouring youngsters best at ingratiating themselves with others, setting in motion a causal chain of adaptive evolution that began with development⁴². Art by L. M. Ruttan and used with permission.

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In this contribution, we reconstruct how growing up in such a social environment may have impacted dependent immatures along with the cascading consequences this would have had on uniquely human forms of learning and language. We start by asking: How would dependent immatures respond to the challenges of eliciting vital, but facultatively proffered, maternal and allomaternal attentions? What would this little ape need to do? Since none of us can go back in time to observe how early hominin infants would have behaved, we draw on evidence for how non-human ape and modern human babies responded in ‘virtual’ experiments with and without allomaternal care to test assumptions made here about how hominin infants would have behaved with it⁴³, as well as on evidence from callitrichid monkey infants reared in a cooperative context.

Although inevitably speculative, this reconstruction is informed by both comparative evidence and a growing understanding of the survival challenges hominin infants confronted. As our point of departure though, we begin with callitrichid monkeys, the only extant primates besides humans with extensive alloparental in addition to parental care and provisioning of infants. Callitrichids face similar challenges to those hominin infants would have although they do so endowed with far smaller brains. Callitrichid mothers customarily give birth to twins, and owing to postpartum oestrus are immediately pregnant again^{44,45}. They are thus lactating and gestating at the same time, and the new set of offspring is born before the previous one is fully independent. This costly reproduction is only possible because other group members act as allomothers and help by carrying infants, protecting them and substantially provisioning them⁴⁶. Like human mothers, callitrichid mothers are highly tolerant towards other group members interested in carrying their babies, and they adjust their maternal investment relative to how much help is available^{47,48}. Helpers provisioning immatures exhibit highly proso-

⁴³ Hrdy SB. 2016 Development plus social selection in the emergence of ‘emotionally modern’ humans. In *Childhood: origins, evolution and implications* (eds Meehan CL, Crittenden AN), pp. 11-44. Albuquerque, NM: School for Advanced Research and University of New Mexico Press. **Google Scholar**

⁴⁴ Erb WM, Porter LM. 2017 Mother’s little helpers: what we know (and don’t know) about cooperative infant care in callitrichines. *Evol. Anthropol.* **26**, 25-37. (doi:10.1002/evan.21516) **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁵ Garber P. 1997 One for all and breeding for one. *Evol. Anthropol.* **7**, 187-199. (doi:10.1002/(SICI)1520-6505(1997)5:6<187::AID-EVAN1>3.0.CO;2-A) **Crossref, Google Scholar**

⁴⁶ Guerreiro Martins EM, Moura ACA, Finkenwirth C, Griesser M, Burkart JM. 2019 Food sharing patterns in three species of callitrichid monkeys (*Callithrix jacchus*, *Leontopithecus chrysomelas*, *Saguinus midas*): individual and species differences. *J. Comp. Psychol.* **133**, 474-487. (doi:10.1037/com0000169) **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁷ Hrdy SB. 1999 *Mother nature*. New York, NY: Pantheon. **Google Scholar**

⁴⁸ Bardi M, Petto AJ, Lee-Parritz DE. 2001 Parental failure in captive cotton-top tamarins (*Saguinus oedipus*). *Am. J. Primatol.* **54**, 159-169. (doi:10.1002/ajp.1020) **Crossref, PubMed, Web of Science, Google Scholar**

cial motivations^{49,50}. Within the social group, all members are characterized by high levels of tolerance and prosociality compared with independently breeding primates⁵¹. Youngsters born to hominin mothers who, when conditions permitted, similarly produced more closely spaced young (in ‘as-if’ litters), confronted challenges similar to those callitrichid twins face. Thus did infants in distantly related species converge upon similar modes of eliciting succour from allomothers as well as mothers. But how might such solutions be extended and transformed if dependent immatures were endowed with much more powerful ape cognitive systems to begin with?

⁴⁹ Guerreiro Martins EM, Moura ACA, Finkenwirth C, Griesser M, Burkart JM. 2019 Food sharing patterns in three species of callitrichid monkeys (*Callithrix jacchus*, *Leontopithecus chrysomelas*, *Saguinus midas*): individual and species differences. *J. Comp. Psychol.* **133**, 474-487. (doi:10.1037/com0000169) **Crossref, PubMed, Web of Science, Google Scholar**

⁵⁰ Brügger RK, Kappeler-Schmalzriedt T, Burkart JM. 2018 Reverse audience effects on helping in cooperatively breeding marmoset monkeys. *Biol. Lett.* **14**, 20180030. (doi:10.1098/rsbl.2018.0030) **Link, Web of Science, Google Scholar**

⁵¹ Burkart JM et al. 2014 The evolutionary origins of human hyper-cooperation. *Nat. Commun.* **5**, 4747. (doi:10.1038/ncomms5747) **Crossref, PubMed, Web of Science, Google Scholar**

2. The hominin infant's to-do list

(a) First order of business: appeal to mother

Although born with open eyes, able to blurrily seek the eyes of someone else, newborn apes are otherwise altricial, utterly dependent on others for warmth, protection, locomotion and food¹². Fortunately, apes enjoy the built-in mammalian advantage of being born to a mother who during gestation was suffused by hormones lowering her threshold for responding to sounds and smells of a warm, wriggling, fluid-covered baby. If only the newborn can make it to maternal nipples, root, suck and stimulate lactation, ensuing surges in oxytocin and prolactin further enhance her nurturing impulses. With lactation underway, even an inexperienced first-time ape mother becomes increasingly bonded to this newcomer. But over the course of hominin evolution, increasing maternal reliance on allomaternal assistance would have rendered mothers increasingly sensitive to cues of available social support. In the absence of social support, the commitment of even the most experienced human mother falters (see especially³⁴⁵).

Over evolutionary time, more contingent commitment preadapted human mothers to become more discriminating than other apes. In addition to their parity, prior experience, physical condition and likely social support, mothers began to respond to specific physical attributes of each infant. Consciously or not, each costly infant was in competition not only with still nutritionally dependent older siblings, but also with subsequent infants a mother might bear under ecologically more opportune conditions if only she retrenched upon investment in this one, or bailed out altogether, and resumed cycling sooner. Over the course of the Pleistocene (perhaps earlier?), hominin

¹ Bard K. 2012 Emotional engagement: how chimpanzee minds develop. In *The primate mind* (eds de Waal F, Ferrari FP), pp. 224-245. Cambridge, MA: Harvard University Press. **Crossref**, **Google Scholar**

² Tomonaga M, Tanaka M, Matsuzawa T, Myowa-Yamakoshi M, Kosugil M, Mizuno Y, Okamoto S, Yamaguchi MK, Bard KA. 2004 Development of social cognition in infant chimpanzees (*Pan troglodytes*): face recognition, smiling, gaze, and the lack of triadic interactions. *Jap. Psychol. Res.* **46**, 227-235. (doi:10.1111/j.1468-5584.2004.00254.x) **Crossref**, **Web of Science**, **Google Scholar**

³ Hrdy SB. 1999 *Mother nature*. New York, NY: Pantheon. **Google Scholar**

⁴ Hrdy SB. 2016 Variable postpartum responsiveness among humans and other primates with 'cooperative breeding': a comparative and evolutionary perspective. *Horm. Behav.* **77**, 272-283. (doi:10.1016/j.yhbeh.2015.10.016) **Crossref**, **PubMed**, **Web of Science**, **Google Scholar**

⁵ Bugos PE, McCarthy ML. 1984 Ayoreo infanticide: a case study. In *Comparative and evolutionary perspectives on infanticide* (eds Hausfater G, Hrdy S), pp. 503-520. Hawthorne, NY: Aldine. **Google Scholar**

babies came under increasing pressure to look good and sound vigorous right at birth, advertising that they were full-term, robust, good bets for survival, worth further investment. This challenge may help explain why, over the course of hominin evolution, fetuses began to stockpile adipose tissue at an unlikely time, just prior to squeezing through what were becoming increasingly narrow birth canals. By now, human neonates are born much fatter than other apes (*ca* 10–14% body fat contrasted with 3–4% for chimpanzees). No doubt, an extra dollop of energy was initially beneficial for thermoregulation and fuelling fast-growing brains, contributing to the emergence in mothers of sensory biases favouring plump babies⁶. Over time, plumpness may also have come to serve as an infantile equivalent of sex appeal, seducing mothers into embarking on a long, exorbitantly costly, endeavour⁷, ch. 21].

Once increasingly discriminating hominin mothers began to notice associations between birth weight and later outcomes, one of evolution’s more consequential self-reinforcing feedback loops would be underway. With runaway social selection (*sensu* West-Eberhard) for neonatal plumpness underway, extra energy stores became available for brain development, in turn rendering allomaternal provisioning even more essential. Over generations, allomothers as well became attuned to cues of neonatal viability, adjusting levels of commitment accordingly⁸.

This brings us to the hominin infant’s *second order of business*.

(b) Attract others

Because hominin mothers as well benefitted from allomaternal assistance, it behooved females to reside near trusted others, matrilineal kin and/or adult males who were probable fathers. Unlike exceedingly possessive great ape mothers, mothers in traditional human societies not only tolerate, but often encourage postpartum contact with infants. Whether this shift was due to innately more tolerant temperaments, to greater autonomy in selecting whom to live among, or both, is not clear. In any event, maternal tolerance facilitated intimate exposure of trusted group members to infantile smells and sounds, generating maternal-like affiliation-promoting neurophysiological

⁶ Kuzawa CW et al. 2014 Metabolic costs and evolutionary implications of human brain development. *Proc. Natl Acad. Sci. USA* **111**, 13 010-13 015. (doi:10.1073/pnas.1323099111) **Crossref**, **Web of Science**, **Google Scholar**

⁷ Hrdy SB. 1999 *Mother nature*. New York, NY: Pantheon. **Google Scholar**

⁸ Hrdy SB. 2016 Variable postpartum responsiveness among humans and other primates with ‘cooperative breeding’: a comparative and evolutionary perspective. *Horm. Behav.* **77**, 272-283. (doi:10.1016/j.yhbeh.2015.10.016) **Crossref**, **PubMed**, **Web of Science**, **Google Scholar**

transformations in male and female allomothers alike⁹¹⁰¹¹¹². Among humans, only a few hours of intimate contact with grandparents is sufficient to produce surges in oxytocin and rearrange priorities¹³. (Among marmosets, similarly, oxytocin increases not only in mothers, but in all group members after the birth of new babies¹⁴.)

But other factors also enter in, including the allomother's own physical condition and past caretaking experiences, and alternatives available, as well as the infant's vulnerability and level of need. Facing this uncertainty, cues from infants themselves to elicit allomaternal involvement would again be paramount. Over time, human allomothers become sensitive to the same viability cues that mothers respond to. Magnetic resonance images of the brains of modern humans reveal that even nulliparous women find the faces of plump, healthy-looking (read full-term) babies 'cuter' and more rewarding to look at¹⁵. Not only physical viability cues, but also behavioural interactions, will attract carers. Humans are born with neurological capacities comparable with those of other apes, but differences soon emerge¹⁶. At birth, both chimpanzee and human newborns seek out eyes, are capable of mutual gazing, and caught just right, may imitate someone else's outstretched tongue or other facial expressions¹⁷. Both species exhibit reflexive 'fairy smiles', soon to be replaced by more open-eyed 'social smiles' in response to someone else. Among newborn chimpanzees however, that someone else

⁹ Hrdy SB. 2009 *Mothers and others: the evolutionary origins of mutual understanding*. Cambridge, MA: Belknap Press. **Google Scholar**

¹⁰ Abraham E, Gilam G, Kanat-Maymon Y, Jacob Y, Zagoory-Sharon O, Hendler T, Feldman R. 2017 The human coparental bond implicates distinct corticostriatal pathways: longitudinal impact on family formation and child well-being. *Neuropsychopharmacology* **42**, 2301-2313. (doi:10.1038/npp.2017.71) **Crossref, PubMed, Web of Science, Google Scholar**

¹¹ Bales K, Kim AJ, Lewis-Reese AD, Carter CS. 2004 Both oxytocin and vasopressin may influence alloparental behavior in male prairie voles. *Horm. Behav.* **45**, 354-361. (doi:10.1016/j.yhbeh.2004.01.004) **Crossref, PubMed, Web of Science, Google Scholar**

¹² Carter CS, Perkeybile A. 2018 The monogamy paradox: what do love and sex have to do with it? *Front. Ecol. Evol.* **8**, 202. (doi: 10.3389/fevo.2018.00202.) **Crossref, Web of Science, Google Scholar**

¹³ Hrdy SB. 2019 The transformative power of nurturing. In *Power and care* (eds Singer T, Ricard M), pp. 15-27. Cambridge, MA: MIT Press. **Google Scholar**

¹⁴ Finkenwirth C, Martins E, Deschner T, Burkart JM. 2016 Oxytocin is associated with infant-care behavior and motivation in cooperatively breeding marmoset monkeys. *Horm. Behav.* **80**, 10-18. (doi:10.1016/j.yhbeh.2016.01.008) **Crossref, PubMed, Web of Science, Google Scholar**

¹⁵ Glocker ML, Langleben DD, Ruparel K, Loughead JW, Valdez JN, Griffin MD, Gur RC, Sachser N. 2009 Baby schema modulates the reward system in nulliparous women. *Proc. Natl Acad. Sci. USA* **106**, 9115-9119. (doi:10.1073/pnas.0811620106) **Crossref, PubMed, Web of Science, Google Scholar**

¹⁶ Lonsdorf EV, Ross SR, Matsuzawa T (eds). 2010 *The mind of the chimpanzee: ecological and experimental perspectives*. Chicago, IL: University of Chicago Press. **Crossref, Google Scholar**

¹⁷ Myowa-Yamakoshi M. 2010 Early social cognition in chimpanzees. In *The mind of the chimpanzee: ecological and experimental perspectives* (eds Lonsdorf EV, Ross SR, Matsuzawa T), pp. 23-31. Chicago, IL: University of Chicago Press. **Google Scholar**

would always be their own mother¹⁸. In traditional human societies, however, blearily gazing newborns engage a wider audience^{19,20}. Over time as infants grow accustomed to and learn to trust specific allomothers, the sort of emotional bonds primate infants forge with mothers prove sufficiently elastic to encompass multiple attachment figures, an average of six attachment figures among the Central African Aka hunter-gatherers Courtney Meehan studied²¹. It is not known whether human infants are more prone to forge multiple attachments than are other apes if cared for by both mothers and others because the latter virtually never are.

A challenge unique to immatures of cooperatively breeding primates is that they are not in continuous contact with their carer. This can be buffered by proactive caring motivations by adults, as in callitrichids, where group members check babies on carriers, eager to take over when necessary²², or proactively announce that they have found food and are ready to share it. Such provisioning is different from food sharing patterns in other primates, where at most, immatures are passively tolerated when taking their mother's food^{23,24}. Nevertheless, without being in constant body contact with a single carer, cooperatively breeding immatures face the chronic risk of being overlooked.

Among apes such as chimpanzees, gorillas or orangutans, newborns constantly held by mothers in direct skin-to-skin contact have less need to smile or vocalize. Calling would only be useful if separated, or later, at weaning, as youngsters object to maternal rejections. Otherwise, low, scarcely audible sounds make more sense than loudly advertising to predators 'vulnerable baby here!' Among primates with shared care, life tends to be noisier. Infants need to stay 'in touch without touch' and may complain to

¹⁸ Matsuzawa T. 2010 The chimpanzee mind: bridging fieldwork and laboratory work. In *The mind of the chimpanzee: ecological and experimental perspectives* (eds Lonsdorf EV, Ross SR, Matsuzawa T), pp. 1-19. Chicago, IL: University of Chicago Press. **Google Scholar**

¹⁹ Konner M. 2010 *The evolution of childhood: relationships, emotion, mind*. Cambridge, MA: Belknap Press. **Google Scholar**

²⁰ Konner M. 1972 Aspects of the foraging ecology of a foraging people. In *Ethological studies of child behavior* (ed. Blurton-Jones N), pp. 285-304. Cambridge, UK: Cambridge University Press. **Google Scholar**

²¹ Meehan CL, Hawks S. 2013 Cooperative breeding and attachment among Aka foragers. In *Attachment reconsidered: cultural perspectives on a Western theory* (eds Quinn N, Mageo JM), pp. 85-114. New York: NY: Palgrave Macmillan. **Crossref, Google Scholar**

²² Yamamoto ME, Box HO. 1997 The role of non-reproductive helpers in infant care in captive *Callicebus jacchus*. *Ethology* **103**, 760-771. (doi:10.1111/j.1439-0310.1997.tb00184.x) **Crossref, Web of Science, Google Scholar**

²³ Brown GR, Almond RE, Bergen YV. 2004 Begging, stealing, and offering: food transfer in nonhuman primates. *Adv. Study Behav.* **34**, e295. (doi:10.1016/S0065-3454(04)34007-6) **Web of Science, Google Scholar**

²⁴ Jaeggi AV, Dunkel LP, van Noordwijk MA, Wich SW, Sura AAL, van Schaik CP. 2010 Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *Am. J. Phys. Anthropol.* **72**, 62-71. (doi:10.1002/ajp.20752) **Google Scholar**

prompt maternal retrievals. Infant langur monkeys spend up to 50% of their first day of life being held and carried by females-other-than-mothers, calling incessantly²⁵.

Life is even noisier in animals with biparental and alloparental provisioning, where babies beg for treats. This correlation is best documented in birds²⁶, but it also holds for callitrichids and humans, who fall among the most voluble of primates²⁷. Vocalizing starts early in marmosets and tamarins, becoming more frequent and specialized over the course of development. Begging calls spike around weaning, when allomaternal provisioning is most critical^{28,29}. But these infants not only are noisy beggars, but also engage in babbling-like behaviors, by producing repetitive, random-sounding streams of elements of adult vocalizations that can last for more than a minute. This babbling-like behaviour comes with likely cost because it is noisy and makes infants conspicuous to predators. It peaks around weaning, when allomaternal provisioning is most critical, and turns out to be an effective attention getter, as adults are more likely to approach and interact with immatures that are babbling³⁰.

Something similar goes on in humans, with the onset of babbling around the time (in hunter-gatherers at least) when allomothers begin providing edible treats (discussed below). Within weeks of birth, human infants emit engaging noises. Learning progresses more rapidly if infants notice others reacting. By 10 weeks some actually take turns vocalizing. The sound of a baby laughing generates an especially powerful stimulus, audible at some distance and signalling emotional engagement^{31,32}. As babies put two

²⁵ Hrdy SB. 1977 *The langurs of Abu: female and male strategies of reproduction*. Cambridge, MA: Harvard University Press. **Google Scholar**

²⁶ Leighton GM. 2017 Cooperative breeding influences the number and type of vocalizations in avian lineages. *Proc. R. Soc. B* **284**, 20171508. (doi:10.1098/rspb.2017.1508) **Link, Web of Science, Google Scholar**

²⁷ Burkart JM, Martins EG, Miss F, Zuercher Y. 2018 From sharing food to sharing information: cooperative breeding and language evolution. *Interact. Stud.* **19**, 136-150. (doi:10.1075/is.17026.bur) **Crossref, Web of Science, Google Scholar**

²⁸ Brown GR, Almond RE, Bergen YV. 2004 Begging, stealing, and offering: food transfer in nonhuman primates. *Adv. Study Behav.* **34**, e295. (doi:10.1016/S0065-3454(04)34007-6) **Web of Science, Google Scholar**

²⁹ Rapaport L, Brown G. 2008 Social influences on foraging behavior in young nonhuman primates: learning what, where and how to eat. *Evol. Anthropol.* **17**, 189-201. (doi:10.1002/evan.20180) **Crossref, Web of Science, Google Scholar**

³⁰ Elowson AM, Snowdon CT, Lazaro-Perea C. 1998 Babbling and social context in infant monkeys: parallels to human infants. *Trends Cogn. Sci.* **2**, 31-37. (doi:10.1016/S1364-6613(97)01115-7) **Crossref, PubMed, Web of Science, Google Scholar**

³¹ Parsons CE, Young KS, Bhandari R, van IJzendoorn MH, Bakermans-Kranenburg MI, Stein A, Kringelbach ML. 2013 The bonnie baby: experimentally manipulated temperament affects perceived cuteness and motivation to view infant faces. *Dev. Sci.* **17**, 257-269. (doi:10.1111/desc.12112) **Crossref, PubMed, Web of Science, Google Scholar**

³² Riem Madelon ME, van IJzendoorn MH, Parsons CE, Young KS, De Carli P, Kringelbach ML, Bakermans-Kranenburg MJ. 2017 Experimental manipulation of infant temperament affects amygdala functional connectivity. *Cogn. Affect. Behav. Neurosci.* **71**, 858-868. (doi:10.3758/s13415-017-0518-8) **Crossref, Web of Science, Google Scholar**

and two together, conditioning plus early glimmerings of inter-subjectivity³³ lead them to incorporate sensory biases and preferences of potential caretakers into their own expanding repertoires for ingratiating themselves with others³⁴. By nine months, little humans go out of their way to be helpful. Human youngsters clearly care about what others think of their performance³⁵.

(c) Vocal control and more flexible vocalizing

Old World monkeys and apes are sophisticated communicators. Vervet monkeys, for example, emit one kind of call to alert group-mates of raptors, a different alarm call for terrestrial enemies. They are also sensitive to context, taking into account who is listening and who is out of range, modifying calls accordingly³⁶. Apes, particularly chimpanzees and bonobos, also make extensive use of hands and arms to communicate what they want, extending an arm palm up when requesting something. Even so, their vocal repertoires never achieve the richness, sophistication and flexibility of their gesturing³⁷. Rather, non-human apes seem surprisingly limited in the kinds of vocalizations they emit³⁸, a marked contrast with humans, who early in development increase vocal control and start to build larger and more flexible vocal repertoires³⁹. So how did this get started?

One important element developed elsewhere concerns the challenges that adults, rather than the immatures of cooperative breeders, are confronted with^{40,41}. They face

³³ Trevarthen C. 1993. The self born in intersubjectivity. In *The perceived self: ecological and interpersonal sources of self-knowledge* (ed. Neisser U), pp. 121-173. Cambridge, UK: Cambridge University Press. **Google Scholar**

³⁴ Gopnik A. 2020 Childhood as a solution to explore-exploit tensions. *Phil. Trans. R. Soc. B* **375**, 20190502. (doi:10.1098/rstb.2019.0502) **Link, Web of Science, Google Scholar**

³⁵ Warneken F, Tomasello M. 2006 Altruistic helping in human infants and young chimpanzees. *Science* **311**, 1301-1303. (doi:10.1126/science.1121448) **Crossref, PubMed, Web of Science, Google Scholar**

³⁶ Cheney D, Seyfarth R. 1990 *How monkeys see the world: inside the mind of another species*. Chicago, IL: University of Chicago Press. **Crossref, Google Scholar**

³⁷ Pollick AS, De Waal F. 2007 Ape gestures and language evolution. *Proc. Natl Acad. Sci. USA* **104**, 8184-8189. (doi:10.1073/pnas.0702624104) **Crossref, PubMed, Web of Science, Google Scholar**

³⁸ Slocombe K, Zuberbühler K. 2010 Vocal communication in the chimpanzee. In *The mind of the chimpanzee: ecological and experimental perspectives* (eds Lonsdorf EV, Ross SR, Matsuzawa T), pp. 192-207. Chicago, IL: University of Chicago Press. **Google Scholar**

³⁹ Zuberbühler K. 2012 Cooperative breeding and the evolution of vocal flexibility. In *The Oxford handbook of language evolution* (eds Tellerman M, Gibson K), pp. 71-81. New York, NY: Oxford University Press. **Google Scholar**

⁴⁰ Burkart JM, Martins EG, Miss F, Zuercher Y. 2018 From sharing food to sharing information: cooperative breeding and language evolution. *Interact. Stud.* **19**, 136-150. (doi:10.1075/is.17026.bur) **Crossref, Web of Science, Google Scholar**

⁴¹ Snowden CT. 2001 Social processes in communication and cognition in callitrichid monkeys: a review. *Anim. Cogn.* **4**, 247-257. (doi:10.1007/s100710100094) **Crossref, PubMed, Google Scholar**

increasing necessity to coordinate their activities, such as for instance infant transfers, with others and their prosociality motivates them to share not only food with others, but also information that is useful for them. Vocal communication is a prime candidate to provide a solution to exactly these type of challenges, and accordingly, the large vocal repertoires of cooperatively breeding birds are driven by an increase in contact and alarm calls⁴². But a critical element is added by immatures, who grow up in an increasingly voluble environment.

From a comparative perspective, it seems clear that shared care with babies carried by others increases vocalization frequency. Allomaternal provisioning and contingent reinforcement raises the stakes, with begging leading to more calling, especially if immatures have to compete for rewarding attentions^{43,44}. Through the expression of otherwise latent capacities and their subsequent shaping, attention-getting and begging set the stage for selection to favour enhanced vocal control accompanied by goal-oriented shaping of acoustic structure. Indeed, as in marmosets, vocal development in humans occurs earlier than motor development⁴⁵. By contrast, infants in constant close contact with single-mindedly dedicated mothers (as in independently breeding species such as chimpanzees) would more often be called upon to cling than cry.

Experiments with marmosets undertaken by Asif Ghazanfar and his team demonstrate how contingent responsiveness by caretakers generates turn-taking and also speeds development of specialized, more mature-sounding calls⁴⁶. For 40 min a day during the first two months of life, each of a pair of marmoset twins was separated from their parents and allowed to call. Whereas one twin was provided consistent feedback from taped parental calls, the other twin received less consistent feedback. The more reliable the feedback, the more rapidly infants progressed from the coarse, random-sounding vocalizations typical of immatures to cleaner, more tonal, adult-like

⁴² Leighton GM. 2017 Cooperative breeding influences the number and type of vocalizations in avian lineages. *Proc. R. Soc. B* **284**, 20171508. (doi:10.1098/rspb.2017.1508) **Link, Web of Science, Google Scholar**

⁴³ Leighton GM. 2017 Cooperative breeding influences the number and type of vocalizations in avian lineages. *Proc. R. Soc. B* **284**, 20171508. (doi:10.1098/rspb.2017.1508) **Link, Web of Science, Google Scholar**

⁴⁴ Goldstein MH, King AP, West MJ. 2003 Social interaction shapes babbling: testing parallels between birdsong and speech. *Proc. Natl Acad. Sci. USA* **100**, 8030-8035. (doi:10.1073/pnas.1332441100) **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁵ Gustison ML, Borjon JI, Takahashi DY, Ghazanfar AA. 2019 Vocal and locomotor coordination develops in association with the autonomic nervous system. *eLife* **8**, e41853. (doi:10.7554/eLife.41853) **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁶ Takahashi DY, Fenley AR, Ghazanfar AA. 2016 Early development of turn-taking with parents shapes focal acoustics in infant marmoset monkeys. *Phil. Trans. R. Soc. B* **371**, 20150370. (doi:10.1098/rstb.2015.0370) **Link, Web of Science, Google Scholar**

phee calls^{47,48}. By two to three months of age, their utterances resembled the turn-taking ‘conversations’ human babies engage in with their caretakers. Chow *et al.*⁴⁹ further showed that parents actively intervene when immatures make typical mistakes while learning to engage in turn-taking. If immatures get timing wrong and ‘interrupt’ their parents, parents add an extra break before responding. When immatures respond with a wrong call type, the parents themselves interrupt them with the correct *phee* call. In another example of convergent evolution between human cooperative breeders and these tiny-brained, distantly related New World monkeys, Takahashi and colleagues noted that infant marmosets responding to contingent reinforcement rely on one of the same circuits to guide their *phee* calls that humans use in speech. The patterning of FoxP2 expression in marmosets’ cortico-striatal circuit turns out to be analogous to that in both humans and songbirds⁵⁰. Moreover, a role of oxytocin has recently been proposed for the social motivation and evolution of vocal learning and language⁵¹, which is consistent with the increase of oxytocin in all group members after the birth of marmoset immatures⁵² and its link with prosociality among group members⁵³.

Observations of golden lion tamarins (*Leontopithecus rosalia*) in Brazil illustrate how these increasingly complex, two-way conversations function in natural habitats⁵⁴. Solitary adults traverse the treetops hunting for spiders, insects, and small frogs, prying prey from inside holes or tangled foliage. Youngsters learn to locate, stalk, and dexterously extract and dispatch struggling, sometimes biting or stinging, prey. Learning takes time and practice as immatures grow more adept at responding to adults

⁴⁷ Takahashi DY, Fenley AR, Ghazanfar AA. 2016 Early development of turn-taking with parents shapes focal acoustics in infant marmoset monkeys. *Phil. Trans. R. Soc. B* **371**, 20150370. (doi:10.1098/rstb.2015.0370) **Link, Web of Science, Google Scholar**

⁴⁸ Takahashi DY, Liao DA, Ghazanfar AA. 2017 Vocal learning via social reinforcement by infant marmoset monkeys. *Curr. Biol.* **27**, 1844-1852. (doi:10.1016/j.cub.2017.05.004) **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁹ Chow CP, Mitchell JF, Miller CT. 2015 Vocal turn-taking in a non-human primate is learned during ontogeny. *Proc. R. Soc. B* **282**, 20150069. (doi:10.1098/rspb.2015.0069) **Link, Web of Science, Google Scholar**

⁵⁰ Takahashi DY, Liao DA, Ghazanfar AA. 2017 Vocal learning via social reinforcement by infant marmoset monkeys. *Curr. Biol.* **27**, 1844-1852. (doi:10.1016/j.cub.2017.05.004) **Crossref, PubMed, Web of Science, Google Scholar**

⁵¹ Theofanopoulou C, Boeckx C, Jarvis ED. 2017 A hypothesis on a role of oxytocin in the social mechanisms of speech and vocal learning. *Proc. R. Soc. B* **284**, 20170988. (doi:10.1098/rspb.2017.0988) **Link, Web of Science, Google Scholar**

⁵² Finkenwirth C, Martins E, Deschner T, Burkart JM. 2016 Oxytocin is associated with infant-care behavior and motivation in cooperatively breeding marmoset monkeys. *Horm. Behav.* **80**, 10-18. (doi:10.1016/j.yhbeh.2016.01.008) **Crossref, PubMed, Web of Science, Google Scholar**

⁵³ Finkenwirth C, Burkart JM. 2017 Long-term-stability of relationship structure in family groups of common marmosets, and its link to proactive prosociality. *Physiol. Behav.* **173**, 79-86. (doi:10.1016/j.physbeh.2017.01.032) **Crossref, PubMed, Web of Science, Google Scholar**

⁵⁴ Rapaport LG. 2011 Progressive parenting in wild golden lion tamarins. *Behav. Ecol.* **22**, 745-754. (doi:10.1093/beheco/arr055) **Crossref, PubMed, Web of Science, Google Scholar**

volunteering prey. Deliveries peak near the end of weaning, when up to 90% of their diets are provided by (mostly male) allomothers⁵⁵. Food transfers are often initiated by youngsters begging. But when adults locate food, provisioners too emit staccato ‘food-offering calls’. Mothers, probable fathers, and other helpers extract the food and call the infant to come and get the food out of their hands. As prey-catching efficiency improves, but before youngsters reach adult proficiency, mentors switch from ‘come and get it’ calls, to ‘hey, look here’. Adult calls direct older immatures’ attention to a particular patch of substrate where prey have been detected. The finder then waits nearby while the young locate and extract it for themselves. Such adjustment of adults to immature skill levels has also been found in other callitrichids in captive studies (cotton-top tamarins⁵⁶, common marmosets^{57,58}). As infants increasingly associate an allomother’s particular call with a particular reward, they register regularities in how others respond to particular sounds they themselves make.

Opportunities to link own vocal productions to regularities in how others respond to them are particularly evident for babbling (humans) or babbling-like behaviours (callitrichids). In humans, babbling emerges spontaneously at around five to seven months, about the same time as the emergence of milk teeth, which among hunter–gatherers often coincides with allomothers beginning to offer premasticated and other (sometimes ‘kiss-fed’) treats to infants⁵⁹. At some level (consciously or not), children recognize that babbling attracts rewarding attention. This may help explain why older children revert to ‘baby talk’ after the birth of a younger sibling (S. B. Hrdy 2019, personal observation). Interestingly, babbling in marmosets not only attracts carers, but also speeds up the acquisition of adult-like forms of vocalizations. Moreover, babbling similarly can resume and spike among juvenile marmosets following the birth of new infants in their group⁶⁰. Apparently, the same message is being conveyed: ‘pay attention to *me!*’

‘If babbling changes adult behaviour in predictable, infant-oriented ways’, as Goldstein and colleagues propose, ‘infants should be able to recognize changes in others’

⁵⁵ Rapaport LG. 2011 Progressive parenting in wild golden lion tamarins. *Behav. Ecol.* **22**, 745–754. (doi:10.1093/beheco/arr055) **Crossref, PubMed, Web of Science, Google Scholar**

⁵⁶ Humle T, Snowdon CT. 2008 Socially biased learning in the acquisition of a complex foraging task in juvenile cottontop tamarins, *Saguinus oedipus*. *Anim. Behav.* **75**, 267–277. (doi:10.1016/j.anbehav.2007.05.021) **Crossref, Web of Science, Google Scholar**

⁵⁷ Chow CP, Mitchell JF, Miller CT. 2015 Vocal turn-taking in a non-human primate is learned during ontogeny. *Proc. R. Soc. B* **282**, 20150069. (doi:10.1098/rspb.2015.0069) **Link, Web of Science, Google Scholar**

⁵⁸ Dell’Mour V, Range F, Huber L. 2009 Social learning and mother’s behavior in manipulative tasks in infant marmosets. *Am. J. Primatol.* **71**, 503–509. **Crossref, PubMed, Web of Science, Google Scholar**

⁵⁹ Hrdy SB. 2009 *Mothers and others: the evolutionary origins of mutual understanding*. Cambridge, MA: Belknap Press. **Google Scholar**

⁶⁰ Snowdon C, Elowson AM. 2001 ‘Babbling’ in pygmy marmosets: development after infancy. *Behaviour* **138**, 1235–1248. (doi:10.1163/15685390152822193) **Crossref, Web of Science, Google Scholar**

actions as a result of their vocalizations’⁶¹, p. 8034], launching more goal-oriented vocal control. As with other apes, humans are born with limited motor control over articulation, but beginning around six months humans gain increased vocal control, including more tongue involvement with vocal tracts continuing to develop over the first 15 months, contributing to greater vocal flexibility and larger vocal repertoires in humans than other apes⁶². Impressed by the coincidence in timing between increased vocal control and the transition from baby-calls to babbling-like streams of consonants and vowels, Klaus Zuberbühler makes a compelling case that increased control derived from hominin infants’ need to attract allomaternal attentions⁶³, pp. 71, 77–79]. Although ‘babbling’ is widely assumed to have first emerged in human children in preparation for the acquisition of spoken language, akin to Mother Nature adding training wheels on a bicycle, it makes more sense (and is far less teleological) to consider the initial emergence of traits like babbling as byproducts of infantile needs to attract carers. A key innovation here was increased motor control over articulation. Once vocalizations become subject to voluntary control they can be shaped via conditional reinforcement, critical preadaptation for the eventual evolution of spoken language.

(d) Incorporate others’ preferences

These novel capacities emerged within broader sociocognitive contexts where apes were already endowed with rudimentary Theory of Mind^{64,65,66}, already using rich gestural repertoires⁶⁷, already employing tools and devising new modes of extracting food. By the Late Pleistocene, selection pressures from a range of new subsistence and so-

⁶¹ Goldstein MH, King AP, West MJ. 2003 Social interaction shapes babbling: testing parallels between birdsong and speech. *Proc. Natl Acad. Sci. USA* **100**, 8030-8035. (doi:10.1073/pnas.1332441100) **Crossref, PubMed, Web of Science, Google Scholar**

⁶² Zuberbühler K. 2012 Cooperative breeding and the evolution of vocal flexibility. In *The Oxford handbook of language evolution* (eds Tellerman M, Gibson K), pp. 71-81. New York, NY: Oxford University Press. **Google Scholar**

⁶³ Zuberbühler K. 2012 Cooperative breeding and the evolution of vocal flexibility. In *The Oxford handbook of language evolution* (eds Tellerman M, Gibson K), pp. 71-81. New York, NY: Oxford University Press. **Google Scholar**

⁶⁴ Hermann EA, Call J, Hernandez-Loreda MV, Hare B, Tomasello M. 2007 Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* **317**, 1360-1366. (doi:10.1126/science.1146282) **Crossref, PubMed, Web of Science, Google Scholar**

⁶⁵ Krupenye C, Kano F, Hirata S, Call J, Tomasello M. 2016 Great apes anticipate that other individuals will act according to false beliefs. *Science* **354**, 110-114. (doi:10.1126/science.aaf8110) **Crossref, PubMed, Web of Science, Google Scholar**

⁶⁶ Tomasello M. 2019 *Becoming human: a theory of ontogeny*. Cambridge, MA: Harvard University Press. **Crossref, Google Scholar**

⁶⁷ Pollick AS, De Waal F. 2007 Ape gestures and language evolution. *Proc. Natl Acad. Sci. USA* **104**, 8184-8189. (doi:10.1073/pnas.0702624104) **Crossref, PubMed, Web of Science, Google Scholar**

cioecological challenges also favoured greater inter-individual coordination⁶⁸⁶⁹⁷⁰⁷¹. It is within this broader context that recent proposals need to be understood that link cooperative breeding to the evolution of enhanced capacities not only for joint attention⁷² but also for language⁷³⁷⁴⁷⁵.

Social selection favouring more flexible communication coincided with other co-evolving feedback loops. But, by themselves, neither larger brains nor increased uses for cooperation are sufficient to explain the evolution of language. As psychiatrist Peter Hobson reminds us ‘before language there (had to be) something else ... that could evolve in tiny steps ... that something else was *social engagement with each other*. The links that can join one person’s mind with the mind of someone else are, especially to begin with, emotional links’ (⁷⁶, p. 2]; emphasis in original). But what about the foundational steps? Klaus Zuberbühler’s speculations point us in a promising direction: ‘Once vocal control has evolved to help infants secure care, it is only a small step to producing utterances in context-specific ways’⁷⁷, p. 80]. But, Zuberbühler adds, such a transformation ‘may only be possible against a background of other psychological skills, such as the ability to share intentions and attention’⁷⁸, and well-developed com-

⁶⁸ Guerreiro Martins EM, Moura ACA, Finkenwirth C, Griesser M, Burkart JM. 2019 Food sharing patterns in three species of callitrichid monkeys (*Callithrix jacchus*, *Leontopithecus chrysomelas*, *Saguinus midas*): individual and species differences. *J. Comp. Psychol.* **133**, 474-487. (doi:10.1037/com0000169) **Crossref, PubMed, Web of Science, Google Scholar**

⁶⁹ Tomasello M, Kruger AC, Ratner HH. 1993 Cultural learning. *Behav. Brain Sci.* **16**, 495-552. (doi:10.1017/S0140525X0003123X) **Crossref, Web of Science, Google Scholar**

⁷⁰ Boehm C. 2012 *Moral origins: the evolution of virtue, altruism and shame*. New York, NY: Basic Books. **Google Scholar**

⁷¹ Tomasello M. 2018 How we learned to put our fate in one another’s hands: the origins of morality. *Scient. Am.* **319**, 70-75. **Web of Science, Google Scholar**

⁷² Ben Mocha Y, Mundry R, Pika S. 2019 Joint attention skills in wild Arabian babblers (*Turdoides squamiceps*): a consequence of cooperative breeding? *Proc. R. Soc. B* **286**, 20190147. (doi:10.1098/rspb.2019.0147) **Link, Web of Science, Google Scholar**

⁷³ Burkart JM, Martins EG, Miss F, Zuercher Y. 2018 From sharing food to sharing information: cooperative breeding and language evolution. *Interact. Stud.* **19**, 136-150. (doi:10.1075/is.17026.bur) **Crossref, Web of Science, Google Scholar**

⁷⁴ Zuberbühler K. 2012 Cooperative breeding and the evolution of vocal flexibility. In *The Oxford handbook of language evolution* (eds Tellerman M, Gibson K), pp. 71-81. New York, NY: Oxford University Press. **Google Scholar**

⁷⁵ Knight C. 2016 *Decoding Chomsky*. New Haven, CT: Yale University Press. **Google Scholar**

⁷⁶ Hobson P. 2004 *The cradle of thought: exploring the origins of thinking*. Oxford, UK: Oxford University Press. (doi:10.1002/ajp.20682) **Google Scholar**

⁷⁷ Zuberbühler K. 2012 Cooperative breeding and the evolution of vocal flexibility. In *The Oxford handbook of language evolution* (eds Tellerman M, Gibson K), pp. 71-81. New York, NY: Oxford University Press. **Google Scholar**

⁷⁸ Tomasello M. 2008 *Origins of human communication*. Cambridge, MA: MIT Press. **Crossref, Google Scholar**

prehension'⁷⁹, p. 80]. He expands on Tomasello's insight regarding a 'major difference'⁸⁰ between humans and other primates, involving (as Tomasello would later phrase it) capacities for 'intersubjective sharing'⁸¹, pp. 121–122].

Eagerness to ingratiate themselves with others would be enhanced by allomaternal care, an interpretation consistent with observations of captive chimpanzees who, when co-reared by responsive human caretakers (allomothers of a different species) as well as their mothers, become more eager than wild chimpanzees are to engage in targeted helping of others (⁸²⁸³; reviewed in⁸⁴). Even though human-tended chimpanzees do not acquire spoken language and other distinctively human traits, they nevertheless develop greater concern for the intentions and goals of others, learning the power that particular gestures, facial expressions and utterances exert on others. For example, human-reared chimpanzees point to what they want in ways that wild apes almost never do⁸⁵. The expression of such interactive potentials in ape phenotypes would increase opportunities to share and increase effectiveness of helping. Over the course of human evolution, such opportunities may have increased selection favouring neuroendocrine systems conducive to prosocial responses, including the increasingly 'dopamine dominated' striatal systems being documented by palaeontologists working in concert with neuroscientists⁸⁶. Interactions with processes that opened parental neural care systems to a wider range of social stimuli might have resulted in more unsolicited food sharing and general prosociality⁸⁷. Apes who needed to be more interested in the preferences of others would also find it more emotionally rewarding to do so. This chain of

⁷⁹ Zuberbühler K. 2012 Cooperative breeding and the evolution of vocal flexibility. In *The Oxford handbook of language evolution* (eds Tellerman M, Gibson K), pp. 71-81. New York, NY: Oxford University Press. **Google Scholar**

⁸⁰ Tomasello M. 1999 *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press. **Google Scholar**

⁸¹ Tomasello M, Carpenter M. 2007 Shared intentionality. *Dev. Sci.* **10**, 121-125. (doi:10.1111/j.1467-7687.2007.00573.x) **Crossref, PubMed, Web of Science, Google Scholar**

⁸² Bard K. 2012 Emotional engagement: how chimpanzee minds develop. In *The primate mind* (eds de Waal F, Ferrari FP), pp. 224-245. Cambridge, MA: Harvard University Press. **Crossref, Google Scholar**

⁸³ Yamamoto S, Tatyana H, Tanaka M. 2012 Chimpanzees' flexible targeted helping based on an understanding of conspecific goals. *Proc. Natl Acad. Sci. USA* **109**, 3588-3592. (doi:10.1073/pnas.1108517109) **Crossref, PubMed, Web of Science, Google Scholar**

⁸⁴ Hrdy SB. 2016 Development plus social selection in the emergence of 'emotionally modern' humans. In *Childhood: origins, evolution and implications* (eds Meehan CL, Crittenden AN), pp. 11-44. Albuquerque, NM: School for Advanced Research and University of New Mexico Press. **Google Scholar**

⁸⁵ Tomasello M. 2019 *Becoming human: a theory of ontogeny*. Cambridge, MA: Harvard University Press. **Crossref, Google Scholar**

⁸⁶ Raghanti M-A, Edler MK, Stephenson AR, Munger EL, Jacobs B, Hof PR, Sherwood CC, Holloway RL, Lovejoy CO. 2018 A neurochemical hypothesis for the origin of hominids. *Proc. Natl Acad. Sci. USA* **115**, e1108-e1116. (doi:10.1073/pnas.1719666115) **Crossref, PubMed, Web of Science, Google Scholar**

⁸⁷ Numan M. 2015 *Neurobiology of social behavior: toward an understanding of the prosocial and antisocial brain*. Amsterdam, The Netherlands: Elsevier/Academic Press. **Google Scholar**

admittedly speculative reasoning brings us to a key component to the hominin infant's to-do list.

(e) Add psychological dimensions to *Kindchenschema*

Like all other catarrhine primates, apes in the line leading to the genus *Homo* would grow up keenly aware of kin ties, alliances, statuses and friendships as well as competencies and reliability of group-mates⁸⁸⁹. The quantitative skills and manipulative capabilities of a chimpanzee or orangutan fall in the same ballpark as those of two-and-a-half-year-old humans. They too exhibit rudimentary capacities for theorizing about what others know⁹⁰⁹¹⁹². Our Last Common Ancestors with these apes were already beginning to register what others intended or wanted.

So imagine such an ape growing up reliant on the competencies and motivations of others. If contingent reinforcement from allomothers encourages turn-taking and speeds up acquisition of adult vocalizations in tiny-brained marmosets with only minimal awareness of what another marmoset knows⁹³⁹⁴, how much more sensitive to the thoughts and preferences of others would apes already attuned to the thoughts and intentions of others become? Contingent allomaternal responses generate new psychological dimensions to *Kindchenschema* as apes growing up this way are conditioned to become more aware that others have preferences worth appealing to.

Youngsters would be conditioned not only to monitor the intentions of others, but increasingly to probe their thoughts and feelings so as to better conform to their preferences. Over time, learning which facial expressions, sounds or conversational

⁸⁸ Perry S. 2020 Behavioural variation and learning across the lifespan in wild white-faced capuchin monkeys. *Phil. Trans. R. Soc. B* **375**, 20190494. (doi:10.1098/rstb.2019.0494) [Link](#), [Web of Science](#), [Google Scholar](#)

⁸⁹ Cheney D, Seyfarth R. 2007 *Baboon metaphysics: the evolution of the social mind*. Chicago, IL: University of Chicago Press. [Crossref](#), [Google Scholar](#)

⁹⁰ Hermann EA, Call J, Hernandez-Loreda MV, Hare B, Tomasello M. 2007 Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* **317**, 1360-1366. (doi:10.1126/science.1146282) [Crossref](#), [PubMed](#), [Web of Science](#), [Google Scholar](#)

⁹¹ Krupenye C, Kano F, Hirata S, Call J, Tomasello M. 2016 Great apes anticipate that other individuals will act according to false beliefs. *Science* **354**, 110-114. (doi:10.1126/science.aaf8110) [Crossref](#), [PubMed](#), [Web of Science](#), [Google Scholar](#)

⁹² Tomasello M. 2020 The adaptive origins of uniquely human sociality. *Phil. Trans. R. Soc. B* **375**, 20190493. (doi:10.1098/rstb.2019.0493) [Link](#), [Web of Science](#), [Google Scholar](#)

⁹³ Burkart JM, Martins EG, Miss F, Zuercher Y. 2018 From sharing food to sharing information: cooperative breeding and language evolution. *Interact. Stud.* **19**, 136-150. (doi:10.1075/is.17026.bur) [Crossref](#), [Web of Science](#), [Google Scholar](#)

⁹⁴ Burkart JM, Heschl A. 2007 Perspective taking or behaviour reading? Understanding of visual access in common marmosets (*Callithrix jacchus*). *Anim. Behav.* **73**, 457-469. (doi:10.1016/j.anbehav.2006.05.019) [Crossref](#), [Web of Science](#), [Google Scholar](#)

rhythms result in solicitude would mature into more sophisticated understanding of how others perceived their own intentions, behaviours, and thoughts and to begin to care about their ‘reputations’.

3. New dimensions to social learning

(a) Expanded avenues

All apes are endowed with inordinate behavioural flexibility along with aptitudes for manipulating objects and imitating others. In the case of chimpanzees and orangutans, knowledge about what to eat, where to find and how to process it, is transmitted vertically during 5–8 years of intimate association with one other trusted individual, their mother. Mothers set the stage for socially induced independent practice¹²³ or, as in the case of chimpanzee nut-cracking, very occasionally make helpful adjustments⁴⁵. The processes by which little apes copy and learn from others are however primarily self-initiated⁶. Provisioning and shared care broadens this initial context for social learning.

From an early age, youngsters with shared care observe a wider range of role models. For example, cooperatively breeding magpie jays with many helpers become more adept

¹ Jaeggi AV, Dunkel LP, van Noordwijk MA, Wich SW, Sura AAL, van Schaik CP. 2010 Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *Am. J. Phys. Anthropol.* **72**, 62-71. (doi:10.1002/ajp.20752) **Google Scholar**

² Schuppli C, Forss SI, Meulman EJ, Zweifel N, Lee KC, Rukmana E, Vogel ER, van Noordwijk M, van Schaik CP. 2016 Development of foraging skills in two orangutan populations: needing to learn or needing to grow?. *Front. Zool.* **13**, 43. (doi:10.1186/s12983-016-0178-5) **Crossref, PubMed, Web of Science, Google Scholar**

³ Whiten A. 1999 Parental encouragement in gorilla in comparative perspective: implications for social cognition and the evolution of teaching. In *The mentalities of gorillas and orangutans: comparative perspective* (eds Taylor Parker S, Mitchell RW, Miles HL), pp. 342-366 Cambridge, UK: Cambridge University Press. **Google Scholar**

⁴ Matsuzawa T. 2010 The chimpanzee mind: bridging fieldwork and laboratory work. In *The mind of the chimpanzee: ecological and experimental perspectives* (eds Lonsdorf EV, Ross SR, Matsuzawa T), pp. 1-19. Chicago, IL: University of Chicago Press. **Google Scholar**

⁵ Boesch C. 2012 *Wild cultures: a comparison between chimpanzee and human cultures*. Cambridge, UK: Cambridge University Press. **Crossref, Google Scholar**

⁶ Humle T, Snowdon CT, Matsuzawa T. 2009 Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Anim. Cogn.* **12**, 37-48. (doi:10.1007/s10071-009-0272-6) **Crossref, PubMed, Web of Science, Google Scholar**

at harvesting arthropods than jays growing up with few⁷. Furthermore, demonstrators among cooperative breeders tend to be more prosocial, even deliberately helpful⁸⁹. Recall that golden lion tamarin allomothers (often probable or possible progenitors) provide the majority of food for nearly weaned infants. First, adults call when they have food to offer, but with older immatures, they call them to places where prey is hidden and the immatures have to do the extraction themselves. As performance levels plateau, food calls cease. Rapaport¹⁰, p. 746] compares the progressive, developmentally sensitive behaviours and vocalizations tracking the needs and skills of youngsters that allomothers use to provide foraging assistance to ‘teaching-like’ behaviour (cf.¹¹ for cooperatively breeding meerkats).

Incorporating situation-dependent vocalizations enhances effectiveness of demonstrations while contingently delivered food rewards rivets the attention of mentees. Anyone who has ever tried to habituate wild creatures, or even skittish domestic ones, know that food rewards provide the quickest short-cut to taming or training them. Now add to this prosocial–provisioning–vocalizing mix mentalizing mentees eager to accommodate their mentors. Possibilities for information transfer expand exponentially.

(b) Emotionally modern and mentalizing mentees

Even in the absence of detectable Theory of Mind, tiny-brained marmosets prove remarkably prosocial, sharing food or rushing to assist others. Marmosets coordinate with others to crack open tough fruits. They take babies from mothers then voluntarily return them for nursing¹²¹³¹⁴. Tamarins even use guided demonstrations ac-

⁷ Langen TA, Vehrencamp SL. 1998 Ecological factors affecting group and territory size in white-throated magpie-jays. *Auk* **115**, 327-339. (doi:10.2307/4089191) [Crossref](#), [Web of Science](#), [Google Scholar](#)

⁸ Burkart JM, Hrdy SB, van Schaik CP. 2009 Cooperative breeding and human cognitive evolution. *Evol. Anthropol.* **18**, 175-186. (doi:10.1002/evan.20222) [Crossref](#), [Web of Science](#), [Google Scholar](#)

⁹ Burkart JM, van Schaik CP. 2012 Group service in macaques, capuchins and marmosets: a comparative approach to identifying proactive prosocial motivations. *J. Comp. Psychol.* **127**, 212-225. (doi:10.1037/a0026392) [Crossref](#), [PubMed](#), [Web of Science](#), [Google Scholar](#)

¹⁰ Rapaport LG. 2011 Progressive parenting in wild golden lion tamarins. *Behav. Ecol.* **22**, 745-754. (doi:10.1093/beheco/arr055) [Crossref](#), [PubMed](#), [Web of Science](#), [Google Scholar](#)

¹¹ Thornton A, McAuliffe L. 2006 Teaching in wild meerkats. *Science* **313**, 227-229. (doi:10.1126/science.1128727) [Crossref](#), [PubMed](#), [Web of Science](#), [Google Scholar](#)

¹² Burkart JM, Hrdy SB, van Schaik CP. 2009 Cooperative breeding and human cognitive evolution. *Evol. Anthropol.* **18**, 175-186. (doi:10.1002/evan.20222) [Crossref](#), [Web of Science](#), [Google Scholar](#)

¹³ Garber P. 1997 One for all and breeding for one. *Evol. Anthropol.* **7**, 187-199. (doi:10.1002/(SICI)1520-6505(1997)5:6<187::AID-EVAN1>3.0.CO;2-A) [Crossref](#), [Google Scholar](#)

¹⁴ Burkart JM et al. 2014 The evolutionary origins of human hyper-cooperation. *Nat. Commun.* **5**, 4747. (doi:10.1038/ncomms5747) [Crossref](#), [PubMed](#), [Web of Science](#), [Google Scholar](#)

centuated by vocalizations to transmit age-appropriate information¹⁵. In this respect, tiny-brained callitrichids converge on something close to what ethnographers studying hunter–gatherers term ‘natural pedagogy’¹⁶. Yet even as tamarins adjust demonstrations to the skill level of pupils, they do so without mentalizing what another knows. Marmosets who readily follow the gaze of another individual do so without registering *what* that individual is seeing¹⁷.

So what would happen if instead of the reflexive responsiveness of marmosets, the primates undertaking shared care and provisioning of young were already larger-bodied, bipedal, tool-users possessed of rudimentary Theory of Mind, with brains in the process of doubling from the 400 cm³ of chimpanzees or australopiths to the more expansive brains typical of *H. erectus*? And what if novel contexts for social development coincided with new foraging tactics, more valuable food packets, and with these, a raised ‘grey ceiling’ so that over time, whenever—and for whatever reasons—they became favoured, even costlier brains could evolve¹⁸¹⁹? Little hominins growing up as cooperative breeders would have opportunities to observe group members of different ages and sexes²⁰²¹²², trust them as their mothers do, gauge their competencies and intentions, decide who was likely to be helpful or not—something modern humans begin to do from as early as three months old²³²⁴. And what if at the same time these infants were

¹⁵ Rapaport LG. 2011 Progressive parenting in wild golden lion tamarins. *Behav. Ecol.* **22**, 745-754. (doi:10.1093/beheco/arr055) **Crossref, PubMed, Web of Science, Google Scholar**

¹⁶ Hewlett BS, Fouts HN, Boyette AH. 2011 Social learning among Congo Basin hunter–gatherers. *Phil. Trans. R. Soc. B* **366**, 1168-1178. (doi:10.1098/rstb.2010.0373) **Link, Web of Science, Google Scholar**

¹⁷ Burkart JM, Heschl A. 2007 Perspective taking or behaviour reading? Understanding of visual access in common marmosets (*Callithrix jacchus*). *Anim. Behav.* **73**, 457-469. (doi:10.1016/j.anbehav.2006.05.019) **Crossref, Web of Science, Google Scholar**

¹⁸ Isler K, van Schaik CP. 2012 Allomaternal care, life history and brain size evolution in mammals. *J. Hum. Evol.* **63**, 52-63. (doi:10.1016/j.jhevol.2012.03.009) **Crossref, PubMed, Web of Science, Google Scholar**

¹⁹ Isler K, van Schaik CP. 2012 How our ancestors broke through the gray ceiling: comparative evidence for cooperative breeding in early Homo. *Curr. Anthropol.* **53**, S453-S465. (doi:10.1086/667623) **Crossref, Web of Science, Google Scholar**

²⁰ Hawkes K. 2020 Cognitive consequences of our grandmothering life history: cultural learning begins in infancy. *Phil. Trans. R. Soc. B* **375**, 20190501. (doi:10.1098/rstb.2019.0501) **Link, Web of Science, Google Scholar**

²¹ Deffner D, McElreath R. 2020 The importance of life history and population regulation for the evolution of social learning. *Phil. Trans. R. Soc. B* **375**, 20190492. (doi:10.1098/rstb.2019.0492) **Link, Web of Science, Google Scholar**

²² Gurven MD, Davison RJ, Kraft TS. 2020 The optimal timing of teaching and learning across the life course. *Phil. Trans. R. Soc. B* **375**, 20190500. (doi:10.1098/rstb.2019.0500) **Link, Web of Science, Google Scholar**

²³ Hamlin JK, Wynn K, Bloom P. 2007 Social evaluation by preverbal infants. *Nature* **450**, 557-559. (doi:10.1038/nature06288) **Crossref, PubMed, Web of Science, Google Scholar**

²⁴ Hamlin JK, Wynn K, Bloom P. 2010 Three-month-olds show a negativity bias in their social evaluations. *Dev. Sci.* **13**, 923-929. (doi:10.1111/j.1467-7687.2010.00951.x) **Crossref, PubMed, Web of Science, Google Scholar**

beginning to monitor the intentions of others, seeking to conform to their preferences, even beginning to internalize their preferences, and at the same time also developing larger and more flexible vocal repertoires?

Many factors were involved in the evolution of language. Some clearly had to do with the unusual way apes in the line leading to *H. sapiens* were reared. Learning language is a highly social endeavour. Anyone who has ever spent time with babies knows that their mother is not the only person who speaks to them in high-pitched ‘motherese’. It is from eagerly listening to others that youngsters acquire new phonemes and words. Immatures learn new sounds better in the presence of someone else than if by themselves. As young as nine months, babies watching instructive videos more readily discriminate sounds and learn foreign phonemes when another child is present²⁵.

Not only current interactions but also past experiences with others influence children’s readiness to mentalize what someone else knows. When experimenters set up a computer game where 5-year-olds must explain to someone else where to collect a digital prize, they were told that the unseen other (really the experimenters’ confederate) was either a toddler or another 5-year-old. Subjects adjusted instructions accordingly. When told their partner was a toddler, subjects spent longer explaining the game than when they assumed the other child was older. The more days between birth and age four that the subject had spent with others in daycare, the readier that child was to take the others’ level of understanding into account, mentalizing what they were likely to already know²⁶.

(c) Concern for reputation and learning

Within the first year of life, hominins approaching this emotional modernity would, like behaviourally modern humans today, actively seek to become the object of someone else’s attention, and feel at least a glimmer of pride when approved of, and shame when disapproved of^{27,28}. After a year or so these youngsters may have already been disposed to spontaneously offer something interesting or desirable to someone else, the way 14-month-old behaviourally modern humans do today, even proffering an item

²⁵ Lytle SR, Garcia-Sierra A, Kuhl PK. 2018 Two are better than one: infant language learning from video improves in the presence of peers. *Proc. Natl Acad. Sci. USA* **115**, 9859-9866. (doi:10.1073/pnas.1611621115) **Crossref, PubMed, Web of Science, Google Scholar**

²⁶ Stolk A, Hunnius S, Bekkering H, Toni I. 2013 Early social experience predicts referential communicative adjustments in five-year-old children. *PLoS ONE* **8**, e72667. (doi:10.1371/journal.pone.0072667) **Crossref, PubMed, Web of Science, Google Scholar**

²⁷ Trevarthen C. 1993. The self born in intersubjectivity. In *The perceived self: ecological and interpersonal sources of self-knowledge* (ed. Neisser U), pp. 121-173. Cambridge, UK: Cambridge University Press. **Google Scholar**

²⁸ Reddy V. 2003 On being the object of attention: implications for self-other consciousness. *Trends Cogn. Sci.* **7**, 397-402. (doi:10.1016/S1364-6613(03)00191-8) **Crossref, PubMed, Web of Science, Google Scholar**

differing from their own preference²⁹. Today’s behaviourally modern Western children readily absorb and follow normative rules³⁰, pp. 224–225], expect others to do so, and care desperately about their own reputations³¹. When someone is trying to teach them something they not only feel pride at success, but want others to know ‘I did it!’ Equipped with sophisticated language these same children as early as 3 or 4 years of age employ flattery to cultivate the goodwill of others³². By early adulthood, behaviourally modern humans find it so pleasurable to talk about themselves that among contemporary Westerners, it stimulates the same neural regions as anticipating something delicious to eat would³³. This concern with presentation of self, reputation and impressing others may fuel tendencies to register the intentions and preferences of others who are modelling behaviour and then conform. This may explain why human children, but not other apes, do not just imitate demonstrators, but sometimes ‘over-imitate’ them, adding all the same ritualized bells and whistles even if these exceed procedures needed to accomplish a task^{34,35,36}. Acute sensitivity to the intentions, thoughts and preferences of others, eagerness for their approval, and a rush of dopamine and other neurochemical rewards when sensing approval, add new dimensions to social learning.

Primatewide, youngsters learn to conform to social rules while growing up, for example internalizing proper etiquette for approaching a dominant group member. But human children display special eagerness to ingratiate themselves with others and internalize their preferences, adding subjective dimensions to this quest. Evolutionary psychiatrist Randolph Nesse hypothesizes that runaway social selection favouring self-consciousness and concern with reputation in creatures already interested in mentaliz-

²⁹ Repacholi BM, Gopnik A. 1997 Early reasoning about desires: evidence from 14- and 18-month-olds. *Dev. Psychol.* **33**, 12-21. (doi:10.1037/0012-1649.33.1.12) **Crossref, PubMed, Web of Science, Google Scholar**

³⁰ Gopnik A. 2010 *The philosophical baby: what children’s minds tell us about truth, love, and the meaning of life*. New York, NY: Farrar, Straus, and Giroux. **Google Scholar**

³¹ Englemann JM, Herrmann E, Tomasello M. 2012 Five-year olds, but not chimpanzees, attempt to manage their reputations. *PLoS ONE* **7**, e48433. (doi:10.1371/journal.pone.0048433) **Crossref, PubMed, Web of Science, Google Scholar**

³² Fu G, Lee K. 2007 Social grooming in the kindergarten: the emergence of flattery behavior. *Dev. Sci.* **10**, 255-265. (doi:10.1111/j.1467-7687.2007.00583.x) **Crossref, PubMed, Web of Science, Google Scholar**

³³ Tamir D, Mitchell J. 2012 Disclosing information about the self is intrinsically rewarding. *Proc. Natl Acad. Sci. USA* **109**, 8038-8043. (doi:10.1073/pnas.1202129109) **Crossref, PubMed, Web of Science, Google Scholar**

³⁴ Gopnik A. 2010 *The philosophical baby: what children’s minds tell us about truth, love, and the meaning of life*. New York, NY: Farrar, Straus, and Giroux. **Google Scholar**

³⁵ Nielsen M, Tomaselli K. 2010 Overimitation in Kalahari Bushman children and the origins of human cultural cognition. *Psychol. Sci.* **21**, 729-736. (doi:10.1177/0956797610368808) **Crossref, PubMed, Web of Science, Google Scholar**

³⁶ Whiten A, McGuigan N, Marshall-Pescini S, Hopper LM. 2009 Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Phil. Trans. R. Soc. B* **364**, 2417-2428. (doi:10.1098/rstb.2009.0069) **Link, Web of Science, Google Scholar**

ing what others think explains why our ancestors evolved the internal self-monitoring known as ‘a conscience’³⁷³⁸.

Whether or not such ingratiating tendencies encourage humans to behave in fair, generous, or civic-minded rather than more self-serving ways probably depends more on socioecological contexts and immediate goals than on what are sometimes taken to be hard-wired moral sensibilities³⁹⁴⁰⁴¹. As early as six months, long before language, infants exhibit preferences for helpful versus hurtful others⁴². However, it is unclear how prosocial versus self-interested such preferences are. In experiments simulating *voir dire* in an imaginary courtroom, Melnikoff & Bailey⁴³ asked adult subjects who they would prefer in the jury, depending on whether they served as lawyer for the defence or for the prosecution. The researchers were struck by how conditional on peoples’ current goals their preferences for moral versus immoral actors could be. Whatever standards prevail, quests to demonstrate mental and behavioural responses conforming to others’ preferences pave the way for internalizing group norms⁴⁴ and for behaviour that others consider ‘moral’⁴⁵⁴⁶. It is exactly this third party perspective that is strikingly lacking in non-human primates⁴⁷, who otherwise exhibit various building blocks of morality⁴⁸⁴⁹. Other primates may conform to local traditions, but they do not seem to care if *others*

³⁷ Nesse R. 2019 *Good reasons for bad feelings: insights from the frontier of evolutionary psychiatry*. New York, NY: Penguin/Random House. **Google Scholar**

³⁸ Nesse RM. 2007 Runaway social selection for displays of partner value and altruism. *Biol. Theor* **2**, 143-155. (doi:10.1162/biot.2007.2.2.14) **Crossref, Google Scholar**

³⁹ Hamlin JK, Wynn K, Bloom P. 2010 Three-month-olds show a negativity bias in their social evaluations. *Dev. Sci.* **13**, 923-929. (doi:10.1111/j.1467-7687.2010.00951.x) **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁰ Bloom P. 2013 *Just babies: the origins of good and evil*. New York, NY: Crown. **Google Scholar**

⁴¹ Hamlin JK, Wynn K. 2011 Young infants prefer prosocial to antisocial others. *Cogn. Dev.* **26**, 30-39. (doi:10.1016/j.cogdev.2010.09.001) **Crossref, PubMed, Web of Science, Google Scholar**

⁴² Hamlin JK, Wynn K. 2011 Young infants prefer prosocial to antisocial others. *Cogn. Dev.* **26**, 30-39. (doi:10.1016/j.cogdev.2010.09.001) **Crossref, PubMed, Web of Science, Google Scholar**

⁴³ Melnikoff DE, Bailey AH. 2018 Preferences for moral vs. immoral traits in others are conditional. *Proc. Natl Acad. Sci. USA* **115**, e592-e600. (doi:10.1073/pnas.1714945115) **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁴ Gavrilites S, Richerson PJ. 2017 Collective action and the evolution of social norm internalization. *Proc. Natl Acad. Sci. USA* **114**, 6068-6073. (doi:10.1073/pnas.1703857114) **Crossref, PubMed, Web of Science, Google Scholar**

⁴⁵ Boehm C. 2012 *Moral origins: the evolution of virtue, altruism and shame*. New York, NY: Basic Books. **Google Scholar**

⁴⁶ Tomasello M. 2016 *A natural history of human morality*. Cambridge, MA: Harvard University Press. **Crossref, Google Scholar**

⁴⁷ Burkart JM, Brügger RK, van Schaik CP. 2018 Evolutionary origins of morality: insights from nonhuman primates. *Front. Sociol.* **3**, 17. (doi:10.3389/fsoc.2018.00017) **Crossref, Google Scholar**

⁴⁸ De Waal F. 2006 *Primates and philosophers: how morality evolved*. Princeton, NJ: Princeton University Press. **Crossref, Google Scholar**

⁴⁹ Silk JB, House BR. 2016 The evolution of altruistic social preferences in human groups. *Phil. Trans. R. Soc. B* **371**, 20150097. (doi: 10.1098/rstb.2015.0097) **Link, Web of Science, Google Scholar**

do so or not, and even unusually prosocial primates such as marmosets do not manage their reputations by increasing helping efforts when observed by others⁵⁰. Humans, being able to represent how their behaviour appears to others (perhaps as a result of their great ape cognitive heritage)⁵¹, appear distinctively motivated to care about their reputations. The same would be advantageous for marmosets too, but they may simply not be able to cognitively represent how they appear to others.

⁵⁰ Burkart JM, Brügger RK, van Schaik CP. 2018 Evolutionary origins of morality: insights from nonhuman primates. *Front. Sociol.* **3**, 17. (doi:10.3389/fsoc.2018.00017) **Crossref, Google Scholar**

⁵¹ Krupenye C, Kano F, Hirata S, Call J, Tomasello M. 2016 Great apes anticipate that other individuals will act according to false beliefs. *Science* **354**, 110-114. (doi:10.1126/science.aaf8110) **Crossref, PubMed, Web of Science, Google Scholar**

4. Conclusion

Across taxa, longer spans of post-weaning or post-fledging dependence are predictable corollaries of cooperative breeding. In the case of the cooperatively breeding apes in the line leading to the genus *Homo*, reliance on care and provisioning from alloparents as well as parents conditioned dependent immatures to develop un-ape-like eagerness to monitor and care about the intentions of others, mentalize what they were thinking and feeling, and seek to ingratiate themselves with them, leading to the expression and refinement of otherwise latent ape potentials. This novel context for development and social learning coincided with directional social selection¹² favouring youngsters best at ingratiating themselves with protectors, mentors and providers. By 2 Ma this combined process of development-plus-social selection was already contributing towards the emergence of ape cognitive and emotional phenotypes very different from those among our Last Common Ancestors with chimpanzees and other apes.

Without any foresight on Mother Nature's part concerning how important questing for intersubjective engagement and escalating concerns with reputations would eventually turn out to be, *H. erectus* infants would have been conditioned to monitor and care about what others were thinking, including thinking about them, and rewarded for internalizing their preferences in ways others apes were not. Reputational concerns make having a conscience increasingly useful. Long before the emergence of *anatomically modern* big-brained humans by 300 000 years ago³, or before behaviourally modern humans with symbolic thought and language, these emotionally different apes were already eager to appeal to and help others. Furthermore, observation of humans today suggests that these tendencies emerge early and in both sexes, with girls if anything better able to interpret others' expressions and feelings than boys⁴.

By the Late Pleistocene, when cooperative hunting of big game, division of labour and sharing of food became important, hominins of both sexes must *already* have become predisposed to read the intentions of others in order to coordinate with and per-

¹ West-Eberhard MJ. 2003 *Development, plasticity and evolution*. Oxford, UK: Oxford University Press. **Crossref, Google Scholar**

² West-Eberhard MJ. 1983 Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**, 155-183. (doi:10.1086/413215) **Crossref, Web of Science, Google Scholar**

³ Hublin J-J et al. 2017 New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. *Nature* **546**, 289-292. (doi:10.1038/nature22336) **Crossref, PubMed, Web of Science, Google Scholar**

⁴ Geary DC. 2018 Autism in the broader context of cognitive sex differences. *Proc. Natl Acad. Sci. USA* **115**, 12 089-12 091. (doi:10.1073/pnas.1817772115) **Crossref, Web of Science, Google Scholar**

haps help them⁵⁶⁷⁸. By the time coordinated hunting of large animals was established in the human repertoire—whether by 400 000 years ago as in Tomasello’s reconstruction or closer to Chris Boehm’s ‘magic number’⁹, p. 313] of 250 000 years ago—it was probably accompanied by ‘punitive social selection’ against stingy or overly domineering men, as documented for most well-studied hunter–gatherer societies¹⁰, p. 164,¹¹¹². If so, these members of the genus *Homo* would have already become motivationally very different from their more self-centred, solipsistic ape ancestors. In Boehm’s account, sanctions against bullies could extend to exile or even execution, pressuring group members to conform and adopt normative ‘moral’ behaviour. But with internalization of norms already underway, archaic humans were, from an early age already sensitive to what others felt and thought about them, concerned about personal reputations, and eager to cooperate. They were preadapted to internalize ways of behaving and expressing themselves that others preferred.

With higher quality food sources and with multiple provisioners continuing to buffer weanlings from recurring shortages, the grey ceiling limiting energy available for brains was raised. The stage was set for these *emotionally modern* early humans to meet Late Pleistocene social and ecological challenges in ways that would favour the evolution of even more costly, anatomically modern, brains. Accompanying motivations would also lead to the emergence of more sophisticated modes of vocal communication that would vastly expand both the ability to learn from multiple others (via gossip and teaching) and the reach and importance both of normative ways of doing things¹³ and of reputations. Such processes would stress conformity and further favour the internalization of group norms and human indoctrinability, hallmarks of *behaviourally modern* humans.

⁵ Hrdy SB. 2009 *Mothers and others: the evolutionary origins of mutual understanding*. Cambridge, MA: Belknap Press. **Google Scholar**

⁶ Hrdy SB. 2016 Development plus social selection in the emergence of ‘emotionally modern’ humans. In *Childhood: origins, evolution and implications* (eds Meehan CL, Crittenden AN), pp. 11–44. Albuquerque, NM: School for Advanced Research and University of New Mexico Press. **Google Scholar**

⁷ Hawkes K. 2014 Primate sociality to human cooperation: why us and not them? *Hum. Nat.* **25**, 28–48. (doi:10.1007/s12110-013-9184-x) **Crossref, PubMed, Web of Science, Google Scholar**

⁸ Tomasello M, Gonzalez-Cabrera I. 2017 The role of ontogeny in the evolution of human cooperation. *Hum. Nat.* **28**, 274–288. (doi:10.1007/s12110-017-9291-1) **Crossref, PubMed, Web of Science, Google Scholar**

⁹ Boehm C. 2012 *Moral origins: the evolution of virtue, altruism and shame*. New York, NY: Basic Books. **Google Scholar**

¹⁰ Boehm C. 2012 *Moral origins: the evolution of virtue, altruism and shame*. New York, NY: Basic Books. **Google Scholar**

¹¹ Tomasello M. 2018 How we learned to put our fate in one another’s hands: the origins of morality. *Scient. Am.* **319**, 70–75. **Web of Science, Google Scholar**

¹² Tomasello M. 2016 *A natural history of human morality*. Cambridge, MA: Harvard University Press. **Crossref, Google Scholar**

¹³ Richerson PJ, Boyd R. 2020 The human life history is adapted to exploit the adaptive advantages of culture. *Phil. Trans. R. Soc. B* **375**, 20190498. (doi:10.1098/rstb.2019.0498) **Link, Web of Science, Google Scholar**

Data accessibility

This article has no additional data.

Authors' contributions

S.B.H. drafted the manuscript, and S.B.H. and J.M.B. critically revised it together.

Competing interests

We have no competing interests.

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