

Review

Setting the occasion for adolescent inhibitory control



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ABSTRACT

During adolescence, individuals experience a broad range of dynamic environments as they strive to establish independence. Learning to respond appropriately in both new and previously encountered environments requires that an individual identify and learn the meaning of cues indicating that a behavior is appropriate, or alternatively, that it should be altered or inhibited. Although the ability to regulate goal-directed behavior continues to develop across adolescence, the specific circumstances under which adolescents experience difficulty with inhibitory control remain unclear. Here we review recent findings in our laboratory that address how adolescents learn to proactively inhibit a response. Much of our research has utilized a negative occasion setting paradigm, in which one cue (a feature) gates the meaning of a second cue (a target). The feature provides information that resolves the ambiguity of the target and indicates the appropriate behavioral response to the target. As such, we have been able to determine how adolescents learn about ambiguous stimuli, such as those whose meaning changes in accordance with other features of the surrounding environment. We consider why adolescents in particular exhibit difficulty in negative occasion setting compared to either pre-adolescents or adults. In addition, we review findings indicating that a balance in neural activity between orbitofrontal cortex and nucleus accumbens is necessary to support normal negative occasion setting. Finally, we consider aspects of associative learning that may contribute to adolescent inhibitory control, as well as provide insight into adolescent behavior as a whole.

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1. Introduction

Adolescence is marked by dramatic changes in brain function as well as behavior. For instance, adolescent humans and other ani-

mals typically exhibit heightened exploration and novelty-seeking behavior compared to other age groups (Adriani, Chiarotti, & Laviola, 1998; Somerville, 2013; Stansfield & Kirstein, 2006). These behavioral tendencies serve a number of adaptive functions and promote independence, making them essential for the successful transition into adulthood (Crone & Dahl, 2012; Spear, 2010). At the same time, they can also lead to risky and impulsive behaviors that increase the vulnerability to substance

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abuse and the risk of injury or even premature death (Arnett, 1999; Casey & Jones, 2010; Chambers, Taylor, & Potenza, 2003; Spear, 2011). Accordingly, there is significant interest in understanding the interplay between the specific neurobiological and behavioral factors that characterize adolescence and in identifying why particular individuals are susceptible to negative outcomes.

One factor that has been the focus of substantial research on risk-taking and impulsivity during adolescence is the capacity to inhibit a response e.g., (Brown et al., 2015). Indeed, there is substantial evidence that adolescent humans and laboratory rodents experience difficulty inhibiting maladaptive or inappropriate behavioral responses. In particular, adolescents are often less able, compared to other age groups, to successfully use environmental cues that signal that a response should be withheld (Adriani & Laviola, 2003; Anderson, Anderson, Northam, Jacobs, & Catroppa, 2001; Andrzejewski et al., 2011; Burton & Fletcher, 2012; Lin, Chen, Yang, Hsiao, & Tien, 2000; Liston et al., 2006; Meyer & Bucci, 2014, 2016c; Pinkston & Lamb, 2011; Sun, Cocker, Zeeb, & Winstanley, 2012). Notably, these difficulties are particularly apparent in experiments that involve increases in the appetitive (Douglas, Varlinskaya, & Spear, 2004; Galván, 2013; Hare et al., 2008; Somerville, Hare, & Casey, 2011) or aversive (Cohen-Gilbert & Thomas, 2013) nature of task-related stimuli. This is consistent with an emerging theory that age-related differences in behavioral control are correlated with cognitive load, which increases alongside the emotional salience of the surrounding environment (Cohen et al., 2016; Mills, Dumontheil, Speekenbrink, & Blakemore, 2015).

To date, most research on inhibitory processes has focused on the ability to *abort* a response that has already been initiated, a process referred to as 'reactive' inhibition (Aron, 2011; Braver, 2012; Meyer & Bucci, 2016d). Reactive inhibition is most commonly assessed using the Stop-Signal Task (SST) Logan & Cowan, 1984; Logan, 1994 in which a 'stop-signal' (e.g., a tone) indicates that the pre-potent response to a previously-presented 'go-signal' (e.g., a visual stimulus presented on a computer screen) should be aborted. Yet, perhaps surprisingly, most studies indicate that reactive inhibition is similar in adolescents and adults (Liston et al., 2006; Simon, Gregory, Wood, & Moghaddam, 2013; Somerville et al., 2011). In comparison, significantly less research (particularly in adolescents) has focused instead on the ability to use environmental cues that signal that a response should *not be initiated in the first place*, a process termed 'proactive' inhibition (Aron, 2011; Braver, 2012; Jaffard et al., 2008; Meyer & Bucci, 2016d). To address this gap in the literature, our laboratory has recently conducted a set of studies to examine proactive inhibitory processes during development and to determine the neural systems that support proactive inhibition.

2. Negative occasion setting

An essential feature of adaptive behavior and a key developmental milestone is the ability to detect and use cues that signal the changing demands of complex environments. For example, some environmental cues indicate the conditions under which a response to another stimulus should be emitted or omitted. To illustrate, in the daily life of an adolescent the stimulus of seeing a friend will in many cases elicit the response of engaging in conversation, with the anticipated outcome of a gratifying social exchange. However, if the friend is encountered in a classroom setting, environmental cues such as the teacher standing in front of the class indicates that this behavior is inappropriate and will likely not result in the desired outcome. Cues such as the teacher are commonly referred to as occasion setters, as they 'set the occasion' for the meaning of an otherwise ambiguous 'target' stimulus

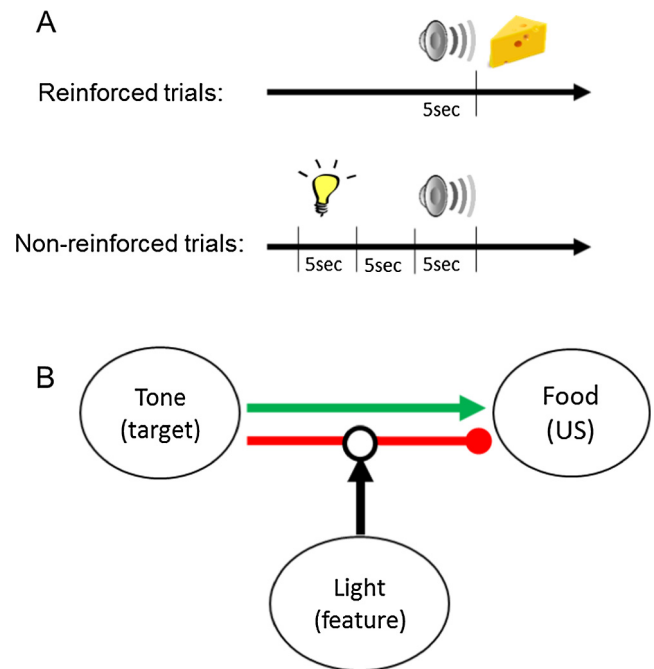


Fig. 1. (A) Illustration of the two types of training trials used in a standard negative occasion setting procedure with rats. The feature (light) and target (tone) are each presented for 5 s and the interval between them on non-reinforced trials is also 5 s. On reinforced trials, food is delivered immediately after the tone is terminated. (B) Model of the associations that are thought to be formed during negative occasion setting (Bouton & Nelson, 1998). Red and green lines indicate inhibitory and excitatory relationships, respectively (US = unconditioned stimulus). The feature stimulus acts to gate, or 'set the occasion' for the meaning of the target stimulus and indicates that a response should be withheld during the subsequent presentation of the target. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and modulate behavior that is directed to it (Bouton, 2006; Holland, 1992; Skinner, 1938). In this way, occasion setters enable an individual to categorize and retain multiple incongruent experiences with stimuli in the environment (Swartzentruber, 1995). Moreover, this hierarchical organization facilitates the representation of events that an individual has experienced and helps to ensure that expectations and responses are appropriate to the present environment.

In the specific case of *negative* occasion setting, the cue indicates that the response to an upcoming stimulus should be withheld. Thus, negative occasion setting has direct bearing on inhibitory control. Moreover, presentation of an occasion setting cue *prior* to the onset of the target stimulus models a key aspect of proactive inhibition in that the cue indicates that a response should not be initiated in the first place. Despite the importance of negative occasion setters for guiding adaptive behavior, very little prior research has considered the developmental timecourse of this form of learning. As described below, we recently addressed this by conducting a series of experiments using laboratory rats to test for age differences in the ability to use negative occasion setters to withhold behavior.

In the negative occasion setting procedure used in our studies (Fig. 1A), a target stimulus (e.g., a tone) is presented by itself on some trials and followed immediately by reinforcement (reinforced trials). On other trials, a 'feature' stimulus (e.g., a light) is presented just before the target and no reinforcement occurs on those trials (non-reinforced trials). Thus, the feature stimulus acts to set the occasion, or the context, for the meaning of the target stimulus (Bouton & Nelson, 1998; Bueno & Holland, 2008; Holland & Morell, 1996). Over the course of training, rats learn to

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