



Discussion

Commentary on the Special Issue on the Adolescent Brain: Incentive-based striving and the adolescent brain



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This special issue on adolescent brain development, one of many to be published in the last decade, is to be applauded, not only because of Spear and Silveri's major accomplishment in updating the field on leading issues but also because of their care in attending to both preclinical and human/clinical work in support of each topic. Animal work has been vital to human studies of adolescence (for instance, in outlining mechanistic aspects of pubertal change: McCormick et al., 2010; Schulz and Sisk, 2016), in illuminating neural circuits and regions of interest that now guide human investigations (as in seminal studies of the human reward system: Olds and Milner, 1954; Schutz et al., 1997), and in probing complex cellular mechanisms (e.g. inflammation; microbiome: papers by Brenhouse and Schwarz (2016), Neufeld et al. (2016), and Rao and Pak (2016)) that interact in previously inconceivable ways to guide expressions of human behavior. As one who has advocated for a theoretically grounded mechanistic account of neural changes that accompany adolescent development (Luciana et al., 2012; Wahlstrom et al., 2010a), I find this approach to be most welcome. From unique vantage points and with admirable conceptual and methodological rigor, in this issue's contributors have converged on behaviors that we wish to understand in the context of normal development (e.g., van Duijvenvoorde et al.'s analysis of motivation and reward sensitivity), how these behaviors are neurally mediated (e.g., Stevens' paper on the developmental connectome), and what can go wrong to create affective and cognitive

vulnerabilities that lead to frank manifestations of psychopathology (Gomes et al., 2016; Lichenstein et al., 2016; Silveri et al., 2016).

Attention to the full dimension of behavioral and neural expression, from "typical" to pathological, and from multiple levels of analysis is reminiscent of the developmental psychopathology perspective (Cicchetti and Rogosh, 2002), a core tenet of which is that an in-depth knowledge of normal behavior is vital to the understanding of psychopathology. Moreover, to appreciate what is expected or typical, it is essential to view adolescence from a lifespan perspective, to identify the developmental tasks that must be negotiated in the achievement of optimal functioning, and to place those tasks within a coherent temporal framework. This involves comprehensive analysis of the progression from childhood into adolescence as well as comparison of adolescents to young adults, adults, and the elderly. The same behavior may have different meanings and distinct neurobehavioral consequences when expressed at different developmental periods and perhaps within different contexts within the same developmental period. Adolescent risk-taking represents one good example.

1. Adolescence as a significant life period for incentive-based striving

As van Duijvenvoorde and colleagues indicate, a useful starting point is to consider what motivates the adolescent. Based on work cited in their review regarding patterns of heightened reward sensitivity (c.f., Urošević et al., 2012) as well as the activation of motivational drives (Satterthwaite et al., 2012), a reasonable conclusion is that a fundamental goal for youth as they transition into adulthood is learning to dynamically engage motivation

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to purposefully formulate and pursue distal goals. Indeed, this is something that most, if not all of us, regardless of age, aspire to achieve—a *productive forward momentum that is grounded in meaning and personal choice*. Our group's perspective is that this developmental task is positive in tone and that it can be understood at an evolutionarily-derived neurobehavioral systems level (Depue and Collins, 1999; Luciana et al., 2012; Luciana and Collins, 2012; Wahlstrom et al., 2010a). Specifically, we have argued that incentive motivation emerges from activity in a neural system organized within the limbic forebrain and basal ganglia utilizing dopamine as a modulator (see Depue and Collins, 1999; Luciana et al., 2012 for reviews). Importantly, the brain circuitry for this type of motivation (reflecting the drive to “get up and go”, a sense of curiosity, the striving to achieve beyond immediate means; hope and desire) is linked to striatal regions implicated in movement. As indicated in the paper by Stevens (2016), novel brain imaging techniques now allow us to discern how the functional dynamics of complex circuitry change with increasing maturation.

From a behavioral perspective, it may be that the activation of incentive motivation in adolescence facilitates a salient developmental process: the seeking of experience. Within this framework, the quest itself is a positive reinforcer. Experience seeking may well represent the means through which an individual learns and ultimately develops individual preferences and identity. As inferred through the analysis provided by Lichenstein et al. (2016), the inability to engage this realm of behavior is potentially devastating to affective development and to neural organization of key nodes in the brain's regulatory network (e.g., the anterior cingulate cortex). As knowledge is gained and as one's identity and preferences become evident, goals that are increasingly longer-range in their focus and that are grounded in those preferences can be adaptively formulated. Accordingly, with increased maturity, the drive toward future incentives emerges coincident with executive capacities for long-range planning and coincident with a refinement of the network-based organization of striatal and regulatory networks (Stevens, 2016; Caballero and Tseng, 2016).

van Duijvenvoorde et al. (2016) and Guyer et al. (2016) both emphasize the social reorientation that takes place during adolescence and the profound emotional upheaval that accompanies it. Novel fMRI-based assessments of how the presence of others impacts reward sensitivity reinforce the salience of peers as a source of reward (Chein et al., 2011), the more regulatory roles that adult attachment figures might play (Telzer et al., 2015), and how peer salience confers vulnerability to risk-taking. Given the need for species survival, long-range goals would be expected to encompass opportunities to form new social/romantic connections.

Learning what one wants and how to mobilize internal and external resources to achieve it can perhaps be appreciated as the “what” of adolescence—the lifespan developmental task to be accomplished.

2. Neural underpinnings

How does nature assure that this quest for relevant experience will take place? Our contention has been that it is through age-driven elevations in *incentive motivation*, achieved through heightened activity in the striatal dopamine (DA) system (Luciana and Collins, 2012; Luciana, 2013). Ascending DA projections originate in the ventral tegmental region of the midbrain and project to regions such as the amygdala, nucleus accumbens (ventral striatum), medial and orbitofrontal cortices, and the anterior cingulate cortex. Links between DA activation in the ventral striatal region and incentive motivation have been strongly supported within the animal and human literatures, and findings are suggestive that

adolescence represents a unique period of dopamine system reorganization for this system (see Wahlstrom et al., 2010b; Luciana et al., 2012; Spear, 2011 as well as van Duijvenvoorde et al. (2016), Gomes et al. (2016), and Caballero and Tseng (2016)). Increases in striatal dopamine tone (that is, tonic activity: see Goto and Grace, 2007) early in the adolescent period heightens incentive motivation above basal levels, provoking the drive to explore and providing a means through which the individual and his/her environment will interact.

Context thus becomes critically important. The environment provides opportunities for instrumental learning. Instrumental reward learning at a basic biological level involves momentary activations of phasic dopamine and the recruitment of limbic and frontal circuits that interact to guide calculations of expected value, perceptions of risk, and ultimately the decision to act (Schutz et al., 1997). We have asserted that as outcomes become more predictable through a culmination of experience, phasic and subsequently tonic levels of dopamine stabilize to what will then characterize adult trait levels (Luciana and Collins, 2012). Neuroimaging-based evidence for a peak in reward system activity during adolescence is reviewed by van Duijvenvoorde et al. (2016) (see also the meta-analysis by Silverman et al., 2015).

Perhaps one of the most salient unresolved issues in understanding this proposed sequence concerns how it is that increased incentive motivation interacts with the developing regulatory control system to influence behavior (Kilford et al., 2016). As observed by Teslovich et al. (2014), cited in van Duijvenvoorde et al., 2016, cognitive control may be most actively recruited under conditions of high reward salience. We have suggested that the exuberance of incentive motivation leads to experiential learning and that through ongoing recruitment of regulatory circuits, activity in frontal region becomes “conditioned” (Luciana, 2013) so that over time, regulatory circuits respond proactively when opportunities for reward present themselves or are pursued. Murty et al. (2016) emphasize the importance of hippocampal-prefrontal connectivity in this process. Dopamine's modulation of cognitive control processes, such as working memory, is well-accepted (see review by Caballero and Tseng (2016)), and circuit-based models to account for its activity patterns have become refined over time to identify the laminar distribution of DA targets and their interactions with other major neurochemical systems. DA action in the PFC is determined by the functional state of local excitatory and inhibitory activity (regulated by GABA, glutamate and perhaps cannabinoids) throughout the period of cortical maturation, including adolescence (Caballero and Tseng, 2016). It is speculated that subcortically modulated motivational drives ultimately impact this balance of inputs and serve to shape, through experience, the final bursts of development of executive functions. Developmental studies of interactions between subcortical (e.g., limbic) and cortical (PFC) DA circuits, both of which are actively changing through adolescence, are needed.

In summary, increased incentive motivation may be the starting point for a developmental cascade through adolescence and into young adulthood that culminates in the ability to learn about one's place within the overarching environment through engagement in instrumental action.

Intuitively, it stands to reason that the surge in gonadal hormones that accompanies reproductive maturity contributes greatly to the increased motivation necessary to pursue social (and especially romantic) strivings, as suggested by van Duijvenvoorde et al. (2016), Guyer et al. (2016), and Kilford et al. (2016), contributing to the salience of peers as sources of reward and to the pursuit of social dominance as a fundamental human drive. As noted by Guyer et al. (2016), reinforced by van Duijvenvoorde et al. (2016), and supported by animal models of risk-taking behavior (Spear, 2016), adolescent behavior even within the same individual varies as a

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