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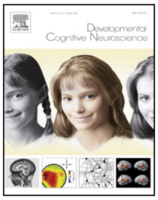

Review

Social re-orientation and brain development: An expanded and updated view

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ABSTRACT

Social development has been the focus of a great deal of neuroscience based research over the past decade. In this review, we focus on providing a framework for understanding how changes in facets of social development may correspond with changes in brain function. We argue that (1) distinct phases of social behavior emerge based on whether the organizing social force is the mother, peer play, peer integration, or romantic intimacy; (2) each phase is marked by a high degree of affect-driven motivation that elicits a distinct response in subcortical structures; (3) activity generated by these structures interacts with circuits in prefrontal cortex that guide executive functions, and occipital and temporal lobe circuits, which generate specific sensory and perceptual social representations. We propose that the direction, magnitude and duration of interaction among these affective, executive, and perceptual systems may relate to distinct sensitive periods across development that contribute to establishing long-term patterns of brain function and behavior.

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1. Introduction

Humans evolved in an environment where integration with the social world was critical for survival. Because many factors moderate social dynamics (e.g., dominance relations, alliance formation, cooperation, deception (de Wall, 1996)), the need to maintain social cohesion under such complex conditions necessitated the dedication of substantial neuronal resources to processing social signals in the environment (Pinker, 2002; Shultz and Dunbar, 2007; Dunbar, 2012). Social cognition, like many complex cognitive processes, is not fully functional at birth, but rather matures slowly across development. One remarkable feature of human social behavior, and one that we believe is a key aspect of normative maturation, is the dramatic change in social focus across development.

Social behavior is the culmination of input from many neural networks that mediate different aspects of responding to various classes of social stimuli or contexts (Kennedy and Adolphs, 2012). For example, distinct brain networks have been identified for social processes such as motor mimicry (Gallese et al., 2004), joint attention (Happe and Frith, 2014), mentalizing (Saxe and Baron-Cohen, 2006), empathy (Singer and Lamm, 2009), fairness (Guroglu et al., 2011), social bonding (Insel, 2010), and even deception (Yang et al., 2014). Thus, the neural mechanisms underlying social behavior do

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not reflect a single "social brain", but rather distinct neural circuits that are implicated in fundamentally different and dissociable functional brain processes that evolve and adapt to the social demands of a given environment and a specific phase of development. In a previous review on adolescent neurodevelopment, we argued that the brain processes governing social behavior could be parsed into three broad functional clusters or nodes: the perceptual node; the affective node; and the cognitive-regulatory node (Nelson et al., 2005). This provided a framework for mapping changes in social behavior during adolescence onto maturational changes that take place in the brain. The present paper has two primary goals. The first is to expand the scope of this social re-orientation perspective beyond adolescence to encompass a number of other inflection points in social development. The second is to update the empirical evidence described in the original review and highlight important gaps that need to be addressed in future work.

2. Beyond adolescence: other periods of social re-orientation

We believe at least five distinct social phases occur in development, each of which can be largely defined by the social target and type of social behavior expressed. During *infancy*, sociality primarily consists of engagement with the mother/caregiver. In the *juvenile phase* between weaning and puberty, the mother–infant dyad is gradually replaced with peer-focused play behavior, while maintaining the mother/caregiver as a base. In the *adolescent phase* between puberty and full maturity, social behavior transitions to full integration with larger groups of peers. This transitions into the *reproductive/intimacy* phase, which is accompanied by social bonding and reproductive behavior. Finally, in the *mature adult phase*, social behavior is characterized by interactions within a relatively stable multigenerational group, with the expression of intimate relations, and directed care of offspring. Although this developmental pattern is not universal, it is widely expressed among most primates and in many socially living mammalian species (Hinde and Spencer-Booth, 1967; Biben, 1983; Panksepp et al., 1984; Pusey and Packer, 1987; Spinka et al., 2001; Ekernas and Cords, 2007; Konner, 2010; Zhang et al., 2012). We believe the conservation of this pattern of social phases across development likely indicates that the brain plays an important role in shaping maximally adaptive social behavior.

An important feature of social behavior in each of these phases is that within phase social engagement is highly motivated. Individuals will energetically seek out the developmentally appropriate form of social behavior and they will experience distress when this target is impeded. Highly motivated social engagement is directed at caregivers in infancy, at playmates during the juvenile phase, at integration with peers during adolescence, at potential mates during early adulthood in the social intimacy phase, and at offspring and stable group members in the mature adult phase (Hennessy et al., 1995; Rubin et al., 2010; Trezza et al., 2011; Abrams et al., 2013; Hostinar et al., 2015). This motivation facilitates attention to and behavioral engagement with specific social contexts at developmentally appropriate times. There is even some indication that, like other motivated behaviors, phase specific social behaviors might be under homeostatic control with built-in patterns of compensatory drives and satiation. For instance, periods of maternal separation interspersed with brief, rather than extended maternal contact, elicits heightened distress in both human and rodent infants (Shair et al., 2015). One explanation for this effect is that insufficient time with the mother leaves a hunger like state in the offspring which is blunted if the contact is of sufficient duration to satiate a social need. Likewise, compensatory increases in play behavior have been observed in juvenile rats following periods of social separation, and the longer the separation the more play behavior is expressed. This suggests that rats are motivated to obtain a certain amount of play in this specific developmental phase (Panksepp et al., 1984).

The role of motivation in guiding phase-specific social behavior is also suggested by several studies indicating that when new targets of social behavior emerge, the motivational response to previous social categories diminish. For instance, the duration and intensity of distress during maternal separation declines across infancy for a number of species at the same time that play behavior increases (Hinde and Spencer-Booth, 1967; Barr, 1990; Brunelli and Hofer, 1996; Zhang et al., 2012). Likewise, a recent study in humans demonstrated that maternal presence can blunt the cortisol stress response in young pre-adolescent children, but has no effect on adolescents, who have shifted their motivated behavior toward peer integration (Hostinar et al., 2015). Finally, peer group directed behavior becomes less important for adolescents and young adults after romantic engagements have become established (Collins et al., 2009). Taken together, these data provide evidence that suggests the focus of social goal undergoes systematic shifts across development, and is accompanied by changes in motivation to obtain and maintain specific types of social experience.

Another feature of social behavior within each developmental phase is that the behaviors themselves are malleable and become adapted to the local social environment. This is perhaps most clearly demonstrated in the emergence of face processing biases. A classic example of this phenomenon was demonstrated in cross-species comparisons of face recognition capabilities during the first year of life. While motivation to attend to face-like stimuli is present at birth, experiences during the early infancy phase sculpt subsequent face-processing capabilities. For example, at six months of age, humans and monkeys demonstrate equivalent capacity to recognize differences between individuals of both species. However, over the course of the following six months, recognition capabilities for individuals of one's own species increases while similar capabilities for other species diminishes (Pascalis et al., 2002). Hence, a same-species bias emerges in perceptual processing as a consequence of social experience. Similar tuning of social perception has also been characterized for specific facial features associated with race, gender, and age (Scherf and Scott, 2012). Each processing bias appears to be sculpted by specific contextual experiences during unique developmental windows.

A similar perceptual-tuning process may also occur in the auditory domain. Despite being pre-linguistic, infants are able to respond selectively to emotional content in voices from an early age (Grossmann et al., 2010), and recognize identity based on vocal characteristics. However, these biases are only observed when the speaker uses the infant's native language (Johnson et al., 2011). This suggests that, like experience-tuned biases in face processing, maturation-related biases in voice processing are molded by the contexts a child experiences (Perrachione et al., 2011).

Another example of this context-matching aspect of social behaviors in development can be found in juvenile play. While anthropological studies have revealed that both physical and imaginary play in virtually all human cultures peaks during middle childhood (Konner, 2010), the form that the play takes can vary markedly across cultures. In some cultures, play involves ritualistic dance, in others it has more elements of hunting and chasing, and in still others it involves pretending to take on different adult roles (Whiting and Edwards, 1992; Rogoff, 2003; Konner, 2010). Similarly, during adolescence, adaptation to the peer group often involves adoption of specific cultural norms expressed by specific local groups into which they are attempting to integrate (e.g., "goths" vs "jocks") (O'Brien and Bierman, 1988). These findings suggest that while there is a developmentally specific aspect in the timing of learned social behaviors, the specific form of that