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Negative occasion setting in juvenile rats

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ABSTRACT

Prior findings indicate that adolescent rats exhibit difficulty using negative occasion setters to guide behavior compared to adult rats (Meyer and Bucci, 2014). Here, additional groups of juvenile rats were trained in the same negative occasion setting procedure to further define the development of negative occasion setting. Beginning on either postnatal day(PND) 30, 40, or 50, rats received daily training sessions in which a tone was paired with food reinforcement on some trials, while on other trials a light preceded the tone and no reinforcement was delivered. We found that rats that began training on PND 50 required 10 training sessions to discriminate between the two types of trials, consistent with prior findings with young adult rats. Interestingly, rats in the PND 30 group (pre-adolescents) also required just 10 training sessions (Meyer and Bucci, 2014). Rats that began training on PND 40 (adolescents) also required more sessions than the PND 30 group. These data indicate that the development of negative occasion setting is non-linear and have direct bearing on understanding the behavioral and neural substrates that underlie suboptimal behavioral control in adolescents.

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1. Introduction

An occasion setter is a cue that provides information that resolves the ambiguity of another stimulus and modulates behavior that is directed to it (Pavlov, 1927; Skinner, 1938; Holland, 1992;

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http://dx.doi.org/10.1016/j.beproc.2016.05.003 0376-6357/© 2016 Elsevier B.V. All rights reserved. Bouton, 2006). In the case of a *negative* occasion setter, the cue indicates that the response to another stimulus should be withheld. In this way, negative occasion setters have direct bearing on adaptive behavior in that they indicate the conditions under which a response will not be associated with an anticipated outcome and should be inhibited. Importantly, negative occasion setting reflects a form of learning that is not readily accounted for by standard models of associative learning (e.g., Rescorla and Wagner, 1972). Indeed, there are currently several different theories that have been proposed to explain negative occasion setting (e.g., Holland, 1992;

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Rescorla, 1985; Holland and Coldwell, 1993; Bouton and Nelson, 1994; Bouton, 1997; Bonardi et al., 2012). Moreover, only a few studies have considered the brain systems that support negative occasion setting or the ontogeny of this form of learning.

We recently began to address the latter issue by training adult and adolescent rats in a serial feature negative discrimination procedure that produces negative occasion setting (Holland et al., 1999). Beginning on either postnatal day (PND) 35 (adolescent group) or PND 70 (adult group), rats received daily training sessions consisting of two trial types. On reinforced trials, a 'target' stimulus (a tone) was presented by itself and immediately followed by delivery of food reinforcement. On non-reinforced trials, a light (the 'feature' stimulus) was presented before the tone and on those trials no food was delivered. After 10 daily sessions, adult rats approached the food cup during presentation of the tone significantly more on trials when it was presented alone, compared to trials when it was preceded by the light (Meyer and Bucci, 2014), consistent with prior studies using normal adults rats and the same procedures (Holland et al., 1999; MacLeod et al., 2006, 2010; MacLeod and Bucci, 2010). In comparison, the adolescent group required almost twice as many (~ 18) sessions to successfully discriminate between the two trial types (Meyer and Bucci, 2014). Further, we demonstrated that adolescents could in fact *learn* the dual meaning of the tone in as few sessions as adults, but were unable to express that learning until they reached \sim 53 days old. Interestingly, that age corresponds to the time at which the prefrontal cortex (PFC) is thought to be fully mature in rats (Newman and McGaughy, 2011), suggesting that PFC is necessary for successful negative occasion setting. Indeed, we have also found that lesioning the PFC of adult rats impairs negative occasion setting in that rats could not discriminate between the two types of trials (MacLeod and Bucci, 2010).

In the present study, we trained additional groups of juvenile rats to further investigate the ontogeny of negative occasion setting. One group began training beginning on PND 30 (i.e., preadolescence) (Rice and Barone, 2000), which is earlier than the adolescent group in our prior study. We hypothesized that if a fully mature PFC is necessary and sufficient to exhibit negative occasion setting, then the PND 30 group would require at least as many training sessions to exhibit negative occasion setting as rats that began training on PND 35 in our prior study (18 sessions) (Meyer and Bucci, 2014), suggestive of a linear development of inhibitory-related behavior and functionality of PFC (Casey et al., 2000; May et al., 2004; Blakemore and Choudhury, 2006; Galvan et al., 2006). An alternative outcome was that the PND 30 group would exhibit adult-like performance and discriminate between the two trials types after only \sim 10 sessions. That would be consistent with the alternate theory that certain types of behavior instead develop in a non-linear fashion. Indeed, Casey and others have posited that the differential development of top-down control systems and subcortical reward areas results in a functional imbalance that affects behavioral control specifically during adolescence (Ernst et al., 2006; Casey et al., 2008a,b; Steinberg, 2008; Somerville and Casey, 2010; Mills et al., 2014). The development of PFC lags behind the development of regions such as the nucleus accumbens (NAC) during adolescence and accordingly, activity is disproportionately higher in NAC than PFC during adolescence compared to either childhood or adulthood (Casey et al., 2008a,b; Mills et al., 2014; Sowell et al., 1999; Rosenberg and Lewis, 1994, 1995; Laviola et al., 1999). If this were the case, then rats that began training prior to adolescence (i.e., the PND 30 group) would be expected to be comparable to adults with regard to the number of sessions that are required to exhibit negative occasion setting. In addition, we included a group of rats that began training on PND 50 and predicted that they would exhibit discrimination after ~ 10 sessions, as shown previously (Meyer and Bucci, 2014) because the balance between PFC and NAC is purportedly resolved by that age. We also

included a group of rats that began training on PND 40. Since this group began training as adolescents, like the PND 35 group in our prior study, we expected that they would require more sessions than the PND 50 group but fewer than the PND 35 group in our prior study. This latter prediction was made because rats in the PND 40 group would reach 53 days of age (i.e., maturation of PFC) after fewer training sessions than the PND 35 group.

2. Materials and methods

2.1. Subjects

Male Long Evans rats (n = 36) were obtained from Harlan Laboratories (Indianapolis, IN). Rats were weaned from their dam on PND 21, and were shipped and received on the same day. Rats were housed individually with free access to water at all times during the study. Food (2014 Teklad Global 14% Protein Rodent Maintenance Diet, Harlan Laboratories) was available ad libitum up until four days prior to the first day of training. Rats were handled and weighed daily during the week prior to behavioral training and body weights were gradually reduced over a four day period to 85% of the daily weight of free-feeding age-matched control rats. All groups remained food restricted until completion of behavioral training, with supplemental rat chow provided after each daily session to maintain the target weight. The colony room was maintained on a 14:10-h light-dark cycle and rats were monitored and cared for in compliance with the Association for Assessment and Accreditation of Laboratory Animal Care guidelines and the Dartmouth College Institutional Animal Care and Use Committee.

2.2. Behavioral apparatus

Behavioral procedures took place in standard conditioning chambers $(24 \times 30.5 \times 29 \text{ cm}; \text{Med Associates})$ constructed of aluminum front and back walls, clear acrylic sides and top, and grid floors. Each chamber was outfitted with a dimly illuminated food cup recessed in the center of the front wall, a 2.8-W white panel light located 5 cm above the opening to the food cup, and a speaker located 15 cm above and to the right of the food cup, used to present the 1500 Hz, 78 dB auditory stimulus. Each chamber was enclosed in a sound-attenuating cubicle $(62 \times 56 \times 56 \text{ cm})$ with an exhaust fan to provide airflow and background noise (~68 dB) and a red house-light (mounted on the ceiling) to provide background illumination. Delivery of two 45-mg grain-based food pellets (Bio-serv) served as the unconditioned stimulus. Each chamber was equipped with a pair of infrared photocells located across the entrance to the food cup to monitor entries into the cup and connected to a PCclone computer. The cubicles also contained surveillance cameras used to monitor the rats during behavioral training.

2.3. Behavioral procedure

At the start of every training session rats were weighed and moved in plastic transporters from the colony room to the conditioning chambers. Rats were first trained to eat from the food cup during a single 64 min session in which 45 mg food pellets were randomly delivered 16 times (average intertrial interval (ITI) of 4 min; ranging from 2.5 to 5.5 min). Subsequently, behavioral training in the negative occasion setting paradigm consisted of daily 68-min sessions with four reinforced and 12 non-reinforced trials. During reinforced trials the tone was presented for 5 s and followed immediately by the delivery of two food pellets. Rats received a total of ~0.36 g of food pellet reinforcer per session. On non-reinforced trials, the panel light was presented for 5 s, followed by a 5-s empty period, and then a 5-s presentation of the tone, after which no food was delivered. The two trial types occurred randomly during each

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