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How Evolutionary Theory and Neuroscience Contribute to Understanding the Development of Prosociality: Commentary

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Introduction

The articles on prosocial behaviour provide a fresh and comprehensive perspective on a vibrant domain of research in developmental psychology. Additionally, each piece concludes with a take-away message for parents and social policy, which nicely broadens their scope. I focus my commentary on some aspects that were not sufficiently integrated with the goal to provide empirical and theoretical clarity on the brain-behaviour processes involved in prosocial behaviour, with an emphasis on moral cognition.

Prosocial behaviour usually refers to any action performed by one organism to alleviate another's need or improve their welfare.[1] It is an uncontroversial phenomenon widespread across social species in different taxa. Even insects and fish engage in prosocial behaviour. To advance our

understanding of the mechanisms that underpin such behaviours, as well as their development in children, this construct needs to be more clearly characterized. Generosity, helping, sharing, empathy and moral behaviour should not be used interchangeably (see Malti et al.). In this commentary, I argue that much is to be gained by conceptualizing prosocial behaviour as a multidimensional construct and by integrating evolutionary theory and developmental neuroscience into its study.

Research and conclusion

Taking evolution seriously

Humans are a hyper social species, which is to say we are specialized and adapted for group living. Rules and expectations for social interactions have been established and shaped over our evolutionary history. Behaviours that promote group cohesion and the smooth functioning of the social group, which are arguably the building blocks or precursor to moral cognition, have been documented in other species.[2] Certainly, humans have a large neocortex, which allows for additional computations necessary for working memory, inhibitory control and selective attention (executive functions) to an extent unmatched with other species, as well as for enabling language and self-awareness. It remains, however, that the human capacity for caring for others is a biological adaptation, because it conferred a selective advantage by enhancing social cohesion and cooperation, and thus survival. This explains why early signs of empathic concern emerge very early in ontogeny, as documented by Roth-Hanania and her colleagues with 8-16 months old infants.[3] This capacity for empathic concern does not depend on, or necessitates self-reflexive abilities, theory of mind, or perspective taking, and these results contradict one dominant theory of the development of empathy (see Spinrad et al.).[4]

Importantly, evolution is a continuous process. It did not stop 30,000 years ago, nor did it start with apes and primates. Kinship and reciprocity have shaped the prosocial inclinations of all social species in important ways. Evidence of similarities in prosociality across these species may reflect either analogy or homology from the molecular level all the way up through biological mechanisms and neural circuits. For instance, rescue behaviour has been documented in ants,[5] and similarly in rodents,[6,7] and is preferentially directed to kin in both species. This does not imply that the physiological mechanisms are necessarily the same across species. It does tell us, however, that rescue behaviour has evolved across species because it provides increased fitness to the organisms. From a neuroscience perspective, there is solid evidence that, in mammalian

species, including humans, emotion plays a causal role in eliciting several prosocial behaviours such as attachment, parental care and empathy. It is thus possible and meaningful to examine the molecular and neurobiological mechanisms that underpin these aspects of prosociality. For instance, oxytocin, a neuropeptide synthetized in the brain in all mammals, facilitates bond forming between mother and offspring and motivates caring in rodents, sheep and humans alike.[8] The role of oxytocin in facilitating species-typical social and reproductive behaviours is similar in its structure and expression, although the specific behaviours that it regulates are quite diverse. The common denominator is the special role of this peptide in increasing the salience of social stimuli. Nursing, caring and helping behaviours are associated with activation of the reward and pleasure circuits in both non-human animals and humans.[9-11] This is also the case for altruistic/costly giving in human subjects.[12,13]

Thus, it should come as no surprise that giving to others makes young children happy-even happier than when they are receiving treats themselves.[14] Positive emotion is a powerful proximate mechanism for prosociality.

Different types of prosocial behaviour may not be related

It is critical to consider prosocial behaviour as a multidimensional construct rather than a global concept, and the relations between these various types of behaviours are not simple.[15] While some forms of prosocial behaviours such as helping and consolation can be the outcome of empathy, other behaviours, like sharing, are not necessarily associated with or elicited by empathy.[16,17] Furthermore, while empathy provides a foundation for care-based morality, it is not always a direct avenue for moral behaviour and can, from an early age, interfere with morality by introducing partiality, which leads to amoral or even immoral behaviours (see Diesendruck & Benozio).[18] Neuroscience research demonstrates that the circuits involved in empathy and morality only partially overlap.[19-22] Furthermore, the fact that empathy produces social preferences that can conflict with morality, fairness and justice is coherent with its ultimate cause in evolutionary theory. The roots of empathy are subsumed in the evolution of parental care and group living, and individuals who identify and cooperate with in-group members enjoy numerous benefits, including the fulfillment of many basic psychological needs, but group life is also a source of prejudice, biases, and of social strife.[23]

What developmental neuroscience brings to the study of morality

Studying subcomponents of more complex behaviours can be particularly useful from a developmental perspective, when it is the case that only some components of, or precursors to more complex behaviours are observable. A neurodevelopmental approach to morality is especially important because many brain regions that are germane to moral functioning do not appear to be fully mature until young adulthood. In addition, there are continuities and discontinuities in the developments, reorganizations and transformations of these regions. To make matter more complex, early competencies may serve functions that can be different from later ones. An illustration of such a phenomenon is the so-called empathic cry of the newborn, which is no longer observed at 5 months of age.[24] Rather than being an affective contagious response to another baby crying as often interpreted, this reaction in fact reflects another function that is anything but empathic.[25] It could be that the function of this cry is competitive, a call for the mother to come and nurse the infants rather than someone else's infant, like bird chicks in their nest. This phenomenon in the infant has no relevance to empathy and concern present at 8 and 10 months as documented by developmental psychologists.[26]

Work across various academic disciplines has converged on the view that moral competency emerges from a complex social, emotional, and cognitive integration, which is shaped through cultural exposure.[27,28] In essence, morality concerns harm to other people. Studies using electroencephalography and event-related potentials (EEG/ERPs) in children aged 3-9 years while they were shown stimuli depicting physical injuries to people demonstrate both an automatic neural response (N200), which reflects affective arousal, and a late-positive potential (LPP), indexing cognitive reappraisal, with the latter showing an age-related gain.[29] Another EEG study assessed implicit moral evaluations of antisocial (harming) and prosocial (helping) behaviours in young children (3-5 years).[16] Significant differences were found in early automatic as well as later controlled temporal periods when children viewed the morally-laden scenarios. Importantly, only controlled processes predicted actual prosocial behaviour (i.e., the number of stickers given to another anonymous child). This study demonstrates that children's implicit moral evaluations are the result of an integration of both early and automatic processing of helping and harming scenarios, and later cognitively controlled reappraisal of these scenes. This neural response to interpersonal harm changes with age. Cross-sectional developmental functional MRI studies tested participants ranging from 4 to 37 years of age while they watched video clips of individuals being accidentally or intentionally injured.[30,31] Younger participants showed a stronger response in the amygdala (a region involved in processing emotionally salient stimuli), anterior insula, anterior cingulate cortex and ventromedial prefrontal cortex (vmPFC) when they observed others

in distress. This latter region connected with evolutionarily old emotional systems in the brainstem and amygdala, integrates affective and value-based information necessary for caregiving behaviours and moral decision-making.[32,33] The early engagement of the amygdala, insula, and vmPFC during the perception of others' distress and pain is consistent with the timing of their structural maturation. These interconnected regions, which underlie rapid and prioritized processing of emotion signals and are involved in affective arousal, come online much earlier in development than other neural structures, especially regions of the prefrontal cortex implicated in emotion regulation and moral decision making, which continue to develop until late in adolescence.

Implications

Prosocial behaviours have been selected for in the course of evolution to facilitate social interactions and group living. We learned from evolutionary theory and neuroscience that behaviour is caused by rewards and stopped by punishments, but actually, the former cause behaviour more effectively than punishment stops it in most individuals. Indeed, this is true for both emotion-driven prosocial behaviour and prosocial behaviour that results in emotional benefits. One way to promote the development of prosocial behaviour in children is to emphasize the positive consequences for the self, the other and the society as a whole. Often, parents and teachers tend to show the opposite pattern of emphasis by punishing antisocial behaviour or the lack thereof (which may be necessary in some cases) more than rewarding moral behaviour.

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