Neurocognitive mechanisms of prosociality in childhood

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Abstract

This paper reviews the neurocognitive mechanisms underlying prosocial development in childhood. I begin by arguing that most prosociality is costly. This cost needs to be regulated for prosocial behavior to occur. The precise regulatory mechanisms depend on the type of prosocial behavior and include behavioral control in the case of sharing and emotion regulation in the case of helping. I review evidence that these regulatory mechanisms are subserved by prefrontal cortical circuitry, which depending on the mechanism interacts with different brain regions coding for self- and other-related affect to produce prosocial behavior. I conclude that the maturation of prefrontal cortical circuitry drives the development of both sharing and helping in childhood through supporting the emergence of relevant regulatory mechanisms.

Introduction

Prosocial behavior can take multiple forms, such as sharing resources (i.e. food or money), helping, or comforting others in distress. These forms of prosociality have been documented already in infancy [1], suggesting early and deep-seated ontogenetic roots [2]. While much attention has been dedicated to understanding the origins of prosociality, less research has been conducted on how these behaviors develop throughout childhood and into adulthood. This paper reviews studies on the neurocognitive mechanisms of prosocial development, specifically sharing and helping, during middle and older childhood[1].

I argue that most types of prosocial behavior, and certainly sharing and helping carry a cost. Sharing resources means less for oneself and helping another requires time and physical or psychological effort. At the very least prosocial behavior implies opportunity costs with regards to both resource and recipient. Studies have shown that children are aware of these costs since, their prosocial behavior is modulated by both the potentially incurred cost [3, 4] and the value of the resource [5]. I propose that the development of prosociality can be viewed through a value-based decision-making framework [6], whereby the potential costs of prosociality are weighed up against the possible benefits derived from being prosocial, both in the short- and the long-term. I argue that for decisions to be swayed in favour of prosociality, the costs of being prosocial need to be regulated. These regulatory processes undergo protracted developmental

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[1] The literature on neural correlates of comforting in children and adults is virtually non-existent.

change due to the maturation of the underlying neural circuitry. This paper reviews studies showing that distinct forms of prosociality demand distinct regulatory processes. Thus, sharing needs behavioral control and helping requires emotion regulating. These regulatory processes draw on distinct neural mechanisms, which might also explain the observed lack of positive relationships between the two types of prosociality in development [1, 7].

The neurocognitive mechanisms of sharing

Sharing valuable resources can be observed in toddlers as young as 15 months [8]. At this age sensitivity towards equal distributions and fairness norms also emerges [9, 10]. Around 3 years, children state that sharing equally is the norm and from then on, they increasingly follow such sharing norms with their actual behavior [11]. Complying with social norms constitutes a long-term goal, which conflicts with the more immediate satisfaction of reward maximization [12]. I argue that resolving such conflict in favour of sharing according to the norm requires behavioral control. There is by now increasing evidence that behavioral control is positively correlated to sharing in both preschoolers [13, 14] and school children [11, 15] using a variety of measures of behavioral inhibition (i.e. day-night task, questionnaire measures). More recently, these correlative findings have been extended to show that explicit experimental manipulations of behavioral control impact sharing directly. Thus, in one study, it was shown that children aged 6-9 years shared less after having engaged in a behavioral motor control task compared to sharing after a speeded reaction time task [16]. In another study children aged 6-9 years shared more after having listened to stories priming behavioral control compared to stories that did not [17]. In sum,

there is a sizeable body of literature suggesting that behavioral control aids sharing in accordance with the prevailing social norms during middle childhood.

In adults, it has been shown that social norm compliance relies on lateral prefrontal cortical brain regions [18, 19]. Activity in left and right dorsolateral prefrontal cortex (DLPFC, see Figure 1A) was positively correlated with sharing under threat of punishment [18], while disrupting activity in right DLPFC reduced such sharing [19]. It has been argued that the top-down modulation from DLPFC of subjective value-signals in the ventromedial prefrontal cortex (VMPFC, see Figure 1B) is key for both implementing and complying with social norms [20]. Lateral prefrontal cortical areas are among the brain regions undergoing the most protracted age-related loss of grey matter volume throughout childhood and adolescence [21]. Further, linear age-related increases in structural connectivity are among the most delayed in white matter bordering prefrontal cortex [22], which in turn impacts the extent of functional connectivity [23]. Lateral portions of the prefrontal cortex are involved in actively maintaining task goals, biasing attention and implementing behaviors [24]. The maturation of lateral PFC also underpins the development of these functions in children [25, 26], which make it a suitable candidate region supporting the emergence of behavioral control mediated social norm compliance.

A recent study showed that social norm compliant sharing in children increased between the ages of 6-13 years and this correlated directly with an independent measure of behavioral motor control [27]. Simultaneously recorded brain

activity showed that this age-related increase in social norm compliance correlated positively with activity in the left DLPFC. Further, the age-dependent increase in activity in this region mediated the developmental increase in behavioral motor control, which in turn predicted the increase in social norm compliance throughout childhood. While connectivity analyses were not conducted in this study, it is likely that such decisions to share are supported by increased functional coupling between DLPFC and brain areas that compute the value of decisions, such as the ventromedial prefrontal cortex (VMPFC). Such a mechanism has been shown to support decisions in favour of long-term goals in similar scenarios in both adults [20, 28, 29] as well as during middle childhood [30]. This interpretation is buttressed by findings from a recent study measuring event-related potentials (ERPs), which show an increase of regulatory processes in bringing about sharing during childhood [31]. Thus, in older children the P3, a component reflecting behavioral control mechanisms predicted equal sharing of resources, whereas in younger children this was predicted by the EPN, an early component reflecting affective evaluation.

In sum, the development of behavioral control, supported by the maturation of function and connectivity of prefrontal cortical circuitry can account for the observed changes in sharing during middle and late childhood. Such a mechanism helps to shift decisions away from the immediate desires of reward maximization to complying to social norms of equal sharing.

The neurocognitive mechanisms of helping

Studies on the ontogeny of prosociality have largely focused on helping, showing that this emerges as early as 14 months [32]. Helping others also implies costs in terms of time, effort and opportunities. Two key motivations have been argued to underlie helping. A selfish desire to *reduce one's own distress,* also known as personal distress; and an altruistic desire to *reduce the other's distress*, also known as empathic concern [33, 34]. Whereas personal distress leads to helping only when there is no other recourse of stopping one's own distress (i.e. fleeing the situation), empathic concern leads to helping across a range of situations. Especially in children, only indicators of empathic concern were shown to predict helping [for a review see 34]. It has been argued that empathic concern arises out of the interplay of an emotional response to the need of another and a sufficiently strong regulation of this emotional response [34]. Thus, the literature on the development of helping during childhood suggests that those children both high in emotional responding and emotion regulation are the ones most likely to help [35]. Support for this comes from studies using parental questionnaires, parent and teacher ratings as well as psychophysiological indicators suggesting that empathic concern is a good predictor of helping behavior in childhood.

In adults it has been shown that observing the painful or unpleasant experience of another person activates circuitry that is also recruited when undergoing this experience oneself [36, 37]. This circuitry comprises the bilateral anterior insula and medial/anterior cingulate cortex [see Figure 1; 38]. Activity in the anterior insula was shown to correlate positively with empathic concern ratings [36] and

activity of this region when watching others in pain was positively related to helping behavior, albeit only to in-group members [39]. It has been argued that the anterior insula performs value computations related to prosocial behavior [40]. More recently, it was shown that especially connectivity between the anterior cingulate cortex (ACC) and the anterior insula was positively related to prosocial behavior following an empathy induction [41]. The ACC has been implicated in top-down regulation and control of negative emotions and processing of emotional conflict [42] and in this case might function as affective regulation mechanism to produce empathic concern in turn leading to prosocial behavior.

Several studies on the neurocognitive development of empathic concern and helping have been performed in children. These studies show that children aged 7-12 years activate anterior insula as well as anterior midcingulate when observing the pain of another [43]. Similar activation patterns could be already seen from 4 years of age [44]. A study testing 7-40 year old participants showed that activity in the amygdala in response to seeing others' pain decreased with age, while activity in lateral prefrontal cortex increased, suggesting a potential decrease in distress-related and an increase in emotion regulation related brain functions [45]. A recent longitudinal study in children from 10 to 13 years of age showed that empathic concern at age 10 predicted activation of lateral prefrontal regions, namely the inferior frontal gyrus (IFG), which in turn was linked to helping [46]. Importantly, the IFG activation overlapped with coordinates typically found for cognitively effortful processing. Unpublished data from our lab also shows that age-related changes in empathically driven helping

were strongly linked to increased connectivity between the right anterior insula and lateral and medial prefrontal cortical areas [47].

In sum, the neurocognitive mechanisms of helping during childhood comprise affective responding to the emotional state of another, as coded in the anterior insula, in combination with regulatory mechanisms of the experienced affect, instantiated in prefrontal cortical brain regions.

Summary

This review summarizes the recent literature on the neurocognitive mechanisms that support the development of prosocial behavior in childhood. The review draws on a value-based decision-making framework of social behavior [6] and combines this with developmental neuroscience to examine the regulatory mechanisms that predispose children towards prosocial actions in spite of associated costs. One key finding is that neurocognitive mechanisms differ depending on the prosocial behavior in question. Whereas sharing requires behavioral control, helping needs the regulation of emotions in response to another's distress. These distinct mechanisms draw on distinct neural circuitry, which in turn could explain why different types of prosocial behavior correlate so poorly during development [1].

One important feature of prosocial behavior is that it is vastly context-dependent. From around 5 years, children discriminate who they share with based on group membership, familiarity, similarity, their partner's willingness to share, their partner's needs and reputation concerns [for a review see 48]. A

value-based decision-making framework of prosociality allows ample room for the influence of such contextual variables, since these will affect the value of prosocial behavior depending on the goals of the benefactor.

The present review applies to situations in which prosociality is costly. I contend that even though some experimental settings manage to eliminate the costs of prosocial behavior, the vast majority of real-life situations imply a cost to prosocial behavior. In spite of such costs it has been argued that prosocial behavior does not require any active regulation, but rather occurs effortlessly and automatically [49]. While the idea that prosociality occurs automatically and without any regulation remains contentious [50] the evidence at least during childhood speaks against this. With developmental changes in neurocognitive architecture, it is likely that the mechanisms supporting prosociality change with age, which should preclude definite inferences made from one age group to another.

There is strong evidence that the maturation of prefrontal cortically mediated regulation supports the development of prosocial behavior during childhood. A value-based framework provides a mechanistic account of developmental change in prosocial behavior. Such a framework can simultaneously account for maturational changes in observable behavior and accommodate for the effect of contextual variables likely to influence the computation of costs and benefits associated with the various available social.

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Acknowledgements:

Figures

Figure 1. Overview of brain regions involved in prosocial behavior during childhood A. Lateral slice showing anterior insula (red) and dorsolateral prefrontal cortex (purple). B. Medial slice showing anterior cingulate (red) and ventromedial prefrontal cortex (blue).