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Domain-general neural computations underlying prosociality during infancy and early childhood

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A mounting body of neuroscience research in the social and moral evaluative abilities of infants and young children suggests the coopting of three domain-general processes involved in attention allocation, approach/avoidance, and intention and action understanding. Electrophysiological investigations demonstrate children's preference for prosocial others, that children's individual differences in moral evaluation predict prosocial behaviors, and that parental values may already influence neural sociomoral computations at quite young ages. This review highlights the importance of a developmental neuroscience approach in clarifying our understanding of early prosocial preference and behavior.

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Introduction

Humans live in cooperative societies, interacting with and relying on others from before birth. This context necessitates a set of evaluations of those who 'do good' and what behaviors we ourselves should do to benefit others [1]. This set of cognitions and actions fall under the umbrella concept of prosociality. Historical accounts of prosocial development have oftentimes subsumed it within the larger question of moral development, assuming that behaviors should, but do not always, follow from our cognitions [2]. Recent behavioral investigations of prosociality have differentiated between prosocial knowledge, preference, and behavior, and have detailed some rudimentary aspects of many of these in very young children, but fundamental differences in the development of each across early and middle childhood [3,4].

Children as young as 3 months of age exhibit preferential looking toward characters that treat others well compared to those that harm others [5]. They also manifest this preference for prosocial agents in their own reaching behavior by 6 months of age [6,7] and extend this preference through the first two years of life [8]. Infants and toddlers may also feel distress for the plight of others when viewing these scenarios [9]. Toddlers also express differential looking toward those that are considered 'fair' in their resource distributions and those that are not [10,11]. Such early aspects of social evaluations have been conceptualized as reflecting rudimentary innate elements of a moral sense [12]. The nature of the complexity of these evaluations however is highly debated, with some advocating for a lean interpretation, where developing prosociality is the product of domain-general, non-specific mechanisms, such as self-control, numerical cognition, emotional appraisal, and perspective-taking [13,14] and others a highly developed, and rich interpretation, specific to prosociality and moral cognition [15]. While children as young as 3 months of age exhibit preferences for prosocial agents, behaviors that benefit others emerge much later. Many studies suggest that rudimentary prosocial actions, those of comforting another in distress and assisting in helpful 'pointing' may emerge in the first year of life, but that it is in the second year that children begin to engage in instrumental helping and sharing [3,16]. Moreover, while children's developing exhibition of prosocial behaviors increases throughout the first years of life, equality and equity in resource distribution are not present until early to middle childhood [17,18].

Decades of developmental research have documented changes in prosocial behavior across the first years of life, as well as early emergence of preferences for prosocial others [19]. Recent investigations, detailed elsewhere in this issue, have begun to elucidate related psychophysiological variants in prosocial thought and behavior (e.g. electrodermal activity, heart rate variability, pupillometry) [20]. However, while this work has been crucial in documenting changes involved in these actions and evaluations, and relevant sympathetic and parasympathetic arousal that is linked to such evaluations, little is known about the underlying neural mechanisms. The importance of neurophysiological investigations in understanding developing prosociality lies in its additional ability to differentiate between different extant theories. Namely, given the precise temporal nature of ERPs, coupled with the ability to quantify the amount of activity in certain frequency bands (EEG), developmental neuroscience

Table 1

Spectral measures of infant electroencephalography.

Electroencephalography (EEG)	EEG is a continuous measure of electrical activity of the brain.
EEG power density	EEG power measures the amount of neuronal activation at a specific scalp location. Power densities are divided into frequency-based bins. In infancy, a 6–9 Hz or 5–8 Hz band is usually of interest.
Alpha power density	The infant 'alpha' band (6–9 Hz) is recorded over anterior scalp regions and shows a steady developmental shift toward higher frequencies with peak frequencies occurring around 10 month of age. It is important to note that the alpha band shows an inverse relationship between synchronization and neural activation, where decreased scalp level synchronization is associated with increased cortical level activation (i.e. low alpha power density reflects greater neural activation).
Alpha asymmetry	Alpha asymmetry accounts for the relative difference between left and right 'alpha' power density over the frontal regions. Alpha asymmetries are recorded during EEG resting state measures, where researcher strives to maintain the infants' visual attention by having them watch a bingo wheel filled with colorful balls, or an experimenter blow bubbles, and in task conditions, which involve the presentation of, or engagement with, and emotional stimulus. Differential activation/suppression on the scalp of right versus left are thought to reflect approach and withdrawal emotion regulatory strategies.

investigations contribute distinguish between the automatic versus controlled nature of computations, the degree to which judgments or actions are 'gut,' emotional, or slower, cognitively controlled 'cool' evaluations, and the extent to which individual differences in how much emotional versus cognitive or automatic versus cognitive processing in prosociality predict children's own prosocial behaviors. EEG and ERP complement each other in allowing for both explorations of the timing of neural computations as well as the degree to which well-established neural frequencies (e.g. alpha, beta, gamma) are involved. However, as neuroscientific methods (e.g. EEG, ERP, MRI, fMRI) are still correlational by nature, causal statements cannot be made, yet, such programs of research provide additional levels of analysis in developing prosociality.

In the present paper, we highlight recent avenues of exploration into the underlying neural computations of developing prosociality in infants, toddlers, and preschool children. Whereas in some developmental behavioral investigations, a focus has been on domain-specific processes related to prosociality, developmental neuroscience findings focus on domain-general mechanisms that have dominated this new field in the past five years, including general attention allocation and emotion regulatory tendencies, and argue that both prosocial preference and behavior coopt these extant systems. The domain-general approach in developmental prosocial neuroscience capitalizes upon suggestions from infant and toddler behavioral investigations over the past 30 years that prosocial judgment and behavior may be based on developing notions of self-control and attention [16] or emotion regulation [21].

Due to the practical limitations of testing young infants with neuroimaging methods, most investigations have employed electroencephalography (EEG/ERP). EEG is relatively inexpensive, can recover from excessive head movement that is standard in young child populations, and is useful for investigating how much of certain neural frequencies (see Table 1) are present (spectral EEG) and when processing of certain aspects is occurring (event-related potentials; ERPs; see Table 2). A developmental neuroscience perspective provides evidence for the differential roles of domain-general mechanisms of attention

Table 2

Temporal measures of infant electroencephalography.

Event-related potential (ERP)	ERPs reflect changes in electrical activity in response to a time-locked stimulus or event. ERPs help to elucidate the spatio-temporal dynamics of development and sequence of cognitive processes.
EPN	The EPN component is associated with early visual differentiation of stimuli and occurs around 100–175 ms after a stimulus is presented, optimal over midline parietal electrodes. The EPN reflects relatively automatic attentional or affective responding.
P400	The P4 component occurs between 200 and 600 ms after a stimulus is presented, over temporal and parietal electrodes, and is thought to index early social information processing. The P4 is sensitive to goal directed actions such as grasping, pointing, emotional processing, and gaze direction.
Nc	The negative central (Nc) is a mid-latency ERP component that is recorded over frontal-central scalp electrodes and occurs around 300–500 ms. After a stimulus is presented, over central electrodes. The Nc indexes a general orienting response to salient stimuli, and is greater for aspects that are attended to than non-attended to.
LPP	The LPP is a late-latency component (400–1200 ms) over parietal and occipital electrodes that appears to index increased allocation of resources to processing, with greater positivity for conditions that engender additional processing in older children and is thought to index a comparable function in early development.