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# Gaze into social bonds: Unlocking great ape emotions through eye-tracking

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*Thinking of the day  
When you went away  
What a life to take  
What a bond to break  
I'll be missing you (1)*

The melody from Faith Evans and Sean Combs sends shivers down my spine, occasionally even stirring tears. Tender recollections of my departed beloveds gently rise to the forefront. Do apes have similar feelings when a certain stimulus reminds them of old friends? The ability to identify and remember fellow conspecifics after extended periods is crucial for intricate social interactions, facilitating cooperation (2). Long-term memory in various species of animals facilitates relationship development, hierarchy navigation, and conflict avoidance (3–6). Humans are renowned for remembering names, faces, and social details over decades (7, 8) and tend to cluster people in terms of social relationships (e.g., teacher, friend), rather than attributes (e.g., gender, race, and age) (9). In a computerized eye-tracking experiment designed by Lewis et al., chimpanzees and bonobos were also found to remember former groupmates for extended periods after separation, especially those they had been closely bonded with in the past (10).

Attention tends to be captivated and sustained by stimuli that are pertinent to an individual or its species. Given the universality of attentional processes, biases in attention can be compared across closely related species and may serve as indicators of various mental processes (11). Previous research has shown that bonobos and humans have an attentional bias toward emotional expressions of conspecifics (12, 13), a bias further modulated by the familiarity of the depicted individual (14). This shows that attentional biases can reveal emotional processes. In the context of the study by Lewis et al., the prolonged gaze at familiar former group mates suggests that the apes remembered them. The duration of gaze directed toward the ape displayed on the screen was influenced by the strength of the positive social bond between that ape and the one observing it. It is well known that emotion enhances memory processes, also in chimpanzees (15). The findings of Lewis underscore the role of social-emotional processes in shaping memory and attention among our closest living relatives.

Examining the evolutionary roots of social memory in bonobos, chimpanzees, and humans is essential to ascertain whether specific elements of social memory are distinct or shared in these three closely related species. Lewis et al. included a large sample of both chimpanzees and bonobos in their investigation, but the picture would have

been even more complete if they had included humans as well. While prior human research has revealed that individuals retain information about others for extended periods, it is noteworthy that none of these studies, to my knowledge, employed a similar eye-tracking method to systematically explore attention bias as an indicator of social memory. This raises the question of whether a comparable bias would be observed in humans under similar conditions. Oftentimes, different methods yield different results. For instance, previous research showed that in bonobos, vocal recognition of former groupmates already ceases beyond 5 y, which is much earlier than what has been observed by Lewis et al. using photographs (16). If a human recalls an old friend after years of separation, would this consistently show in an attention bias toward a briefly presented de-contextualized static image on a computer screen, lacking the richness of multimodal information inherent in real-life encounters? Hence, obtaining additional data from humans is imperative. First, it will help determine the extent of any potential underestimation of social memory capacity suggested by the visual attention bias. Second, adding human data would help find out which features of social memory are derived human traits, and which are phylogenetically basal homologies with bonobos and chimpanzees.

Previous studies on social perception have highlighted substantial species differences among different great ape species. For example, the previously mentioned attentional bias toward emotional expressions has not been observed in orangutans (17) and not consistently in chimpanzees (18, 19). An additional significant research milestone would involve replicating the experiment by Lewis et al. in other closely related primate species with varying social structures, such as orangutans (semi-solitary living), gorillas (harem), and gibbons (family structure comparable to humans). The social structure is likely to be a pivotal factor in shaping the importance of connections with both known and unknown conspecifics, impacting how these relationships are retained in memory.

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Louise, the bonobo described by Lewis et al. seems to have remembered her sister and nephew after a span of 26 y of not seeing them. Intriguingly, she exhibited a notable attentional bias toward both relatives. On average, other apes in the sanctuary where she resides also displayed an attention bias toward former group mates, but this general trend was not observed in apes tested at two zoos. This discrepancy might stem from a methodological confound related to the sanctuary apes being more research-experienced and the data being noisier in the two different zoo populations. Notably, even within Louise's group, significant individual differences were observed. The origins of such differences raise questions about potential influences from factors such as early life history, ranking, parenthood, sex, age, empathic skills, and personality and opens avenues for future research.

with photographs of relatives you once shared joyful moments with. It undoubtedly evokes a cascade of emotions (e.g., sorrow; missing them; joy) and thoughts (e.g., are they doing well? How would they look like now? Do they have children?). Like humans, great apes can also experience and express emotions (20, 21) and enter states of anxiety and depression (22), but it remains difficult to assess what precisely they are feeling. The exploration of memory in nonhuman animals has a dark history marked by invasive and cruel experiments that inflicted suffering upon the subjects. Eye-tracking poses a much better alternative to delve into areas of inquiry such as whether apes can experience grief, mourn, comprehend death, or express concern for friends who are no longer visible (23). Especially when combined with noninvasive psychophysiological methods, I am optimistic that thoroughly investigating attentional biases serves as a pathway to eventually enhance our understanding of their feelings.

In conclusion, underscoring the importance of attentional biases as glimpses into the cognitive and emotional realms of non-human primates' social memories, Lewis et al.'s research raises numerous novel questions and is set to inspire further exploration into these intriguing inquiries.

Imagine stepping into Louise's perspective—after 26 y of silence and no information, being suddenly confronted

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1. Puff Daddy [Sean John Combs], vocalist. "I'll Be Missing You." Featuring Faith Evans and 112. MP3 audio. Track 16 on Puff Daddy & The Family, No Way Out. Arista Records (1997).
2. P. H. Crowley et al., Evolving cooperation: The role of individual recognition. *Biosystems* **37**, 49–66 (1996).
3. K. M. Kendrick, A. P. Da Costa, A. E. Leigh, M. R. Hinton, J. W. Peirce, Sheep don't forget a face. *Nature* **414**, 165–166 (2001).
4. S. J. Insley, Long-term vocal recognition in the northern fur seal. *Nature* **406**, 404–405 (2000).
5. K. McComb, C. Moss, S. Sayialel, L. Baker, Unusually extensive networks of vocal recognition in African elephants. *Anim. Behav.* **59**, 1103–1109 (2000).
6. J. N. Bruck, Decades-long social memory in bottlenose dolphins. *Proc. R. Soc. B Biol. Sci.* **280**, 20131726 (2013).
7. C. F. Bond Jr., R. L. Jones, D. L. Weintraub, On the unconstrained recall of acquaintances: A sampling-traversal model. *J. Pers. Soc. Psychol.* **49**, 327 (1985).
8. T. K. Srull, R. S. Wyer, Person memory and judgment. *Psychol. Rev.* **96**, 58 (1989).
9. A. P. Fiske, Social schemata for remembering people: Relationships and person attributes in free recall of acquaintances. *J. Quant. Anthropol.* **5**, 305–324 (1995).
10. L. S. Lewis et al., Bonobos and chimpanzees remember familiar conspecifics for decades. *Proc. Natl. Acad. Sci. U.S.A.*, in press.
11. R. van Rooijen, A. Ploeger, M. E. Kret, The dot-probe task to measure emotional attention: A suitable measure in comparative studies? *Psych. Bull. Rev.* **24**, 1686–1717 (2017).
12. M. E. Kret, L. Jaasma, T. Bionda, J. G. Wijnen, Bonobos (*Pan paniscus*) show an attentional bias toward conspecifics' emotions. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 3761–3766 (2016).
13. M. E. Kret, E. van Berlo, Attentional bias in humans toward human and bonobo expressions of emotion. *Evol. Psychol.* **19**, 14747049211032816 (2021).
14. E. van Berlo, T. Bionda, M. E. Kret, Attention toward emotions is modulated by familiarity with the expressor: A comparison between bonobos and humans. *Emotion* **23**, 1904–1917 (2023).
15. F. Kano, M. Tanaka, M. Tomonaga, Enhanced recognition of emotional stimuli in the chimpanzee (*Pan troglodytes*). *Anim. Cogn.* **11**, 517–524 (2008).
16. S. Keenan et al., Enduring voice recognition in bonobos. *Sci. Rep.* **6**, 1–8 (2016).
17. D. W. Laméris, E. Van Berlo, T. S. Roth, M. E. Kret, No evidence for biased attention towards emotional scenes in Bornean orangutans (*Pongo pygmaeus*). *Affective Sci.* **3**, 772–782 (2022).
18. M. E. Kret, A. Muramatsu, T. Matsuzawa, Supplemental material for emotion processing across and within species: A comparison between humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **132**, 395–409 (2018).
19. D. A. Wilson, M. Tomonaga, Exploring attentional bias towards threatening faces in chimpanzees using the dot probe task. *PLoS One* **13**, 1–17 (2018).
20. M. E. Kret, J. J. Massen, F. De Waal, My fear is not, and never will be, your fear: On emotions and feelings in animals. *Affect. Sci.* **3**, 182–189 (2022).
21. M. E. Kret, E. Prochazkova, E. H. Sterck, Z. Clay, Emotional expressions in human and non-human great apes. *Neurosci. Biobehav. Rev.* **115**, 378–395 (2020).
22. E. Bliss-Moreau, P. H. Rudebeck, Animal models of human mood. *Neurosci. Biobehav. Rev.* **120**, 574–582 (2021).
23. E. G. Nieuwburg, A. Ploeger, M. E. Kret, Emotion recognition in nonhuman primates: How experimental research can contribute to a better understanding of underlying mechanisms. *Neurosci. Biobehav. Rev.* **123**, 24–47 (2021).