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Hedonic sensitivity in adolescent and adult rats: Taste reactivity and voluntary sucrose consumption

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ABSTRACT

Adolescents have been hypothesized to exhibit an age-related partial anhedonia that may lead them to seek out natural and drug rewards to compensate for this attenuated hedonic sensitivity. In the present series of experiments, taste reactivity (TR) and 2 bottle choice tests were used to assess hedonic reactions to sucrose. In Exp 1, total positive taste responses to 10% sucrose solution were significantly higher in adolescent than adult rats during the infusion period. In Exp 2, adolescent animals exhibited a concentration-effect shift that was consistent with a greater hedonic sensitivity compared to adults. Conversely, adolescents exhibited fewer negative responses to quinine. Using a shortened infusion period, adolescents in Exp 3 exhibited a trend for greater positive TR than adults in response to 10 and 34% sucrose. Consistent with the TR results of Exp 1–3, adolescents consumed significantly more sucrose solution (ml/kg) than adults, although no significant age difference in sucrose preference rates emerged.

The results of the current series of experiments do not support the hypothesis that adolescents exhibit an age-related, partial anhedonia, with adolescent animals, under a number of test circumstances showing greater positive taste reactivity and reduced negative responding.

1. Introduction

Adolescence is a developmental period marked by both neural and behavioral changes. Adolescent-associated behavioral changes are surprisingly well conserved across species and include elevations in social interactions with peers, novelty seeking, and risk taking (Csikszentmihalyi et al., 1977; Primus and Kellogg, 1989; Pellis and Pellis, 1990; Pellis and Pellis, 1997; Trimpop et al., 1998). Adolescents exhibit both hyperdipsia and hyperphagia, with humans and rats exhibiting higher caloric intake relative to their body weight than any other time in the life span (Post and Kemper, 1993; Nance, 1983). In humans this developmental period is also the time during which drug use is typically initiated. The physiological mechanisms responsible for increases in consumption of natural reinforcers during adolescence might contribute to the propensity of adolescents to consume drug reinforcers as well, given that natural and drug reinforcer are thought to share common reward pathways (Di Chiara, 1999; Berridge and Robinson, 1998; Wise, 1989).

It is currently unclear if this adolescent-typical increase in the seeking and consumption of appetitive stimuli is related to increases or decreases in the incentive value attributed to rewarding stimuli. On one hand, adolescents might avidly seek out natural and drug rewards in an attempt to compensate for an attenuated sensitivity to hedonic stimuli (Spear, 2000). Some of the limited human data available supporting this hypothesis include the observation that human adolescents demonstrate less ventral striatal activation in response to reward cues and report a greater incidence of depressed mood compared to adults (Bjork et al., 2004; Petersen et al., 1993). Conversely, adolescent-typical increases in consummatory behaviors may be driven by increases in the hedonic value assigned to reinforcers (Ernst et al., 2006; Chambers et al., 2003). Supporting this notion, other functional magnetic resonance imaging (fMRI) work has shown adolescents to exhibit an exaggerated magnitude of activation in the nucleus accumbens (NAc) in response to visual stimuli associated with a monetary reward when compared with younger and older subjects (Galvan et al., 2006).

Traditionally, the consumption of appetitive stimuli has been used to index the hedonic value attributed to those stimuli, effects thought to be mediated through changes in mesolimbic dopamine function/sensitivity (Wise et al., 1978; Wise and Bozarth, 1982). The preference for mildly sweet sucrose solution (~1.0%) is one of the most extensively used behavioral measures of anhedonia, with anhedonia interpreted as a reduction in choice of the sucrose solution over water in two-bottle choice test (Willner et al., 1987).

More recently, Robinson and Berridge have proposed an incentive salience theory of reward that separates reward conceptually and functionally into two component psychological processes mediated by different neural mechanisms: "wanting" and "liking" (Berridge, 1996; Berridge and Robinson, 1998). Wanting refers to the motivational or

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craving element of reward, and is a reward component found to sensitize following repeated exposure to drugs of abuse. Liking, on the other hand refers to the hedonic or pleasure component of reward and is not thought to sensitize. Within this conceptual framework, dopamine is thought to be involved in assigning incentive motivational value to rewarding stimuli (i.e. wanting) (Berridge, 1996; Berridge and Robinson, 1998). Hedonic "liking" properties, on the other hand, are thought to be mediated by a hierarchical system involving opioid, cannabinoid, and to some extent GABA systems (Peciña et al., 2006).

One model that has been extensively employed to examine hedonic sensitivity to appetitive tastants is the taste reactivity (TR) test, which is thought to be a direct measure of the hedonic value attributed to stimuli. In the TR test, a solution is presented to the subject and the oral facial reactions to that tastant are proposed to reflect the palatability of the solutions. Palatable solutions, such as sucrose, elicit appetitive TR behaviors such as rhythmic and lateral tongue protrusions, whereas aversive solutions, such as quinine, elicit aversive TR behaviors (including gapes) (see methods for more details). Both appetitive and aversive taste reactions are highly conserved, with similar oral facial responses to appetitive and aversive stimuli seen in human infants as in mature primates and rodents (Steiner et al., 2001). Across-species differences emerging primarily in the timing at which particular TR behaviors are emitted, with humans and gorillas expressing behaviors much slower than rodents (Steiner et al., 2001).

The current series of experiments used the TR test, as developed for rats by Grill and Norgren (1978), to assess developmental differences in hedonic sensitivity to appetitive and aversive stimuli in adolescent and adult rats, with TR assessed both during and immediately following the infusion period. Developmental differences in voluntary consumption of an appetitive solution were also assessed using a two-bottle choice test.

2. General methods

2.1. Subjects

Male Sprague–Dawley rats (Taconic Farms) bred in our colony were used. All animals were maintained in a temperature-controlled (22 °C) vivarium on a 14-h/10-h light cycle (lights on 0700) with ad libitum access to food (Purina Rat Chow, Lowell, MA) and water. On postnatal day 1 (P1), litters were culled to 7–10 pups. Animals were weaned on P21 and pair-housed with same-sex littermates until the time of the experimental procedures. No more than one animal from a given litter was used in any experimental group. At all times, rats used in these experiments were maintained and treated in accordance with guidelines for animal care established by the National Institutes of Health (1986).

2.2. Taste reactivity

2.2.1. Surgery

At the onset of each experiment, beginning on P 28–29 for adolescents and P 69–70 for adults, animals were anesthetized with isoflurane prior to the implantation of an oral cannula. Each cannula consisted of polyethylene tubing (PE-50) with a heat-flanged tip. A guide needle was used to insert the cannula through the cheek at the level of the 1st maxillary molar. Another guide needle was then used to tunnel the cannula subcutaneously to the dorsal skull surface where the cannula was secured with surgical glue. Following surgery, animals were singly housed to avoid across-animal damage to the cannulas.

2.2.2. Apparatus

Testing was conducted in a Plexiglas cylinder (adolescent — height = 16.0 in, diameter = 8.0 in; adult — height = 16.0 in, diameter = 10.0 in). A mirror was placed at a 45° angle below the Plexiglas floor, providing a ventral view of the rat for video recording. Solutions were infused into animals' cannulas via connection to a calibrated syringe pump controlling rate, duration and volume of the infusion.

2.2.3. Behavioral measures

All taste reactivity behaviors during the infusion period and 30 s post-infusion were scored frame-by-frame. Scoring criteria for each behavior, and rationale for the classification of components into hedonic or aversive categories were based on Berridge and Grill (1983). Positive hedonic reactions included: (a) rhythmic tongue protrusions — the anterior tip of the tongue visibly emerges directly on the midline, covering the upper incisors and is then retracted — movements repeated at an approximate rate of 8.8 cycles/s; (b) lateral tongue protrusions — the tongue protrudes (nonrhythmic) from the side of the mouth followed by a forward extension, generally occurring on alternating sides of the mouth or in one single protrusion; (c) paw licks — any instance of the rat licking its paws, with the exception of paw licking occurring within a grooming sequence; (d) lateral tongue movements — the tongue emerges on the side of the mouth, extending the upper lip/cheek laterally without protruding from the mouth. Aversive reaction patterns included: (a) gapes — the mandible lowers, while the corners of the mouth contract, forming a triangle shaped mouth opening that is held for approximately 83 ms; (b) chin rubbing — the animal rubs its chin on the floor while projecting the body forward; (c) face washing — single or several wipes of the face with the forepaws; (d) head shake — a bout (typically with a duration of <1 s) of rapid (>60 cycles/s) side to side movements of the head; (e) forelimb flails — a brief bout (<1 s) of shaking of the forelimbs at a rate greater than 60 cycles/s; (f) paw treads — planting of the forelimbs on the floor and alternating forceful strokes forward and back. Unless otherwise noted, scoring criterion used was based on those of Berridge (Berridge, 1996, 2000). Discrete actions such as lateral tongue protrusions, gapes, and chin rubbing as well as bouts of head shaking, forelimb flails and paw treads were scored as a single count for each occurrence. Behaviors that typically persist for >1 s were recorded as follows: paw licks, rhythmic mouth movements, grooming and face washing were recorded in 5-s bins (any occurrence of these behaviors within each 5-s time bin was scored as a single count). Rhythmic tongue protrusions were scored similarly, except 2-s bins were used. The final total positive hedonic score was composed of the sum of all rhythmic tongue protrusions, lateral tongue protrusions, paw licking, and lateral tongue movements, whereas total negative hedonic scores were composed of the sum of all gapes, chin rubs, face washing, head shakes, forelimb flails and paw treads.

The experimenter was present during the test sessions to videotape, using a digital camera (JVS, HDD), a close-up view of the oral region during the infusion period and for 30 sec thereafter. An investigator blind to both solution type and age later analyzed the sessions frame-by-frame.

2.2.4. Experiment 1

Following surgery (Experiment [Exp] Day 0), all animals were given 3 days to recover, after which the taste reactivity test was conducted (Exp Day 3—P 33–34 for adolescents ($n = 5$); P 72–73 for adults ($n = 6$)). On test day, following a 15 min habituation to the chamber, each animal received a 45 s continuous infusion of 10% sucrose solution at a rate of 1 ml/min. Total number of positive and negative responses during the 45 s infusion period and for 30 s thereafter were recorded. Number of negative responses to this appetitive tastant was negligible at both ages and assessment periods. Consequently, only positive response data were analyzed.

Total positive taste responses (i.e., the sum of paw licks, rhythmic tongue protrusions, lateral tongue protrusions and lateral tongue movements) to the 10% sucrose solution were significantly higher in adolescent than adult rats during the 45-s infusion period ($t = 2.6$; df = 9; $p < 0.028$) (see Fig. 1).