Fearful apes, happy apes: is fearfulness associated with uniquely human cooperation?

Riddell, C.; Kret, M.; Zijlstra, T.; Nikolic, M.

1. Tobias Grossmann
2. Word Count Abstract: 60
   Word Count Main Text: 996
   Word Count References: 1228
   Total: 2284
3. Title

Fearful apes, happy apes - is fearfulness associated with uniquely human cooperation?: Commentary on Grossmann (2022)

4. Christopher Riddell[1], Mariska Kret[1], Tonko Zijlstra[1], Milica Nikolic[2]
5. [1]Cognitive Psychology Unit, Leiden University; [2]Research Institute of Child Development and Education, University of Amsterdam
6. Wassenaarseweg 52, 2333AK Leiden, the Netherlands
7. +31 71 527 6359
8. c.d.riddell@fsw.leidenuniv.nl; m.e.kret@fsw.leidenuniv.nl; t.w.zijlstra@fsw.leidenuniv.nl; M.Nikolic@uva.nl;
9. https://www.universiteitleiden.nl/en/staffmembers/chris-riddell; https://www.universiteitleiden.nl/en/staffmembers/mariska-kret https://www.universiteitleiden.nl/en/staffmembers/tonko-zijlstra; https://www.uva.nl/en/profile/n/i/m.nikolic/m.nikolic.html;
10. Abstract

In the fearful ape hypothesis, Grossmann (2022) argues that heightened fearfulness increases human-unique cooperation. We suggest that this conclusion, however, may be premature. In particular, we question Grossmann's singling out of fear as *the* affective trait that enhances cooperative care. Additionally, we problematize the extent to which heightened fearfulness in humans, and its association with human-unique cooperation, are supported empirically.

11. Main Text

Grossmann's (2022) fearful ape hypothesis provides a novel and compelling account for the supposed link between heightened fearfulness and enhanced cooperation in humans. We appreciate the author's re-conceptualization of fear as a potentially adaptive response in some contexts, which in previous clinical works has largely been viewed as maladaptive. Despite its novelty, however, we argue that, at present, there is insufficient evidence to conclude that: 1) it is specifically heightened fearfulness (and not other affective traits or emotions in general) that enhances cooperation and 2) that heightened fearfulness is related to enhanced, "uniquely-human", cooperation.

Grossmann singles out fearfulness as the key affective trait that evolved to support "human-unique" levels of cooperation. He suggests that fearful infants evoke more (allo)parental care and, by receiving more care, become more cooperative children, adults and parents themselves. We argue, however, that the influence of affective states on cooperative behaviour may not be bound to fearfulness alone. Other affective states may also be associated with - or even evoke more - cooperation.

Similarly to fear, from early in human ontogeny, infants experience and display positive affect (Messinger, 2002; Mesinger & Fogel, 2007) and can distinguish positive from other facial expressions (De Haan & Nelson, 1998). Furthermore, although results are mixed, there is some evidence that humans also display a perceptual sensitivity bias toward happy faces (Wirth & Wentura, 2020; Zsido et al., 2021). Crucially, although Grossman and others failed to find an association between sensitivity to happy faces and infants' prosociality (Grossmann et al., 2018; Rajhans et al., 2016), there is robust evidence that experienced and displayed positive affect results in more cooperation in child and adult actors (e.g., Aknin et al., 2018; Centorrino et al., 2015; Isen & Levin, 1972; Kushlev et al., 2021; Moore et al., 1973; Rosenhan et al., 1981), as well as observers (including in cooperative parental-care contexts) (e.g., Centorrino et al., 2015; Danvers & Shiota, 2018; Lengua & Kovacs, 2005; Scharlemann et al., 2001). Therefore, it is not only fearful infants, but also happy infants, who may evoke cooperation in others, and may, by receiving more care, themselves become more cooperative adults. The putative effect of fearfulness on cooperation, is therefore not necessarily unique in this regard - and it may also be that happiness, or emotional expressivity more generally, foster cooperation.

Grossmann also argues that humans display and perceive more fearfulness in comparison to other great-ape species, and that this heightened fearfulness evokes increased levels of "human-unique" cooperation (i.e., alloparental care). However, there is not (enough) evidence that: (1) fearfulness is heightened in humans compared to other great apes; and that (2) heightened fearfulness is associated with enhanced "human-unique" cooperation.

Although some studies found that great apes do not show attentional bias to fear specifically (Kret et al., 2016; Kret et al., 2018), other work has found heightened attention towards fear (Pritsch et al., 2017), and towards emotions in general (Wilson & Tomonaga, 2018, 2021; for review, see Kret et al., 2020). Furthermore, the claim that human infants *express* more fearfulness than other great apes is based on one empirical study (Hermann et al., 2011). This study, however, used a human-centred paradigm (sensitivity to novel humans and objects), to contrast the reactions of human children to adult great apes. Herman and colleagues (2011) assumed that showing an unfamiliar human is similarly relevant and meaningful for a captive adult ape (who is likely exposed to unfamiliar humans many times on a daily basis) and a human child (for whom this context may be drastically different). As such, this study might have or

might have not captured the full extent of the fear response in other primates, calling to question Grossman's claims about uniquely human heightened fear production.

Even if displaying and perceiving fear is, on average, heightened in humans, this does not mean that it necessarily evolved for "human-unique" cooperative care purposes (i.e. alloparental care). First, whether alloparental care is uniquely human is questionable considering some evidence for such forms of cooperation in other primate species (Boesch et al., 2010; Fairbanks, 1990; Samuni et al., 2019; Tokuyama et al., 2021). Second, to support the association between fearfulness and "human-unique" cooperation, Grossmann cites research showing associations between enhanced fearfulness sensitivity and cooperation in non-alloparental care contexts, such as parental care of own children (e.g., Kiel & Buss, 2011), and helping/sharing in infants, children, and adults (e.g., Grossmann et al., 2018; Marsh & Ambady, 2007 Rajhans et al., 2016) that are, importantly, not unique to humans. Given that such forms of cooperation exist also in other species (for review, see de Waal & Suchak, 2010), evidence is lacking that heightened fearfulness is associated with "human-unique*"* cooperation.

Grossman further argues that, next to the fight-or-flight response seen in many animals, heightened displayed and detected fearfulness elicits approach behaviours (tend and befriend) in humans in particular. However, the groundwork for a link between fearfulness and cooperation also exists in non-human animals. For example, newborn chimpanzees and bonobos are known to express fearfulness and distress through pout moans and whimpers in the context of maternal care (de Waal, 1988), and adult caregivers comfort offspring who show such signs by embracing and kissing them, similarly to humans (de Waal & Preston, 2017). Furthermore, offspring displaying distress provoke parental cooperative care in other species, including rodents and birds (de Waal & Preston, 2017). Even outside of infant-parent relationships, non-human animals, such as rodents, react to conspecifics displaying fear by engaging in prosocial behaviours (Keysers et al., 2022). Therefore, it seems highly unlikely that heightened fearfulness elicits approach behaviours exclusively in humans.

In sum, singling out fearfulness as *the* affective trait that evolved specifically for cooperative purposes in humans seems premature. Additionally, there is insufficient evidence to conclude that human fear perception and production is significantly increased compared to other non-human animals. Finally, the link between heightened fearfulness and alloparental care awaits first empirical support. To truly examine these facets, it will be critical for future work to take the sensitivities and milieu of both human and non-human animals into account.

12. Acknowledgements statement
13. Conflict of interest statement
    The authors declare no conflicts of interest

14. Funding statement

CR, MEK and TZ were supported by the European Research Council (Starting grant # 804582) awarded to MEK. MN was supported by a NWO VENI grant (Veni.201G.017)

15. Reference list

Aknin, L. B., Van de Vondervoort, J. W., & Hamlin, J. K. (2018). Positive feelings reward and promote prosocial behavior. *Current Opinion in Psychology*, *20*, 55-59. https:/doi.org/10.1016/j.copsyc.2017.08.017

Boesch, C., Bole, C., Eckhardt, N., & Boesch, H. (2010). Altruism in forest chimpanzees: the case of adoption. *PLoS One*, *5*(1), e8901. https://doi.org/10.1371/journal.pone.0008901

Centorrino, S., Djemai, E., Hopfensitz, A., Milinski, M., & Seabright, P. (2015). Honest signaling in trust interactions: Smiles rated as genuine induce trust and signal higher earning opportunities. *Evolution and Human Behavior*, *36*(1), 8-16. https://doi.org/10.1016/j.evolhumbehav.2014.08.001

Danvers, A. F., & Shiota, M. N. (2018). Dynamically engaged smiling predicts cooperation above and beyond average smiling levels. *Evolution and Human Behavior*, *39*(1), 112-119. https://doi.org/10.1016/j.evolhumbehav.2017.10.007

de Haan, M., & Nelson, C. A. (1998). Facial expressions of emotion during infancy. In Slater, A. (Ed.) *Perceptual Development: Visual, Auditory, and Speech Perception in Infancy*. Psychology Press.

de Waal, F., & Preston, S. D. (2017). Mammalian empathy: behavioural manifestations and neural basis. *Nature Reviews Neuroscience*, *18*(8), 498-509. https://doi.org/10.1038/nrn.2017.72

De Waal, F. B. (1988). The communicative repertoire of captive bonobos (Pan paniscus), compared to that of chimpanzees. *Behaviour*, *106*(3-4), 183-251.

Fairbanks, L. A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, *40*(3), 553-562. https://doi.org/10.1016/S0003-3472(05)80536-6

Gartstein, M. A., & Iverson, S. (2014). Attachment security: The role of infant, maternal, and contextual factors. *International Journal of Psychology and Psychological Therapy*, *14*(2), 261-276.

Grossmann, T., Missana, M., & Krol, K. M. (2018). The neurodevelopmental precursors of altruistic behavior in infancy. *PLoS Biology*, *16*(9), e2005281. https://doi.org/10.1371/journal.pbio.2005281

Herrmann, E., Hare, B., Cissewski, J., & Tomasello, M. (2011). A comparison of temperament in nonhuman apes and human infants. *Developmental Science*, *14*(6), 1393-1405. https://doi.org/10.1111/j.1467-7687.2011.01082.x

Isen, A. M., & Levin, P. F. (1972). Effect of feeling good on helping: cookies and kindness. *Journal of Personality and Social Psychology*, *21*(3). https://doi.org/10.1037/h0032317

Kushlev, K., Radosic, N., & Diener, E. (2020). Subjective well-being and prosociality around the globe: Happy people give more of their time and money to others. *Social Psychological and Personality Science*, *13*(3), 849-861. https://doi.org/10.1177/19485506211043379

Keysers, C., Knapska, E., Moita, M. A., & Gazzola, V. (2022). Emotional contagion and prosocial behavior in rodents. *Trends in Cognitive Sciences*, *26*(8), 688-706. https://doi.org/10.1016/j.tics.2022.05.005

Kiel, E. J., & Buss, K. A. (2011). Prospective relations among fearful temperament, protective parenting, and social withdrawal: The role of maternal accuracy in a moderated mediation framework. *Journal of Abnormal Child Psychology*, *39*(7), 953-966. https://doi.org/10.1007/s10802-011-9516-4

Kret, M. E., Muramatsu, A., & Matsuzawa, T. (2018). Emotion processing across and within species: A comparison between humans (Homo sapiens) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *132*(4), 395. https://doi.org/10.1037/com0000108

Kret, M. E., Jaasma, L., Bionda, T., & Wijnen, J. G. (2016). Bonobos (Pan paniscus) show an attentional bias toward conspecifics' emotions. *Proceedings of the National Academy of Sciences*, *113*(14), 3761-3766. https://doi.org/10.1073/pnas.1522060113

Kret, M. E., Prochazkova, E., Sterck, E. H., & Clay, Z. (2020). Emotional expressions in human and non-human great apes. *Neuroscience & Biobehavioral Reviews*, *115*, 378-395. https://doi.org/10.1016/j.neubiorev.2020.01.027

Lengua, L. J., & Kovacs, E. A. (2005). Bidirectional associations between temperament and parenting and the prediction of adjustment problems in middle childhood. *Journal of Applied Developmental Psychology*, *26*(1), 21-38. https://doi.org/10.1016/j.appdev.2004.10.001

Marsh, A. A., & Ambady, N. (2007). The influence of the fear facial expression on prosocial responding. *Cognition and Emotion*, *21*(2), 225-247. https://doi.org/10.1080/02699930600652234

Marsh, A. A. (2015). Neural, cognitive, and evolutionary foundations of human altruism. *Wiley Interdisciplinary Reviews: Cognitive Science*, *7*(1), 59-71. https://doi.org/10.1002/wcs.1377

Marsh, A. A., Kozak, M. N., & Ambady, N. (2007). Accurate identification of fear facial expressions predicts prosocial behavior. *Emotion*, *7*(2), 239. https://doi.org/10.1037/1528-3542.7.2.239

Messinger, D., & Fogel, A. (2007). The interactive development of social smiling. In R. V. Kail (Ed.), *Advances in child development and behavior* (pp. 327–366). Elsevier Academic Press. https://doi.org/10.1016/B978-0-12-009735-7.50014-1

Messinger, D. S. (2002). Positive and negative: Infant facial expressions and emotions. *Current Directions in Psychological Science*, *11*(1), 1-6. https://doi.org/10.1111/1467-8721.00156

Moore, B. S., Underwood, B., & Rosenhan, D. L. (1973). Affect and altruism. *Developmental Psychology*, *8*(1), 99. https://doi.org/10.1037/h0033847

Peltola, M. J., Forssman, L., Puura, K., van IJzendoorn, M. H., & Leppänen, J. M. (2015). Attention to faces expressing negative emotion at 7 months predicts attachment security at 14 months. *Child Development*, *86*(5), 1321-1332. https://doi.org/10.1111/cdev.12380

Pritsch C, Telkemeyer S, Mühlenbeck C, Liebal K. Perception of facial expressions reveals selective affect-biased attention in humans and orangutans. Sci Rep. 2017 Aug 10;7(1):7782. doi: 10.1038/s41598-017-07563-4.

Rajhans, P., Altvater-Mackensen, N., Vaish, A., & Grossmann, T. (2016). Children's altruistic behavior in context: The role of emotional responsiveness and culture. *Scientific Reports*, *6*(1), 1-6. https://doi.org/10.1038/srep24089

Rosenhan, D. L., Salovey, P., & Hargis, K. (1981). The joys of helping: Focus of attention mediates the impact of positive affect on altruism. *Journal of Personality and Social Psychology*, *40*(5), 899. https://doi.org/10.1037/0022-3514.40.5.899

Samuni, L., Wittig, R. M., & Crockford, C. (2019). Adoption in the Taï chimpanzees: costs, benefits and strong social relationships. *The Chimpanzees of the Taï Forest: 40 Years of Research*, 141-158. https://doi.org/10.1017/9781108674218.011

Scharlemann, J. P., Eckel, C. C., Kacelnik, A., & Wilson, R. K. (2001). The value of a smile: Game theory with a human face. *Journal of Economic Psychology*, *22*(5), 617-640. https://doi.org/10.1016/S0167-4870(01)00059-9

Stern, J. A., Kelsey, C. M., Krol, K. M., Grossmann, T., McElroy, J. L., Yancey, H., & Sigdel, S. (in press) (2022). Maternal recognition of positive emotion predicts sensitive parenting in infancy. *Emotion*. https://doi.org/10.1037/emo0001125

Waters, E., Wippman, J., & Sroufe, L. A. (1979). Attachment, positive affect, and competence in the peer group: Two studies in construct validation. *Child Development*, 821-829. https://doi.org/10.2307/1128949

Wilson, D. A., & Tomonaga, M. (2018). Visual discrimination of primate species based on faces in chimpanzees. *Primates*, *59*(3), 243-251. https://doi.org/10.1007/s10329-018-0649-8

Wilson, D. A., & Tomonaga, M. (2021). Search asymmetries for threatening faces in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, *136*(1), 20–34. https://doi.org/10.1037/com0000302.

Wirth, B. E., & Wentura, D. (2020). It occurs after all: Attentional bias towards happy faces in the dot-probe task. *Attention, Perception, & Psychophysics*, *82*(5), 2463-2481. https://doi.org/10.3758/s13414-020-02017-y

Zsido, A. N., Arato, N., Ihasz, V., Basler, J., Matuz-Budai, T., Inhof, O., ... & Coelho, C. M. (2021). "Finding an emotional face" revisited: Differences in own-age Bias and the happiness superiority effect in children and young adults. *Frontiers in Psychology*, *12*, 580565. https://doi.org/10.3389/fpsyg.2021.580565