



## SHORT REPORT

### Adolescent mice, unlike adults, consume more alcohol in the presence of peers than alone

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#### Abstract

*One hallmark of adolescent risk-taking is that it typically occurs when adolescents are with peers. It has been hypothesized that the presence of peers primes a reward-sensitive motivational state that overwhelms adolescents' immature capacity for inhibitory control. We examined this hypothesis using a rodent model. A sample of mice were raised in same-sex triads and were tested for alcohol consumption either as juveniles or as adults, with half in each age group tested alone and half tested with their cagemates. The presence of 'peers' increased alcohol consumption among adolescent mice, but not adults. The peer effect on human adolescent reward-seeking may reflect a hard-wired, evolutionarily conserved process through which the presence of agemates increases individuals' sensitivity to potential rewards in their immediate environment.*

#### Research highlights

Risky and reckless behavior is the leading cause of morbidity and mortality in adolescence. Importantly, experimental and epidemiological research has indicated that adolescents, but not adults, take more risks in the presence of peers than when alone. It has been hypothesized that this phenomenon is due to the impact of peers on reward processing in adolescence and not merely the result of explicit or implicit peer pressure. This paper provides evidence consistent with this proposition, by demonstrating that the peer effect on adolescent reward processing is seen in mice.

#### Introduction

As a rule, teenagers engage in more risky behavior than do children or adults. Adolescents are more likely than older or younger individuals to experiment with alcohol and illicit drugs, have unprotected sex, commit crimes, engage in deliberate self-injurious behavior, drown accidentally,

and be involved in fatal or serious automobile crashes (Centers for Disease Control and Prevention, 2012; Steinberg, 2008). Many experts agree that these preventable behaviors present the greatest threat to the well-being of young people in industrialized societies, and unsurprisingly, considerable resources have been invested in research seeking to explain this developmental pattern, and in efforts – largely unsuccessful – to intervene.

A vital clue to understanding heightened adolescent risk behavior comes from a consideration of the conditions under which adolescent risk-taking is most likely to take place. One hallmark of adolescent risk-taking is that it is much more likely than that of adults to occur in the presence of peers, as evidenced in studies of reckless driving, substance use, and crime (Albert & Steinberg, 2011). It is not difficult to produce a list of intuitive hypotheses for why adolescent drinking and other forms of risk-taking are more likely to take place in the presence of peers, among them, that adolescents spend more time in social settings, they are coerced by the things their friends say, they want to impress their friends with acts of bravado, they are distracted by their friends

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and thus fail to be cognizant of the potential consequences of their actions, and they do things they would not otherwise do in order to avoid social rejection or to gain social status.

Peer influences on adolescent alcohol and drug use are especially strong (Lundborg, 2006). Substance-using adolescents seek substance-using peers, and substance-using peers encourage even more drug use among their friends (Chassin, Hussong & Beltran, 2009). Unlike adults, adolescents rarely drink alone; even in Italy, a country in which many adolescents drink in the presence of family members, adolescents are seven times more likely to drink for the first time with friends than with family and almost never likely to drink for the first time by themselves (Bonino, Cattelino & Ciariano, 2003).

In several previous articles (e.g. Albert & Steinberg, 2011; Albert, Chein & Steinberg, 2013), we have posited a novel explanation for the peer effect on adolescent risk-taking that is grounded in developmental neuroscience. Our view derives from a dual systems model of adolescent risk-taking (Steinberg, 2010), in which adolescents' relatively greater propensity toward risky behavior is seen as reflecting the interaction between two interconnected brain systems: an incentive processing system, which biases decision-making based on the valuation and prediction of potential rewards and punishments; and a cognitive control system, which supports goal-directed decision-making by keeping impulses in check and by providing the mental machinery needed for deliberation regarding alternative choices (Blakemore & Robbins, 2012; Casey, Getz & Galvan, 2008; Luna, Padmanabhan & O'Hearn, 2010; Somerville, Jones & Casey, 2010; Steinberg, 2008; Van Leijenhorst, Moor, de Macks, Rombouts, Westenberg & Crone, 2010a). These systems contribute to decision-making in an interactive fashion, with impulsive or risky choices often coinciding with the increased engagement of incentive processing regions and the decreased involvement of cognitive control activity (Ernst, Nelson, McClure, Monk, Munson, Eshel, Zarah, Leibenluft, Zametkin, Towbin, Blair, Charney & Pine, 2004; Hare, Camerer & Rangel, 2009; Kuhn & Knutson, 2005; Matthews, Simmons, Lane & Paulus, 2004; McClure, Laibson, Loewenstein & Cohen, 2004). Importantly, the incentive processing system evinces dramatic remodeling in early adolescence (Laviola, Pascucci & Pieretti, 2001; Spear, 2009; Luciana, Wahlstrom, Porter & Collins, 2012; Urošević, Collins, Muetzel, Lim & Luciana, 2012), resulting in heightened sensitivity to anticipated rewards (Ernst, Nelson, Jazbec, McClure, Monk, Leibenluft, Blair & Pine, 2005; Ernst, Romeo & Andersen, 2009; Galvan, Hare, Parra, Penn, Voss, Glover & Casey, 2006; Geier, Terwilliger, Teslovich, Velanova & Luna, 2010; Van Leijenhorst, Zanolie, Van

Meel, Westenberg, Rombouts & Crone, 2010b), which may bias adolescents' decision-making toward risky choices (Chein, Albert, Brien, Uckert & Steinberg, 2011; Galvan, Hare, Voss, Glover & Casey, 2007).

Given the elevated reward value of peer interactions in adolescence (Burnett, Sebastian, Kadosh & Blakemore 2011; Crone & Dahl, 2012), the presence of peers may further sensitize the incentive processing system to respond to cues signaling the potential rewards of risky behavior (Albert & Steinberg, 2011; Albert *et al.*, 2013). That is, the activation of reward circuitry in the presence of peers may "prime" a reward-sensitive motivational state that overwhelms the adolescent's immature capacity for inhibitory control. From an evolutionary perspective, it makes sense that during a phase of development in which reproduction is a primary pursuit, individuals would be drawn to peers and especially sensitive to rewarding stimuli in their presence (Ellis, Del Giudice, Dishion, Figueredo, Gray, Griskevicius, Hawley, Jacobs, James, Volk & Wilson, 2012). Consistent with this interpretation, Chein *et al.* (2011) found that adolescents' heightened risk-taking in the presence of peers was associated with relatively stronger activation of brain regions associated with the incentive processing system (ventral striatum and orbitofrontal cortex). In contrast, adults, whose degree of risk-taking was unaffected by the presence of peers, displayed the same pattern of brain activity whether alone or observed by their friends. Along similar lines, in a study of temporal discounting in the presence or absence of peers, O'Brien, Albert, Chein and Steinberg (2011) found that adolescents tested in the presence of peers evinced a significantly stronger preference for immediate rewards than did those tested alone.

To date, studies of the adolescent peer effect in humans have relied on laboratory tasks meant to assess reward-seeking and risk-taking (Gardner & Steinberg, 2005). Although performance on these tasks is correlated with real-world behavior, it is not possible to conduct experimental studies in human adolescents on genuinely harmful behavior, such as alcohol or drug use. However, because all mammalian species experience a juvenile period that is comparable to human adolescence, it is possible to use animal models to examine this issue. The present study develops a rodent model to test the proposition that the presence of peers heightens reward sensitivity during adolescence, but not adulthood.

Juvenile members of other species are similar to their human counterparts in several respects that are relevant to the study of peer influences on reward sensitivity. First, the remodeling of the incentive processing system at adolescence observed among humans has been well-documented in rodents, and, as is the case in humans,

adolescents of other species are relatively more sensitive than are younger or older animals to rewarding stimuli (Spear, 2009). Second, the especially strong reward value during adolescence of peers, in particular, has been highly conserved across species (Calcagnetti & Schechter, 1992; Douglas, Varlinskaya & Spear, 2004; Panskepp & Lahvis, 2007; Trezza, Campolagna & Vanderschuren, 2011). Finally, there is evidence from rodent studies that, during adolescence, social stimuli may amplify the rewarding effects of drugs (Thiel, Sanabria & Neisewander, 2009) but attenuate their aversive effects (Vetter-O'Hagen, Varlinskaya & Spear, 2009). Although rodent models cannot be used to examine all aspects of human risk-taking, they are well suited to study sensitivity to specific stimuli that are known to be rewarding across mammalian species, such as alcohol.

## Method

In the present study, we test the hypothesis that adolescent mice will consume more alcohol in the presence of peers than when alone, and that this peer effect will not be found in adults. The mouse model we developed to assess the impact of peer presence on alcohol consumption used juvenile and adult C57BL/6J mice. This strain was chosen because both male and female C57BL/6J mice are known to self-administer ethanol (Belknap, Crabbe & Young, 1993; Yoneyama, Crabbe, Ford, Murillo & Finn, 2008).

The sample included 86 animals, half male and half female. The mice were housed in same-sex triads from weaning at postnatal day 21 to testing, and were tested for alcohol consumption in a novel environment, either between postnatal day 28 and 30 (the juvenile period in mice) or between postnatal day 84 and 86 (adulthood). As in the human studies that motivated the current experiment, exposure to peers was experimentally manipulated using random assignment, with half of the mice in each age group tested alone (individual condition;  $N_s = 11$  male juveniles, 10 female juveniles, 9 male adults, and 9 female adults), and half tested in triads (peer condition;  $N_s = 9$  male juveniles, 12 female juveniles, 11 male adults, and 12 female adults). The video from one group of male juvenile mice tested in the social condition was unscorable.

Prior to testing, the fur on the back of each mouse was lightened with a peroxide solution to allow identification of each mouse in a triad. Mice were given free access to a 5% v/v ethanol solution for 45 minutes. The ethanol solution was administered through four sipper tubes arranged around the perimeter of a Plexiglas chamber

(20 × 30 × 20 cm). The chamber had two identical compartments that were separated by an arched doorway with two sipper tubes available in each compartment. To test the effect of peer presence on voluntary ethanol consumption, mice were either placed in the chamber alone or with their two cagemates. Because the mice tested in triads were in cages with four available sipper tubes, individuals did not have to compete for access to ethanol.

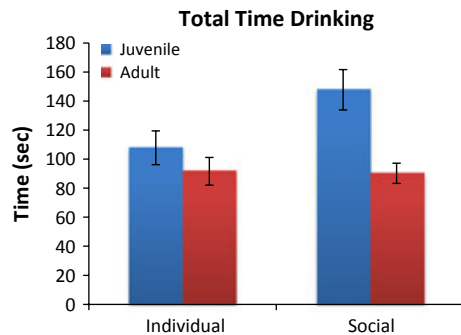
Each session was video recorded for 45 minutes. Video tapes were scored for each mouse's time spent drinking (in seconds), number of visits to any of the four drinking tubes, and, as a measure of basic exploratory behavior, number of transitions through the arched doorway (crosses). For the mice tested with peers, all of the measures were scored for each mouse independently. Duration of drinking bouts was calculated by dividing each individual animal's total time drinking by the number of visits that animal made to a drinking tube.

## Results

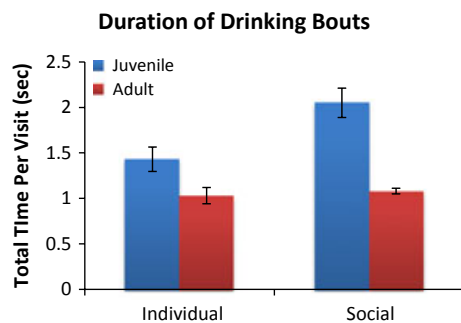
### *Impact of peers on juveniles' and adults' alcohol consumption*

#### Time spent drinking

An omnibus analysis of variance (ANOVA) examining the impact of age, sex, and test condition on individuals' time spent drinking was significant [ $F(7, 85) = 4.05$ ,  $p = .001$ ;  $\eta_p^2 = .27$ ]. Time spent drinking differed across ages [ $F(1, 85) = 13.62$ ,  $p = .000$ ;  $\eta_p^2 = .15$ ], with juvenile mice ( $M = 127.28$ ,  $SD = 61.87$ ) spending more time drinking than adult mice ( $M = 90.86$ ,  $SD = 37.48$ ). Neither the main effect for test condition nor the main effect of sex on time spent drinking was significant ( $p > .05$ ). Importantly, and as hypothesized, the interaction between age and test condition was significant [ $F(1, 85) = 4.35$ ,  $p = .040$ ;  $\eta_p^2 = .05$ ]. Juvenile mice tested with their peers ( $M = 147.71$ ,  $SD = 63.74$ ) spent significantly more time drinking than individually tested juvenile mice ( $M = 107.77$ ,  $SD = 54.50$ ), whereas adult mice in the peer ( $M = 90.22$ ,  $SD = 33.38$ ) and individual ( $M = 91.60$ ,  $SD = 42.60$ ) conditions did not differ (see Figure 1). There was also an interaction between test condition and sex on time spent drinking [ $F(1, 85) = 3.91$ ,  $p = .052$ ;  $\eta_p^2 = .05$ ], with the peer manipulation having a stronger impact on males than females, but the three-way interaction among age, sex, and test condition was not significant ( $p > .05$ ).



**Figure 1** Juvenile mice, but not adults, spend more time drinking alcohol in the presence of peers than when alone.



**Figure 2** Juvenile mice, but not adults, voluntarily spend more time consuming alcohol during each period of consumption when tested with their cage mates.

#### Duration of drinking bouts

The omnibus ANOVA for duration of drinking bouts also was significant [ $F(7, 85) = 8.54, p = .000; \eta_p^2 = .43$ ] (Figure 2). There was a main effect of age [ $F(1, 85) = 37.53, p = .000; \eta_p^2 = .33$ ], wherein juvenile mice ( $M = 1.75, SD = .75$ ) had longer drinking bouts than adult mice ( $M = 1.05, SD = .29$ ). Test condition also had a significant impact on duration of drinking bouts [ $F(1, 85) = 7.86, p = .006; \eta_p^2 = .09$ ] with mice tested in the social condition ( $M = 1.54, SD = .71$ ) averaging longer drinking bouts than mice in the individual condition ( $M = 1.24, SD = .57$ ). There was a main effect for sex [ $F(1, 85) = 4.19, p = .044; \eta_p^2 = .05$ ], wherein females ( $M = 1.53, SD = .70$ ) had longer drinking bouts than males ( $M = 1.25, SD = .59$ ). As with time spent drinking, the interaction between age and test condition was significant [ $F(1, 85) = 6.40, p = .013; \eta_p^2 = .08$ ] (see Figure 2). Juvenile mice tested in the social condition ( $M = 2.05, SD = .74$ ) averaged longer duration drinking bouts than juvenile mice tested individually ( $M = 1.43, SD = .63$ ), whereas adult mice tested in the social ( $M = 1.08, SD = .15$ ) and individual ( $M = 1.03, SD = .40$ ) conditions had shorter and comparably-lengthed drinking bouts. No other interactions were significant ( $p > .05$ ).

#### Number of drinks

Number of drinks was counted when the mouse began drinking from the sipper tube and then moved away or ceased drinking. The omnibus ANOVA for number of drinks was not significant [ $F(7, 85) = .73, p = .647; \eta_p^2 = .06$ ].

#### Peer influences on juveniles' and adults' locomotor activity

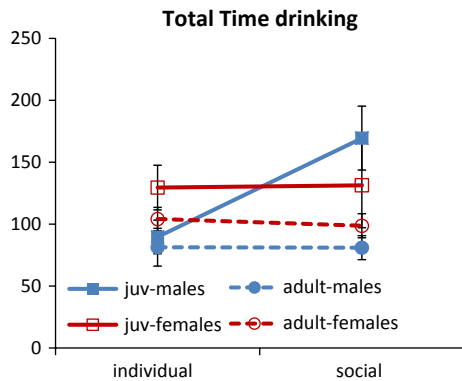
Because the marked difference in average time spent drinking and duration of drinking bouts between juvenile mice tested with their peers versus those tested individually might be due to a higher level of overall activity in the peer condition, we conducted an omnibus ANOVA for locomotor activity level (i.e. crosses between compartments), which was significant [ $F(7, 85) = 3.65, p = .002; \eta_p^2 = .25$ ], with main effects found for age [ $F(1, 85) = 15.60, p = .000; \eta_p^2 = .17$ ] and sex [ $F(1, 85) = 5.65, p = .020; \eta_p^2 = .07$ ]; juvenile mice ( $M = 138.81, SD = 33.71$ ) were less active than adult mice ( $M = 169.97, SD = 38.41$ ) and male mice ( $M = 145.14, SD = 34.55$ ) were less active than female mice ( $M = 163.55, SD = 41.71$ ). However, and importantly, there was no effect of test condition on activity level ( $p > .05$ ) and no significant interactions ( $p > .05$ ). Differences in overall activity could also have impacted the frequency of visits to a drinking spout, but, as noted earlier, there were no differences across any of the groups on this variable.

#### Preliminary evidence for sex differences in the peer effect

The significant interaction between sex and test condition on time spent drinking (but not on duration of drinking bouts) raises the question of whether the presence of peers differentially affects male and female juvenile mice; although the three-way interaction among age, sex, and condition in the prediction of time spent drinking did not reach significance, tests of three-way interactions are often underpowered, and inspection of the results when graphed (see Figure 3) prompted us to examine this issue further. Accordingly, we conducted two-way (age by condition) ANOVAs to analyze the data for each sex separately.

Analysis of the males' total drinking time demonstrated the same pattern as for the sample as a whole [omnibus ANOVA:  $F(3, 42) = 6.29, p = .001; \eta_p^2 = .33$ ]. Time spent drinking differed between male juvenile and adult mice [ $F(1, 42) = 8.97, p = .005; \eta_p^2 = .19$ ], with juvenile males ( $M = 123.86, SD = 72.46$ ) spending more time drinking than adult males ( $M = 81.18, SD = 41.32$ ).





**Figure 3** Total time spent drinking as a function of age, sex, and presence of peers.

In addition, there was a main effect of test condition [ $F(1, 42) = 6.05, p = .018; \eta_p = .13$ ], with male mice tested with peers ( $M = 120.80, SD = 71.42$ ) spending significantly more time drinking than male mice tested individually ( $M = 85.70, SD = 47.84$ ). And, as in the sample as a whole, the interaction between age and test condition was significant [ $F(1, 42) = 6.16, p = .018; \eta_p = .14$ ]. Juvenile males tested in the peer condition ( $M = 169.44, SD = 77.36$ ) spent significantly more time drinking than individually tested juvenile males ( $M = 89.67, SD = 47.11$ ), whereas adult males tested in the peer condition ( $M = 81.00, SD = 32.12$ ) and individually tested adult males ( $M = 81.36, SD = 50.54$ ) did not differ. In contrast, analysis of the females' drinking time did not yield a significant omnibus ANOVA [ $F(3, 42) = 1.68, p = .188; \eta_p = .11$ ], and the only significant contrast effect was in the difference between juvenile females ( $M = 130.55, SD = 51.29$ ) and adult females ( $M = 101.00, SD = 30.77$ ) [ $t$ -test:  $t(41) = 2.28, p = .017$ ]. A similar pattern of results was found for duration of drinking bouts (stronger evidence of peer effect on juveniles but not adults among males than females) but not on number of drinks.

## Discussion

In studying the impact of peers in an animal model we hoped to determine whether the peer effect on reward sensitivity is an evolutionarily conserved characteristic of adolescent behavior, in order to gain further understanding of the specific biological processes that may underlie vulnerability to peer influences on adolescent risk-taking. Like human adolescents, juvenile mice show evidence of increased social orientation during adolescence (Spear, 2009). But unlike human adolescents, mice almost certainly do not have the capacity to mentalize about the beliefs or preferences of conspecifics, or to

tailor their actions in order to increase the likelihood of later social rewards (e.g. group affiliation). Consistent with past studies in humans, which have shown that the presence of peers increases adolescents' risk-taking and reward-seeking, and that drinking during adolescence is mainly a group activity, in the present study, juvenile mice, but not adult mice, consumed more alcohol in the presence of peers than when alone. This suggests that adolescent drinking in the context of the peer group may not be driven solely by explicit peer pressure or perceived peer expectations.

The fact that the presence of peers influenced juvenile mice's alcohol consumption as measured by the total time spent drinking as well as the average duration of drinking bouts, but not their locomotor activity, argues against the notion that the presence of peers affects juvenile mice's drinking through its impact on novelty-seeking or exploratory behavior more generally. The results also cannot be explained in terms of social transmission (e.g. nose to nose touching that in the peer condition that might have signaled the availability of alcohol), since this explanation would have predicted a higher frequency of visits to drinking spouts in the peer condition than in the individual condition, which was not the case. While we cannot rule out other possible accounts of the peer effect observed here (e.g. that the presence of peers induced stress or arousal, which led to greater alcohol consumption), the absence of an effect of peer presence on activity level or exploratory behavior more generally makes these explanations less tenable (nor were any stress responses seen). Moreover, it is important to note that the peers with whom the mice were tested were known conspecifics who had been raised together. Future studies of this phenomenon might compare the impact of unfamiliar versus familiar agemates.

Instead, we believe that the results are consistent with the idea that the presence of peers increases adolescents' reward-seeking. Specifically, the heightened reward value of peers during adolescence, a phenomenon that has been demonstrated in previous studies of humans (Burnett *et al.*, 2011; Crone & Dahl, 2012) as well as rodents (Calcagnetti & Schecter, 1992; Douglas *et al.*, 2004; Panskepp & Lahvis, 2007; Spear, 2009; Trezza *et al.*, 2011), appears to motivate individuals to seek other rewarding experiences when in the company of agemates. Because we did not compare the effect of peer presence on alcohol consumption to its impact on other appetitive behaviors, we do not know whether the observed peer effect is specific to alcohol use or generalizable to other forms of reward-seeking. This is an important question for future research.

Although prior studies of human adolescents showed no indication that the peer effect on risk-taking or reward-seeking is sex specific, in the present study the impact of peers on adolescent alcohol consumption was more vividly seen among males than females. Because the three-way interaction among sex, age, and social condition did not reach statistical significance, we cannot say with certainty that the peer effect on adolescent reward-seeking is stronger among males than females. However, when we split the sample by gender, we detected a significant peer effect on alcohol consumption within the male, but not female, subsample. One possible explanation for the weaker peer effect on drinking among female mice is that the mean level of ethanol consumption among female juveniles is so high in general that there is little room for peers to elevate it further; other studies have found that female mice consume more alcohol than male mice (e.g. Middaugh, Kelley, Brandy & McGroarty, 1999; Rhodes, Ford, Yu, Brown, Finn, Garland & Crabbe, 2007). Another possibility is that in social settings the reward-seeking behavior of female adolescents may be relatively more influenced by extrinsic factors, such as peer approval, than is the case among males, whose behavior may be relatively more influenced by intrinsic factors. In a mouse model, extrinsic factors such as peer approval are absent, resulting in a reduced peer effect on females. Future research might explore this issue by using a behavioral outcome whose baseline level is comparable among male and female juveniles when they are tested alone.

As we noted earlier, one characteristic of adolescent risk-taking is that it typically occurs when adolescents are with their peers. The present investigation sheds light on one potential biological mechanism that may underlie this phenomenon. Although it is no doubt the case that a certain amount of risk-taking during this stage is in response to explicit pressures that teenagers place on each other or the result of adolescents' desire to gain the admiration or acceptance of their peers, it is clear that these conscious processes cannot account entirely for the fact that adolescents take more risks when they are with their friends than when they are alone. Rather, the impact of peers on adolescent drinking and other forms of risk-taking may be in part the result of a hard-wired, evolutionarily conserved process through which the presence of agemates increases adolescents' sensitivity to potential rewards in their immediate environment. Although the adaptive value of this peer effect on adolescent reward sensitivity is that it likely encourages mating with same-aged conspecifics during a period of relatively higher fecundity, it may also incline adolescents to engage in other risky activities when in the presence of their friends. The present findings should open the door

to further research into the neural mechanisms of this phenomenon, and profitably inform preventive interventions designed to decrease teenagers' dangerous and health-compromising behavior.

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