The evolutionary origins of group-mindedness: comparative studies with apes and equines

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Introduction

Humans work together and collaborate on massive scales nearly unparalleled elsewhere in nature. They also kill, wage wars, and commit genocide. While these behaviours are often considered antithetical, evolutionary considerations suggest a common history. In my doctoral thesis, I aimed to conduct a systematic empirical investigation of the roots of "group-mindedness," through studies of our closest relatives and closest companions. To do this, I studied group-mindedness from three levels: the behavioural products (group cohesion), the selection pressures (especially intergroup competition), and the proximate hormonal mechanisms (highlighting the neuropeptide oxytocin). In particular, I studied where these levels intersect, focusing on how oxytocin affects group cohesion, how oxytocin interacts with responses to outgroup sensory cues, and how outgroup cues themselves affect group cohesion. Methods consisted of high-resolution eye-tracking as well as broader-scale observation of free interaction. As study species, I worked with captive bonobos and chimpanzees, and semi-free ranging domestic horses. Bonobos and chimpanzees (our two closest relatives) differ drastically in group-based behaviour despite relatively recent divergence. Horses are phylogenetically more distant, but share with us a history of domestication and, like us, form complex multi-level societies in natural conditions. These species thus make ideal targets for comparative research on the evolution of group-mindedness.

Methods

In the first set of studies, the effect of outgroup vocalizations on ingroup social behaviour was compared to control (crow vocalizations). Observation was conducted before, during, and after presentation of stimuli. The first study focused on chimpanzees, while the second focused on bonobos. In the chimpanzees study, semi-monopolizable bundles of food were given to group after stimuli played, while in the bonobo study this was replaced by a silent period of observation.

The second set of studies aimed to validate oxytocin administration as a tool for researching social cognition in great apes. A non-invasive procedure to administer exogenous oxytocin to great apes was developed. In the first of these studies, participants watched stimuli from a wide variety of social contexts after administration of oxytocin or placebo while their eye-gaze was recorded. In the second study, the same administration procedures were used to investigate how oxytocin affects the allocation of attention to ingroup and outgroup stimuli. Matched-sex image pairings were presented, each featuring headshots of one ingroup member and one outgroup member. In the third ape oxytocin study, whole subgroups of female bonobos simultaneously were given either oxytocin or placebo, after which their naturalistic social behaviour was recorded.

Finally, in the last study, horse positioning across five groups was recorded in large fields after receiving either oxytocin or placebo control, administered using a custom-designed detachable mask. Group-level metrics of association were then analyzed for each experimental day, as well as association between dyads.

Results

In the first playback experiment, results showed that despite higher vigilance (more self-directed behaviour, less rest), chimpanzee groups were more cohesive after hearing the outgroup sounds (spending time in closer proximity, grooming more, fighting over food less). A similar, although weaker, pattern was found in bonobos, with groups tending to become more socially cohesive in the outgroup compared to control condition.

In the first oxytocin study, the hormone was found to promote eye contact in bonobos, but not chimpanzees. In chimpanzees, attention instead tended to shift towards the mouth. These opposite effects enlarged existing species differences. In the second, results showed that oxytocin promoted outgroup, but not ingroup, attention, and that this effect was limited to stimuli depicting the sex primarily involved in intergroup encounters (female bonobos and male chimpanzees). The third oxytocin study found an increase in social grooming, alongside a decrease in self-directed behaviour, in the oxytocin compared to placebo condition.

In the final study, horse groups became overall less dense in the oxytocin condition, but also less clustered and more centralized. On the dyadic level, interindividual distances increased on average, but bonds additionally became more even across the groups. The closest dyads drew further apart, while the more distant dyads instead drew closer together.

Discussion

The results of the first study indicate that the link between perceived outgroup threat and ingroup cohesion in humans is shared with chimpanzees, while the second extends this to bonobos and therefore across the *Pan-Homo* lineage. These results suggest a potentially ancestral emergence of the common enemy effect, which therefore is suggestive of intergroup competition at least as far back as the last common ancestor of humans, bonobos, and chimpanzees.

Given the central importance of eye contact in initiating social behaviour, the third study suggests that oxytocin may play an important facilitatory role in species-typical sociality. The fourth study reinforces the importance of oxytocin to intergroup behaviour across hominini, and further supports the notion that oxytocin may act through conserved general roles (e.g. eye contact and intergroup behaviour), but divergent instantiations (e.g. direction of effect, form of intergroup behaviour). The fifth study suggests that exogenous oxytocin can affect gross behaviour in non-human great apes, validates that it can promote group cohesion in at least certain contexts, and provides some support to the proposed biobehavioural feedback loop hypothesis of oxytocin in ape bonding.

The results of the final study are consistent with a role of oxytocin in social group organization. The observed changes to group-level metrics of clustering and centrality, along with decreased dyad-level differentiation, suggest that some of oxytocin's effects cannot be reduced to simple dyadic bond reinforcement, and instead could operate in distinctively group-based ways.

Throughout this research, my thesis aimed to investigate the evolution of group-mindedness through comparing species across contexts, linking group cohesion, intergroup competition, and oxytocin. Results were largely consistent with prevailing evolutionary theories, while highlighting core missing evidence and establishing novel methods which can deepen our understanding. There were several important limitations, and many questions remain, but together these studies provide an empirical basis to suggest that group-mindedness may have evolved through social cohesion in the face of outgroup threat, supported in part by the oxytocin system.