

Target BBS article: Dunbar R. Structural and Cognitive Mechanisms of Group Cohesion in Primates. *Behavioral and Brain Sciences*. 2025;48:e162.
doi:10.1017/S0140525X2400030X

Commentary citation: WALLER, B., WHITEHOUSE, J., KAVANAGH, E. 2025. Facial expression is a group cohesion solution, *Behavioral and Brain Sciences*, 48

Title: Facial expression is a group cohesion solution

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ABSTRACT

Facial expression has evolved as a solution to the primate group living problem. A growing body of empirical evidence suggests that the evolution of facial expression has been driven by the need to bond. Dunbar's theories of group cohesion are therefore key to understanding primate (including human) facial expression.

MAIN TEXT

Facial expression has evolved as a solution to the primate group living problem. Involving both behavioural and cognitive processes, primate facial expression has diverged in complexity from those of mammalian relatives. We are only just starting to understand how facial expression functions in the form and maintenance of primate social relationships, but the evidence we have so far suggests that the evolution of facial expression has been driven by the need to bond (Schmidt & Cohn, 2001). Dunbar's theories of group cohesion are therefore key to understanding primate (including human) facial expression.

Dunbar proposes that primates need structural, behavioural and cognitive solutions to avoid group fragmentation (strategies which are not mutually exclusive). Facial expression is a prime candidate solution, operating across these strategies in three ways. First, facial expressions act as cues to an individual's future behaviour (Waller et al., 2017). Whether this is underpinned by cognitive reading of intentions, or simpler associative learning, is an interesting question, but the

function is the same. Knowing how others are likely to act next allows individuals to prepare an optimal response, synchronise behaviour, and (importantly) avoid conflict. Illustrating this, primates predict a peaceful outcome when they see others using any facial signals, including facial threats (Waller et al., 2016), presumably as the sharing of the potential willingness to engage in conflict allows all parties to act promptly to diffuse the aggression. Second, the facial expressions of others can be used to understand third parties and their relationships. There has been an historical focus on thinking of facial expressions as revealing information within a dyadic context (when directed towards ‘you’), but their potential utility within third party dynamics is in many ways much greater. Observing the nonverbal behaviour exchanged between others can be incredibly informative about the nature of their relationship (Bergman & Sheehan, 2013; Dunbar et al., 2022). Again, bystanders can then use this information to avoid potential ensuing conflict, take heed of blossoming alliances, identify the social centrality of other individuals, and manage one’s own relationships with those parties. In particular, this could be a powerful mechanism to keep track of the ‘weak’ ties in the social group (indirect social connections) which Dunbar suggests is important. Third, Dunbar argues that one-trial learning gives anthropoid primates the ability to generalize from single experiences, allowing a more nuanced management of social relationships. We agree, and within the facial expression domain this is particularly important, as an isolated glance, baring of teeth or eyebrow raise between parties can be significant and meaningful, it does not need to be repeated to be indicative of a relationship.

We argue that facial expression, via these processes, acts as a bonding mechanism. This function has been evidenced through analysis of individual differences, whereby individuals who use facial expression well (either as a producer or observer) leverage social advantages. Macaque groups lead by facially expressive males have greater social cohesion, and expressive male macaques occupy more central positions in their social groups (thus recipients of social advantages) (Whitehouse et al., 2024). Similarly, facially expressive humans are more likeable, and can be better at negotiating during conflict (Kavanagh et al., 2024). Dunbar points out that demonstrating how individual differences in specific skills correlate with relationship management is difficult, and we agree, this body of evidence in relation to facial expression is building. Other forms of communication, such as vocalization and gesture, could function similarly, but unlike facial expression there is little data at present showing how individuals differ in their communicative capacity in these other domains, and whether they leverage this to navigate their social worlds better.

Human and non-human primate facial expression has been of interest to scientists for decades, featuring heavily in Darwin’s early comparisons of behaviour across species (Darwin, 1872). Why, then, are studies relating to its social cohesion function in relative infancy? We argue that the dominant emotional framework (Ekman, 1992) in which facial expression is commonly approached tends to distract from this approach. If facial expressions are seen only as ‘expressions’ of subjective feeling state (which is currently heavily debated: Barrett et al., 2019),

it is hard to envisage (and test) how they operate as solutions to the group living problem. In contrast, if they are approached as predictive (Fridlund, 1994) and adaptive (Williams, 2002) signals, this better explains how they might help individuals avoid conflict, cooperate and synchronise behaviour.

One outstanding question is whether human facial expression is different to that of other primates. Did humans leverage the primate facial expression mechanism to break a glass ceiling in group size? Humans produce approximately 100 facial movements per minute during conversational social interaction (Rollings et al., 2024) which appears much higher than other primates (e.g. 67 facial movements per minute in rhesus macaques during affiliation: Whitehouse et al., unpublished data), but there is no current evidence that absolute function differs. One possibility, however, is that the evolution of language has shifted the function of primate facial expression in humans, by entwining facial movement with language and creating a more multimodal, communicatively rich social interaction where intentions, goals and predictive cues are shared accurately and rapidly (Jack & Schyns, 2015). The reality is that the discrete, basic universal expressions (happy, angry, sad, disgusted, surprised, fearful) are rarely used in spontaneous social interaction (with the exception of smiling which may not necessarily indicate actual happiness: Kavanagh et al., 2024) and instead facial movements pepper conversations allowing individuals to predict each other's responses (Emmendorfer & Holler, 2025). These real-world behaviours need to be studied within an evolutionary framework, with explicit comparison to those of other primates, if we are to understand whether this represents a step-change social bonding mechanism. Dunbar's theories about the mechanisms of group cohesion are important to help generate and test predictions about human behaviour, particularly to understand the differences between humans and other primates, and not just the similarities.

This project has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (Grant agreement No. 864694 to B.W.).

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