

Research



Cite this article: Engelmann JM, Herrmann E, Proft M, Keupp S, Dunham Y, Rakoczy H. 2022 Chimpanzees consider freedom of choice in their evaluation of social action. *Biol. Lett.* **18**: 20210502.
<https://doi.org/10.1098/rsbl.2021.0502>

Received: 20 September 2021
Accepted: 2 February 2022

Subject Areas:
behaviour

Keywords:
chimpanzees, freedom of choice, social evaluation, theory of mind

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5847080>.

Animal behaviour

Chimpanzees consider freedom of choice in their evaluation of social action

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Judgements of wrongdoing in humans often hinge upon an assessment of whether a perpetrator acted out of free choice: whether they had more than one option. The classic inhibitors of free choice are constraint (e.g. having your hands tied together) and ignorance (e.g. being unaware that an alternative exists). Here, across two studies, we investigate whether chimpanzees consider these factors in their evaluation of social action. Chimpanzees interacted with a human experimenter who handed them a non-preferred item of food, either because they were physically constrained from accessing the preferred item (Experiment 1) or because they were ignorant of the availability of the preferred item (Experiment 2). We found that chimpanzees were more likely to accept the non-preferred food and showed fewer negative emotional responses when the experimenter was physically constrained compared with when they had free choice. We did not, however, find an effect of ignorance on chimpanzee's evaluation. Freedom of choice factors into chimpanzees' evaluation of how they are treated, but it is unclear whether mental state reasoning is involved in this assessment.

1. Introduction

Like humans, chimpanzees live in highly variable social environments. Much of the complexity of chimpanzee social life is a direct result of the flexible ways in which chimpanzees form, maintain and repair their various social connections [1–6]. At the root of these relational strategies lie social evaluations. Chimpanzees have to assess various social interactions on a daily basis. Did my partner invest sufficient time grooming me? Can I rely on my ally during an intergroup encounter? Why did not I receive support during my recent conflict with a rival? Correctly evaluating these different situations is a crucial prerequisite for navigating a complex social life. Chimpanzees draw on both direct interactions [7] and the observation of third-party interactions [8–10] in evaluating social agents.

That chimpanzees evaluate social actions (i.e. how they are treated by others) is well supported by findings from controlled experiments [11–15] and from observations in the wild [16,17]. *How* chimpanzees assess social interactions and, specifically, which cognitive processes they draw on in doing so, is a question that has received very little attention.

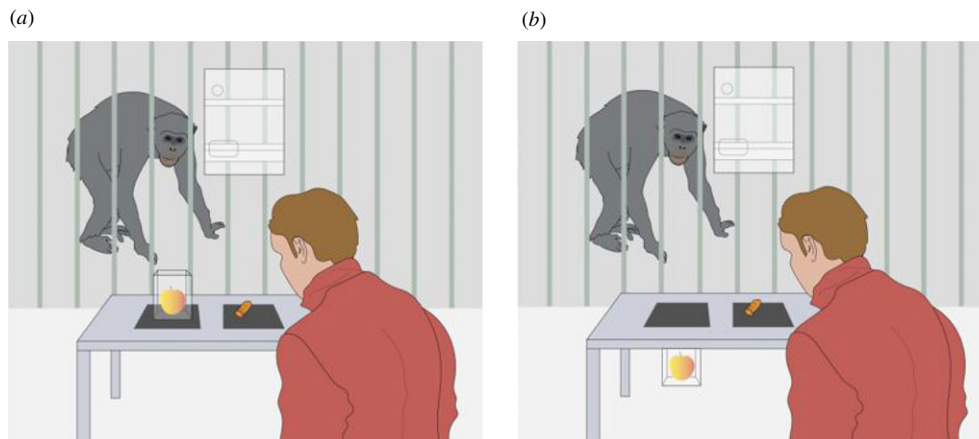


Figure 1. (a) Schematic drawing of the experimental set-up in Experiment 1. Depending on condition, the box containing the apple could either be opened by the experimenter (free choice condition) or not (constrained condition). (b) Experimental set-up in Experiment 2. Note that the box containing the apple is depicted for visualization only. In fact, the experimenter did not have visual access to it (see also electronic supplementary material, figures S3 and S4). In the free choice condition, the experimenter had observed the hiding of the apple. In the ignorant condition, the experimenter was not aware of its availability.

Humans attend to several different variables in their interpretations of social events [18,19]. The most basic dimension is freedom of choice—actions that are freely chosen are evaluated differently from actions that are not. There are two main ways in which agents can be prevented from exercising freedom: constraint and ignorance. In prototypical instances of constraint, an agent is aware of alternative possibilities, but, owing to physical, psychological or social restrictions, is compelled to act in one way. In instances of ignorance, the agent is theoretically free to choose another option, but is not aware that such alternatives exist. Previous work has shown that human adults [20,21], children [22–27] and even preverbal infants [28–30] take freedom of choice into consideration in their assessment of social action. While chimpanzees evaluate various social behaviours that are directed at themselves or others, it is unclear whether the existence of alternative possibilities plays a role in these evaluations. Preliminary evidence that chimpanzees differentiate between voluntary and involuntary actions comes from a study by Call and colleagues ([31], see also [32]), which showed that chimpanzees change their behaviour depending on whether they interact with an ‘unwilling’ or an ‘unable’ experimenter.

In the current studies, we experimentally investigated whether chimpanzees consider the degree of an agent’s freedom of choice in their evaluation of social actions. We made use of a paradigm that has been successfully employed to probe the reactions of chimpanzees to various social behaviours and, in line with prior work, defined social evaluation as an affective behavioural response to treatment by a partner [11,12]. A human experimenter delivered one of two food options (one preferred and one non-preferred) to a chimpanzee subject, who could either accept the offered food by inserting a tool into an apparatus, or alternatively reject the food. Across two experiments, chimpanzees were consistently offered the non-preferred food while we varied the experimenter’s freedom of choice with respect to the preferred option. In Experiment 1, the experimenter was *constrained*: because the preferred food was locked away in a box, they were not free to hand over this option. In Experiment 2, the experimenter was *ignorant*: they were ostensibly unaware of the availability of the preferred food (only the chimpanzee had witnessed the hiding event). Each of these conditions was compared with matched controls—which

we called the *free choice conditions*—in which the experimenter had the option of delivering the preferred food, either because it was not locked away (Experiment 1) or because they too had observed the hiding event (Experiment 2). We assessed chimpanzees’ responses to being offered the non-preferred food by coding (i) whether chimpanzees accepted the food and (ii) the incidence of chimpanzees’ negative emotional reactions towards the experimenter (for details on coding, refer to the electronic supplementary material).

2. Experiment 1: constraint

(a) Methods

(i) Participants

Sixteen chimpanzees (10 females), living at Sweetwaters Chimpanzee Sanctuary, Kenya, ranging in age from 12 to 31 years ($M = 24$ years) participated in this study.

(ii) Procedure

The procedure consisted of three consecutive steps: a food preference test, a familiarization phase and a test phase. Here, we focus on the test phase (for details on all steps, refer to the electronic supplementary material).

In a within-subjects design, subjects first completed two sessions (each comprising six trials) in one condition, and then two sessions (each comprising six trials) in the other condition. Order of condition was counterbalanced across subjects.

The experimenter sat on a chair by the food table, facing the chimpanzee subject (electronic supplementary material, figures S1 and S2; figure 1*a*). In constrained conditions, the experimenter first reached for the right platform, then the left platform, then again the right platform, and, finally, reached for the left platform, placed their hand on the box, tried to open the box five consecutive times by pulling a lever, then placed their hand on the box again, reached for the right platform, grabbed the non-preferred food and placed it in the food apparatus. Next, the experimenter placed a tool on the mesh next to the food apparatus. The trial ended 30 s after the tool had been placed there.

In the free choice condition, the experimenter’s actions were exactly identical to their actions during the constrained

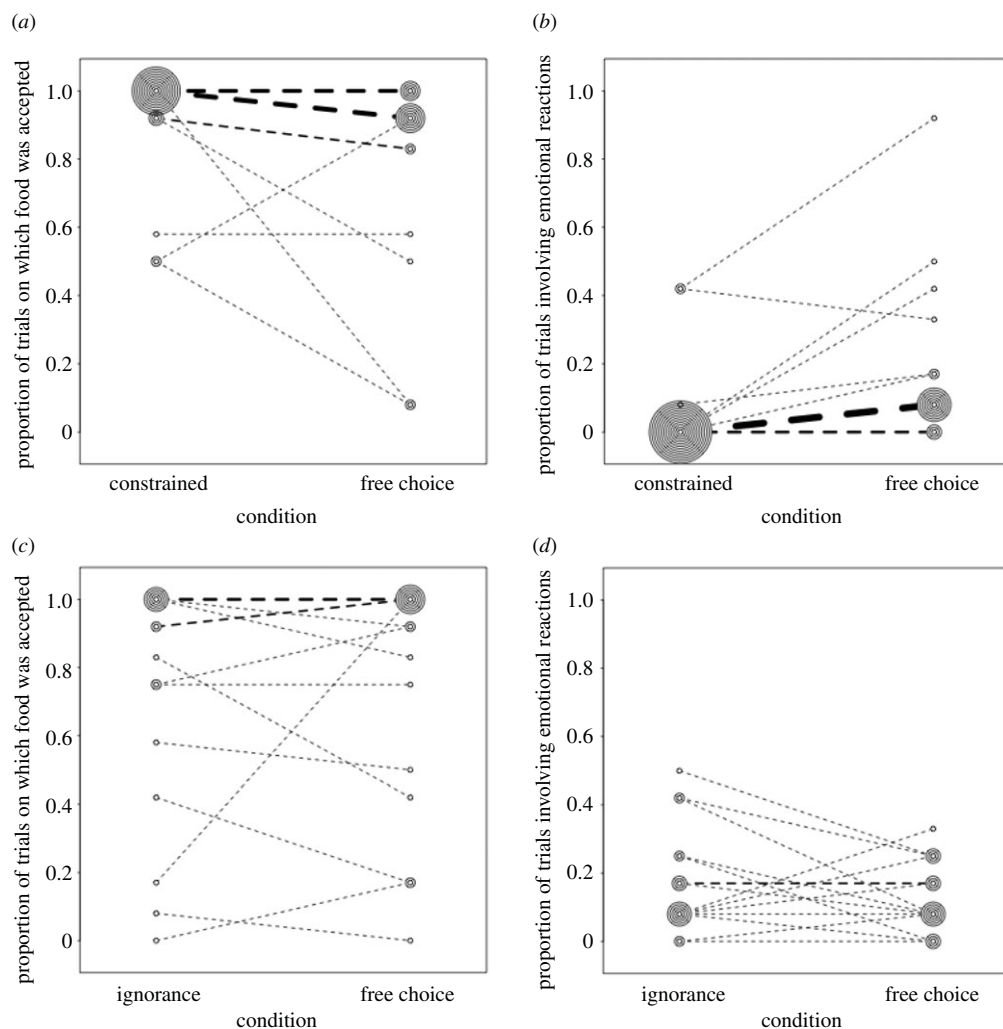


Figure 2. (a) Proportion of trials on which each individual in the constrained and free choice conditions accepted the food. (b) Proportion of trials on which each individual in the constrained and free choice conditions showed a negative emotional reaction towards the experimenter. (c) Proportion of trials on which each individual in the ignorance and free choice conditions accepted the food. (d) Proportion of trials on which each individual in the ignorance and free choice conditions showed a negative emotional reaction towards the experimenter. Each circle represents the behaviour of one individual across 12 trials. Multiple circles at a given number indicate that several subjects showed that score. Dashed lines connect the behaviour of a given subject in the constrained and free choice conditions. Thicker dashed lines indicate that multiple subjects showed a given change across conditions.

condition, except for one difference. During this condition, the experimenter successfully opened the box by pulling the lever, then reached for the food with the other hand, waited for 4 s (the same amount of time it took the experimenter in the constrained condition to try to open the box), closed the box again, and continued as in the constrained condition (placing their hand on the box, reaching for the right platform, grabbing the non-preferred food and placing it in the food apparatus, etc.).

(b) Results

We ran generalized linear mixed models (GLMMs; for details refer to the electronic supplementary material) to investigate the effects of condition, trial number, session and sex. We found that chimpanzees were more likely to accept the low-value food in the constrained compared with the free choice condition: $\chi^2 = 3.6$, d.f. = 1, $p = 0.05$, two-tailed, figure 2a. There were no effects of trial ($\chi^2 = 0.33$, d.f. = 1, $p = 0.56$), session ($\chi^2 = 0.18$, d.f. = 1, $p = 0.67$) or sex ($\chi^2 = 0.09$, d.f. = 1, $p = 0.75$). A second GLMM revealed that chimpanzees displayed more negative emotional responses towards the experimenter in the free choice condition: $\chi^2 =$

7.17, d.f. = 1, $p = 0.007$, two-tailed (figure 2b). Trial ($\chi^2 = 1.12$, d.f. = 1, $p = 0.28$), session ($\chi^2 = 0.12$, d.f. = 1, $p = 0.73$) and sex ($\chi^2 = 0.06$, d.f. = 1, $p = 0.81$) did not reach significance.

3. Experiment 2: ignorance

(a) Methods

(i) Participants

Fifteen chimpanzees (nine females), living at Sweetwaters Chimpanzee Sanctuary, Kenya, ranging in age from 12 to 31 years ($M = 23.2$ years) participated in this experiment.

(ii) Procedure

The general set-up and procedure of Experiment 2 was identical to Experiment 1 (figure 1b). The procedure consisted of three consecutive steps: a food preference test, a familiarization phase and a test phase. We focus here on the test phase (see the electronic supplementary material).

At the beginning of each trial, the second experimenter (E2) placed a piece of carrot on the right platform and a piece of apple in the box below the tabletop. The position

of the first experimenter (E1) during this baiting varied across conditions. In free choice conditions, E1 knelt next to the food table during baiting. This ensured that (i) E1 had full visual access to the hiding of the piece of apple and (ii) E1 and the chimpanzee subject could see each other. Having completed the baiting, E2 moved to a different room, out of sight of E1 and the chimpanzee. Once E2 was out of sight, E1 sat down on the chair next to the table. In ignorance conditions, E1 was in a different room, out of sight of the chimpanzee, while E2 conducted the baiting. Once E2 had finished the baiting and had moved to their room, E1 came out of their room, walked by the table and sat down on the chair. Thus, crucially, in this condition, E1 did not witness the hiding event.

Once E1 was seated on the chair by the food table, facing the chimpanzee subject, the procedure was identical in both conditions. The experimenter engaged in the following series of actions. The experimenter looked at the table, first towards the left, then towards the right, then towards the piece of carrot, and, finally, towards the food apparatus. The experimenter then reached for the right platform, grabbed the non-preferred food and placed it in the food apparatus. Next, the experimenter placed a tool on the mesh next to the food apparatus. The trial ended 30 s after the tool had been placed there.

(b) Results

We found no evidence that chimpanzees were more likely to accept the low-value food in the ignorance compared with the free choice condition (figure 2c): result of the full-null model comparison: $\chi^2 = 0.004$, d.f. = 1, $p = 0.95$. Also, for the second dependent variable—testing whether chimpanzees displayed more negative emotional responses towards the experimenter in the free choice condition—the full model did not fit the data significantly better compared with the null model that lacked the test predictor but included the same random effect structure ($\chi^2 = 1.00$, d.f. = 1, $p = 0.32$). For details on the GLMMs, refer to the electronic supplementary material.

4. Discussion

The current results suggest that chimpanzees respond differently to freely chosen compared with constrained actions. Throughout the experiments reported here, chimpanzees had the possibility of interacting with a human experimenter by exchanging a tool for food. The experimenter consistently behaved in a way that was contrary to the chimpanzees' preferences: they handed over non-preferred food. The main finding was that chimpanzees were more likely to engage in a successful exchange when the experimenter had no alternative to handing over the non-preferred food (because the preferred food was not accessible). Chimpanzees not only were more willing to accept the non-preferred food in these cases but also directed fewer negative emotional reactions at the experimenter, and were less likely to throw the tool at, to spit at and/or to attempt to forcefully grab the experimenter.

This is, to our knowledge, the first demonstration that chimpanzees, like humans, evaluate social treatment not only in terms of outcome—e.g. whether they received a preferred or a non-preferred item—but also with regard to its

causal history. This possibility had been suggested by previous research, in which chimpanzees left a testing station earlier and produced more communicative attempts if they faced an 'unwilling' versus an 'unable' experimenter [31]. While these behaviours might express an evaluation, they can also be interpreted simply in terms of a prediction (e.g. chimpanzees might have left the testing station earlier in the 'unwilling' condition because they predicted that they would not receive food from the experimenter). In the current study, on the other hand, chimpanzees directly expressed their evaluation of the actions of the experimenter, most notably by engaging in the costly—and for chimpanzees very untypical—behaviour of rejecting food. In addition, chimpanzees also showed more negative emotional reactions when the experimenter could hand them the preferred food but chose not to. As in previous studies [11,12], the rate of these behaviours was generally low and while we found a strong effect of condition on chimpanzees' emotional response, the effect on food acceptance was relatively weak. One potential explanation for this difference between the two dependent variables is that showing a negative emotional response is less costly than rejecting food.

We found this pattern of results only in Experiment 1, and not in Experiment 2. Chimpanzees considered freedom of choice when it was operationalized as physical constraint, but not when it was limited owing to ignorance. How might we understand this difference between Experiment 1 and Experiment 2? Potentially our experimental set-up was too complex. Notice that while chimpanzees in Experiment 1 interacted with the same experimenter in both conditions, they were exposed to two different individuals in the two conditions of Experiment 2 (this was necessary because one individual cannot be simultaneously knowledgeable and ignorant). While we cannot rule out the possibility that increased cognitive demands account for the difference between Experiment 1 and 2, we believe that this explanation is unlikely given previous research. There is robust evidence from several experimental paradigms that chimpanzees understand the perception and knowledge of other social agents and successfully use this knowledge to predict their behaviour [33,34]. Another possibility is that the experimenter's two behavioural options were more salient in Experiment 1 (where the experimenter reached for the two food options) than in Experiment 2 (where the experimenter only looked at the two options). Future research should develop other experimental paradigms to assess whether chimpanzees consider knowledge state in their social evaluation. Ideally, these set-ups would not only involve interactions between human experimenters and chimpanzees but also chimpanzee–chimpanzee interactions [35].

As it stands, the extent to which chimpanzees not only predict others' behaviour differently depending on mental state attribution [36–38] but also evaluate others' behaviour differently depending on their knowledge or desires, remains an open question. Nonetheless, even in the absence of conclusive evidence regarding the interaction between social evaluation and mental states, the current results show that chimpanzees evaluate the behaviour of a social partner differently depending on whether it was freely chosen or not.

Ethics. Research at Sweetwaters Chimpanzee Sanctuary was performed in accordance with the recommendations of the Weatherall

Report 'The use of non-human primates in research'. Groups of apes were housed in semi-natural indoor and outdoor enclosures with regular feedings, daily enrichment and water ad libitum. Subjects voluntarily participated in the study and were never food- or water- deprived. Research was conducted in the sleeping and/or observation rooms. No medical, toxicological or neurobiological research of any kind is conducted at Sweetwaters Chimpanzee Sanctuary. Research was non-invasive and strictly adhered to the legal requirements of Kenya. The full procedure of the study was approved by three committees: the local ethics committee at the Sanctuary (the board members and the veterinarian), the Kenya Wildlife Service and the National Council for Science and Technology (NACOSTI), Kenya. Research permits were issued by NACOSTI (P/19/7557/27803; P/18/24055/20857).

Data accessibility. All data are provided in the electronic supplementary material.

Authors' contributions. J.M.E.: conceptualization, investigation, writing—original draft; S.K.: conceptualization, methodology, writing—review and editing; H.R.: conceptualization, methodology, writing—review and editing; E.H.: conceptualization, methodology, project administration, writing—review and editing; M.P.:

conceptualization, methodology, project administration, writing—review and editing; Y.D.: conceptualization, methodology, project administration, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Competing interests. We declare we have no competing interests.

Funding. We thank the Leibniz Science Campus Primate Cognition Göttingen (funded by the Leibniz Association) for awarding us a Seed Fund, and the Whitney and Betty MacMillan Center for International and Area Studies at Yale for awarding us a Faculty Research Grant. J.M.E. was funded by a DAAD P.R.I.M.E. Fellowship.

Acknowledgements. We thank Stephen Ngulu and all the staff of Sweetwaters Chimpanzee Sanctuary for their crucial support. Special thanks go to Martin Kinyua, Steven Mukundi and Charles Mussasia. We also thank OI Pejeta Conservancy, Kenya Wildlife Service (KWS) and the National Council for Science and Technology (NCST) for approving our research. Thanks go to Roger Mundry and Hanna Schleihauf for statistical advice; Alissa Gomez and Joshua Confer for coding; and Christopher Krupenye and Anna-Claire Schneider for helpful comments on previous versions of this manuscript.

References

- de Waal FBM. 2007 *Chimpanzee politics: power and sex among apes*, 25th anniversary edn. Baltimore, MD: Johns Hopkins University Press.
- de Waal FBM. 2002 *Peacemaking among primates*, vol. 1, 6th paperback edn. Cambridge, MA: Harvard University Press.
- Massen JJM, Koski SE. 2014 Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evol. Hum. Behav.* **35**, 1–8. (doi:10.1016/j.evolhumbehav.2013.08.008)
- Muller MN, Wrangham RW, Pilbeam DR. 2017 *Chimpanzees and human evolution*. Cambridge, MA: Belknap Press of Harvard University Press.
- Samuni L, Preis A, Mielke A, Deschner T, Wittig RM, Crockford C. 2018 Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proc. R. Soc. B* **285**, 20181643. (doi:10.1098/rspb.2018.1643)
- Silk J. 2002 Using the 'F'-word in primatology. *Behaviour* **139**, 421–446. (doi:10.1163/156853902760102735)
- Melis AP. 2006 Chimpanzees recruit the best collaborators. *Science* **311**, 1297–1300. (doi:10.1126/science.1123007)
- Herrmann E, Keupp S, Hare B, Vaish A, Tomasello M. 2013 "Direct and indirect reputation formation in nonhuman great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*) and human children (*Homo sapiens*)": correction to Herrmann, Keupp, Hare, Vaish, and Tomasello (2012). *J. Comp. Psychol.* **127**, 32. (doi:10.1037/a0032042)
- Russell YI, Call J, Dunbar RIM. 2008 Image scoring in great apes. *Behav. Process.* **78**, 108–111. (doi:10.1016/j.beproc.2007.10.009)
- Subiaul F, Vonk J, Okamoto-Barth S, Barth J. 2008 Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. *Anim. Cogn.* **11**, 611–623. (doi:10.1007/s10071-008-0151-6)
- Brosnan SF, Schiff HC, de Waal FBM. 2005 Tolerance for inequity may increase with social closeness in chimpanzees. *Proc. R. Soc. B* **272**, 253–258. (doi:10.1098/rspb.2004.2947)
- Engelmann JM, Clift JB, Herrmann E, Tomasello M. 2017 Social disappointment explains chimpanzees' behaviour in the inequity aversion task. *Proc. R. Soc. B* **284**, 20171502. (doi:10.1098/rspb.2017.1502)
- Roughley N. 2018 The empathy in moral obligation: an exercise in creature construction. In *Forms of fellow feeling* (eds N Roughley, T Schramme), pp. 265–291. Cambridge, UK: Cambridge University Press.
- Brosnan SF, de Waal FBM. 2003 Monkeys reject unequal pay. *Nature* **425**, 297–299. (doi:10.1038/nature01963)
- Yamamoto S, Tanaka M. 2009 Do chimpanzees (*Pan troglodytes*) spontaneously take turns in a reciprocal cooperation task? *J. Comp. Psychol.* **123**, 242–249. (doi:10.1037/a0015838)
- Mielke A, Preis A, Samuni L, Gogarten JF, Wittig RM, Crockford C. 2018 Flexible decision-making in grooming partner choice in sooty mangabeys and chimpanzees. *R. Soc. Open Sci.* **5**, 172143. (doi:10.1098/rsos.172143)
- Wittig RM, Crockford C, Weltring A, Langergraber KE, Deschner T, Zuberbühler K. 2016 Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nat. Commun.* **7**, 13361. (doi:10.1038/ncomms13361)
- Scanlon T. 2010 *Moral dimensions: permissibility, meaning, blame*, vol. 1, paperback edn. Cambridge, MA: Belknap Press.
- Wallace RJ. 2019 *The moral nexus*. Princeton, NJ: Princeton University Press.
- Baumeister RF, Masicampo EJ, DeWall CN. 2009 Prosocial benefits of feeling free: disbelief in free will increases aggression and reduces helpfulness. *Pers. Social Psychol. Bull.* **35**, 260–268. (doi:10.1177/0146167208327217)
- Baumeister RF, Mele AR, Vohs KD. 2010 *Free will and consciousness*. Oxford, UK: Oxford University Press.
- Chernyak N, Kushnir T. 2018 The influence of understanding and having choice on children's prosocial behavior. *Curr. Opin. Psychol.* **20**, 107–110. (doi:10.1016/j.copsyc.2017.07.043)
- Josephs M, Kushnir T, Gräfenhain M, Rakoczy H. 2016 Children protest moral and conventional violations more when they believe actions are freely chosen. *J. Exp. Child Psychol.* **141**, 247–255. (doi:10.1016/j.jecp.2015.08.002)
- Killen M, Mulvey KL, Richardson C, Jampol N, Woodward A. 2011 The accidental transgressor: morally-relevant theory of mind. *Cognition* **119**, 197–215. (doi:10.1016/j.cognition.2011.01.006)
- Kushnir T, Gopnik A, Chernyak N, Seiver E, Wellman HM. 2015 Developing intuitions about free will between ages four and six. *Cognition* **138**, 79–101. (doi:10.1016/j.cognition.2015.01.003)
- Proft M, Rakoczy H. 2019 The ontogeny of intent-based normative judgments. *Dev. Sci.* **22**, e12728. (doi:10.1111/desc.12728)
- Yang F, Choi Y-J, Misch A, Yang X, Dunham Y. 2018 In defense of the commons: young children negatively evaluate and sanction free riders. *Psychol. Sci.* **29**, 1598–1611. (doi:10.1177/0956797618779061)
- Choi Y, Luo Y. 2015 13-month-olds' understanding of social interactions. *Psychol. Sci.* **26**, 274–283. (doi:10.1177/0956797614562452)
- Dunfield KA, Kuhlmeier VA. 2010 Intention-mediated selective helping in infancy. *Psychol. Sci.* **21**, 523–527. (doi:10.1177/0956797610364119)
- Hamlin JK. 2013 Failed attempts to help and harm: intention versus outcome in preverbal infants' social evaluations. *Cognition* **128**, 451–474. (doi:10.1016/j.cognition.2013.04.004)
- Call J, Hare B, Carpenter M, Tomasello M. 2004 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Dev.*

- Sci.* **7**, 488–498. (doi:10.1111/j.1467-7687.2004.00368.x)
32. Phillips W, Barnes JL, Mahajan N, Yamaguchi M, Santos LR. 2009 'Unwilling' versus 'unable': capuchin monkeys' (*Cebus apella*) understanding of human intentional action: unwilling vs. unable in capuchin monkeys. *Dev. Sci.* **12**, 938–945. (doi:10.1111/j.1467-7687.2009.00840.x)
33. Call J, Tomasello M. 2008 Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn. Sci.* **12**, 187–192. (doi:10.1016/j.tics.2008.02.010)
34. Hare B, Call J, Tomasello M. 2001 Do chimpanzees know what conspecifics know? *Anim. Behav.* **61**, 139–151. (doi:10.1006/anbe.2000.1518)
35. Hattori Y, Kano F, Tomonaga M. 2010 Differential sensitivity to conspecific and allospecific cues in chimpanzees and humans: a comparative eye-tracking study. *Biol. Lett.* **6**, 610–613. (doi:10.1098/rsbl.2010.0120)
36. Krupenye C, Call J. 2019 Theory of mind in animals: current and future directions. *WIREs Cogn. Sci.* **10**, e1503. (doi:10.1002/wcs.1503)
37. Rosati AG, Santos LR, Hare B. 2010 Primate social cognition: thirty years after Premack and Woodruff. In *Primate neuroethology* (eds M Platt, A Ghazanfar), pp. 117–143. Oxford, UK: Oxford University Press.
38. Premack D, Woodruff G. 1978 Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* **1**, 515–526. (doi:10.1017/S0140525X00076512)