Published in final edited form as:

Alcohol Clin Exp Res. 2011 October ; 35(10): 1884–1890. doi:10.1111/j.1530-0277.2011.01533.x.

Alcohol intake in prairie voles is influenced by the drinking level of a peer

Allison M. J. Anacker, B.S.¹, Jennifer M. Loftis, Ph.D.^{1,2,3}, and Andrey E. Ryabinin, Ph.D.¹

¹ Department of Behavioral Neuroscience, Oregon Health and Science University

² Research and Development Service, Portland Veterans Affairs Medical Center, Portland, OR

³ Department of Psychiatry, Oregon Health & Science University, Portland, OR

Abstract

Background—Peer interactions can have important effects on alcohol drinking levels, in some cases increasing use, and in other cases preventing it. In a previous study we have established the prairie vole as a model animal for the effects of social relationships on alcohol intake, and have observed a correlation of alcohol intake between individual voles housed together as pairs. Here we investigated this correlated drinking behavior, hypothesizing that one animal alters its alcohol intake to match the drinking of its partner.

Methods—Adult prairie voles were tested for baseline drinking levels with continuous access to 10% alcohol and water for four days. In Experiment 1, high alcohol drinkers (>9g/kg/day) were paired with low alcohol drinkers (<5g/kg/day) of the same sex on either side of a mesh divider for four days with continuous access to the same two-bottle choice test. In Experiment 2, high drinkers were paired with high drinkers and low drinkers paired with low drinkers. In both experiments, animals were again separated following pairing and drinking was retested in isolation. In Experiment 3, alcohol-naïve animals were tested for saccharin consumption (0.05%) first in isolation and then in high saccharin drinkers paired with low saccharin drinkers, and then in another isolation period.

Results—In Experiment 1, high drinkers paired with low drinkers significantly decreased their alcohol intake and preference from baseline drinking in isolation, and drinking levels remained significantly lower during isolation following pairing. Interestingly, there was variability between pairs in whether the high drinker decreased or the low drinker increased intake. In Experiment 2, high drinkers paired with high drinkers did not significantly change their intake level or preference, nor did low drinkers paired with low drinkers, and no changes occurred during the subsequent isolation. In Experiment 3, there was no change in saccharin intake or preference when high drinkers were paired with high drinkers or low paired with low, or in the subsequent isolation.

Conclusions—Alcohol drinking of prairie voles can be altered under social conditions, such that one animal changes its alcohol intake to more closely match the intake of the other animal, helping to explain previous findings of correlated alcohol drinking. The effect does not extend to saccharin, a naturally rewarding sweet substance. This behavior can be used to model the peer pressure that can often affect alcohol intake in humans.

Keywords

prairie voles; social behavior; alcohol self-administration; peer influence; *Microtus ochrogaster*

Introduction

Social influences are an important factor in the onset and development of alcohol (ethanol) drinking patterns. An older sibling's drinking is a significant predictor of an early adolescent's drinking (Needle et al., 1986), and the number of alcohol-using friends is the greatest predictor of this behavior (Windle et al., 2008). While selection of friends is often a factor for substance abuse, socialization within a peer group and adoption of norms (real or perceived) are also important influential factors in alcohol use, even more than in use of other drugs (Bot et al., 2005; Kiuru et al., 2010; Knecht et al., 2011; Park et al., 2009). Two of the greatest factors in predicting heavy drinking in social circumstances among adolescents and young adults are the alcohol-related norms of an individual's family and friends, and modeling behavior after observed drinking of family or peers (Oostveen et al., 1996).

Modeling the effects of social influences on alcohol intake in laboratory animals is a challenge, due to species differences in the nature and complexities of relationships. We have previously reviewed this literature (Anacker and Ryabinin, 2010) and found that while mice and rats do exhibit effects of social housing on alcohol intake (e.g., Advani et al., 2007; Schenk et al., 1990; Thorsell et al., 2005; Yanai and Ginsburg, 1976), there is no evidence of effects on changes in alcohol consumption due to influences from a specific animal.

To address this issue, we have previously established a novel animal model to examine the effects of social behaviors on alcohol drinking, using the prairie vole (*Microtus ochrogaster*). Prairie voles, like as few as three percent of mammalian species (Kleiman, 1977), are socially monogamous, highly affiliative animals that form lasting bonds with specific animals (Carter et al., 2008; Getz et al., 1981; Young et al., 2011; Young et al., 2005), and are also unusual in that they will voluntarily self-administer large doses of alcohol (Anacker et al., 2011). In that study, we determined that prairie voles will reach intoxicating levels of blood ethanol concentration similar to those of mice when given the same dose of alcohol. We also showed that prairie voles can demonstrate socially-facilitated alcohol intake, exhibiting a higher preference for alcohol over water when gradually introduced to alcohol housed with a sibling, compared to animals introduced to alcohol in isolation. Interestingly, we observed a correlation of average intake of 10% alcohol over four days between voles housed in sibling pairs, which was not present between siblings housed apart. This correlation was only observed in animals consuming alcohol, but not in animals consuming water or saccharin.

Since individually-housed voles exhibit a substantial variability in their alcohol preference and intake, we hypothesized that the observed correlation in intake between individual members of pairs of animals results from one of the voles altering its level of intake to match the intake of its partner. In the present study we addressed this hypothesis by first measuring alcohol intake in individually-housed voles introduced to a choice between 10% alcohol and water, and then housing animals in pairs based on robust differences in the basal alcohol drinking. After observing significant changes in the drinking levels in pair-housed animals, we tested whether these changes persist when animals are isolated again, and performed control experiments addressing whether these effects are indeed due to social influences and whether they are specific to ethanol.

Materials and Methods

Prairie voles were housed and tested in our breeding colony room at the Portland Veterans Affairs Medical Center Veterinary Medical Unit. The animals were housed under a 12:12 light-dark cycle, weaned at 21 days and housed with the entire litter until sex was

determined at approximately 40 days of age and animals were housed with same-sex siblings. While the 12:12 cycle is not standard for vole studies which commonly use the 14:10 cycle, the 12:12 matches cycles that are typically used in other rodents and that we used in our previous work (Anacker et al., 2011; Anacker and Ryabinin, 2010). Only animals that had been housed with 1–3 siblings prior to testing were used in these experiments. Animals were given *ad libitum* access to water and a diet of mixed rabbit chow (LabDiet Hi-Fiber Rabbit), corn (Nutrena Cleaned Grains) and oats (Grainland Select Grains) throughout the experiments. All animals were experimentally naïve.

In Experiment 1, we tested the hypothesis that one vole alters its alcohol intake to match that of its drinking partner when their drinking levels differ. For this, 81 prairie voles aged 69–100 days at the start of testing, weighing 39.8 ± 0.8 g (mean $\pm$ SEM), were tested in the first phase of the experiment. In this first phase, voles were weighed and then moved into individual housing, where they were given continuous access to two 25 mL glass cylinders fitted with a metal sipper tube and rubber stopper. One bottle contained tap water, and the other contained 10% ethanol (diluted volume/volume with tap water from 95% ethanol) for four days. During this time, the volume of fluid was monitored and refilled every 24 hours, and the position of the bottles was rotated daily to avoid a bias due to side preference.

Each animal's preference for alcohol (volume of alcohol divided by total fluid volume consumed) and dose of alcohol (g/kg body weight) was assessed daily and categorized as high, medium, or low, based on the criteria presented in Table 1. Both preference and dose were normally distributed. The specific criteria were chosen because in preliminary tests they yielded approximately equal numbers of high, medium, and low drinkers. After four days of baseline drinking in isolation, each animal was then categorized by subtracting the number of 'low' scores for preference and dose from the number of 'high' scores. Animals receiving a positive number were labeled 'high drinkers' while those receiving negative numbers were labeled 'low drinkers.' Following categorization from baseline intake, 60 high- or low-drinking prairie voles were used for the study (30 female, 30 male), while the remaining 'medium drinkers' were not tested further.

For the second phase of the experiment, high drinkers were paired with low drinkers of the same sex, which were strangers to each other. Pairs were determined as follows, in order to achieve similar relative differences in alcohol intake between the high drinker and low drinker when compared between pairs. The highest drinker of the high group was paired with the highest drinker of the low group, the second-highest high with the second-highest low, and so on, until the lowest of the high drinkers was paired with the lowest of the low drinkers. The exceptions to this rule were when the pairing would lead to siblings being paired, and in such cases, the closest ranking animals would be switched. Using this method for pairing, there was a relatively similar difference in the drinking levels of the paired animals for each pair.

The paired animals were each housed on one side of a cage with a wire mesh divider that allowed the voles to interact but gave each exclusive access to its own drinking tubes. This housing was identical to our previously validated procedure showing that the voles' alcohol drinking behavior is similar when they are housed in non-divided cages and in cages divided by a mesh (Anacker et al., 2011). The pairs were housed together for four days, with the relative positions of the high and low drinkers within the cage determined randomly. During this period, each animal again had continuous access to 10% alcohol and water. The position of the bottles for each member of a pair was identical (for example, ethanol bottles on the left for both animals on day 1 of pair-housing, and ethanol bottles on the right on day 2). Animals were monitored daily for preference and intake, in order to determine whether any changes in drinking level occurred for each animal.

In the third phase of the experiment, the voles were placed in isolation and drinking was monitored with the same two-bottle choice test for four more days, in order to determine whether any changes in drinking level that occurred during the paired period persist in a subsequent isolation.

In Experiment 2, we tested whether any changes in drinking would occur when paired animals started with similar drinking levels, in order to show that the results of Experiment 1 were due specifically to the presence of the partner drinking at a different level, and not due to the development of an aversion to alcohol that could occur independent of the partner's drinking. The same procedure was performed for the first phase of the experiment, using 51 animals, 71–112 days old, weighing 38.4 ± 0.7 g. Of these, 42 voles (20 female and 22 male) were classified as high and low drinkers and used in the second phase. In this experiment, high drinkers were paired with high drinkers, and low with low, and otherwise the second and third phases of the experiment were performed with the same methods as described for Experiment 1.

Experiment 3 was conducted just as Experiment 1, except that a saccharin solution (0.05%, weight/volume of tap water) was self-administered instead of alcohol, in order to test whether the effects of Experiment 1 were specific to alcohol or would extend to another rewarding substance. We have previously tested saccharin consumption in prairie voles and found that they show a high preference for this substance at the same concentration used here, and that consumption of saccharin is not correlated between partners as was seen for alcohol consumption (Anacker et al., 2011). In this experiment, 39 animals from 67–101 days old, weighing 34.6 ± 1.2 g were used for the first phase, and 34 were labeled high or low for saccharin consumption and went on to the second phase. The criteria for categorization are presented in Table 2.

Since daily alcohol intake for individual animals differ due to common variability as well as the position of the bottle (some voles show a notable side preference), average intake was calculated across the four days at each phase of the experiments. Then, a repeated measures ANOVA was applied to the data from each experiment, using sex and baseline drinking category (high or low) as between subjects factors, the average drinking throughout each of the three four-day sessions (housing type: isolation 1, paired, or isolation 2) as the repeated measure, with dose of alcohol (g/kg) or alcohol preference as the dependent measures. When warranted by a significant main effect or interaction, the data were further assessed by Fisher's PLSD or tests for simple effects. A few animals were eliminated from statistical analysis of alcohol preference, or both preference and dose, due to faulty (leaky) tubes; corresponding degrees of freedom are reported in the results for each test.

Results

Experiment 1 – High and low alcohol drinkers paired

As expected based on categorization, high drinkers exhibited a higher preference for alcohol and a higher intake of alcohol than low drinkers (main effect of drinking category on preference [$F_{(1,46)}=30.73$ $p<0.0001$] and intake [$F_{(1,51)}=42.57$; $p<0.0001$]). Females showed a higher preference for alcohol and a higher intake of alcohol than males (main effect of sex on preference [$F_{(1,46)}=5.17$; $p=0.0277$] and intake [$F_{(1,51)}=8.68$; $p=0.0048$]), but there were no interactions with other variables, and so data are presented in the figures by collapsing across sexes.

There was a significant effect of the repeated measure of housing on preference ($F_{(2,92)}=6.75$; $p=0.0018$) and intake ($F_{(2,102)}=6.75$; $p=0.0018$) of alcohol. Post hoc tests revealed that overall preference and intake were lower in the second isolation period in

comparison to the first isolation (preference: $p=0.0003$; intake: $p=0.0005$) or the paired period (preference: $p=0.0241$; intake: $p=0.0190$).

Importantly, there was a significant interaction between drinking category and the repeated measure of housing type for preference ($F_{(2,92)}=5.92$; $p=0.0038$) and intake ($F_{(2,102)}=6.22$; $p=0.0028$) of alcohol. A test of simple main effects revealed an effect of housing type on preference and intake in high drinkers but not low drinkers (Fig. 1). In high drinkers, drinking during the paired period was lower than in the first isolation (preference: $p=0.0061$; intake: $p<0.0001$), and drinking during the second isolation was also lower in comparison with the first isolation (preference: $p=0.0088$; intake: $p<0.0001$). Thus, our data indicated that animals categorized initially as high drinkers decreased their drinking when housed with animals initially categorized as low drinkers. Moreover, this decrease persisted when animals were again placed in isolation. Although the statistical analysis clearly indicated this change in drinking, there was noticeable variability with some low drinking individuals increasing their alcohol drinking when paired with high drinkers (Fig. 2).

Experiment 2 – Matched alcohol drinkers paired

Initial alcohol intakes and preference in this experiment were very similar to Experiment 1. As in Experiment 1, high drinkers exhibited a higher preference for alcohol and a higher intake of alcohol than low drinkers (main effect of drinking category on preference [$F_{(1,26)}=96.69$; $p<0.0001$] and intake [$F_{(1,27)}=33.65$; $p<0.0001$]). In contrast to Experiment 1, the effect of sex on either preference or intake of alcohol was not significant ($F_{(1,26)}=0.01$; $p=0.93$). There were no interactions of sex with other variables, and so data are presented in figures by collapsing across sexes.

Importantly, in contrast to Experiment 1, there was no effect of the repeated measure of housing type (preference: [$F_{(2,52)}=1.94$; $p=0.15$]; intake: [$F_{(2,54)}=1.05$; $p=0.36$]), or any interaction with drinking category (preference: [$F_{(2,52)}=0.18$; $p=0.84$]; intake: [$F_{(2,54)}=0.06$; $p=0.94$]), indicating that neither the high nor low drinkers significantly altered their alcohol drinking behavior when paired with an animal with similar intake, or in subsequent isolation (Fig. 3).

Experiment 3 – High and low saccharin drinkers paired

As in Experiments 1 and 2 with alcohol, high saccharin drinkers exhibited a higher preference for saccharin and a higher intake than low drinkers (main effect of drinking category on preference [$F_{(1,27)}=20.49$; $p=0.0001$] and intake [$F_{(1,27)}=22.45$; $p<0.0001$]). There was no effect of sex on either preference or intake of alcohol, and there were no interactions of sex with other variables, and so data are presented in figures by collapsing across sexes.

In saccharin drinkers, there was a significant effect of the repeated measure of housing on preference ($F_{(2,54)}=6.55$; $p=0.0029$) and intake ($F_{(2,54)}=5.01$; $p=0.0101$) of saccharin. Post hoc tests revealed that preference and intake were higher in the paired period in comparison to the first isolation (preference: $p=0.0006$; intake: $p=0.0018$), and preference only was lower in the second isolation in comparison to the paired period ($p=0.0277$).

There was no interaction between the repeated measure of housing type and drinking category (preference: [$F_{(2,54)}=2.01$; $p=0.14$]; intake: [$F_{(2,54)}=0.42$; $p=0.66$]), indicating that neither the high nor low drinkers significantly altered their saccharin drinking behavior when paired with an animal with opposite intake, or in subsequent isolation (Fig. 4).

Discussion

In the present studies, we confirm our hypothesis that the alcohol drinking behavior of one prairie vole changes to better match the drinking of the other animal it is housed with. Thus, animals initially categorized as high drinkers decreased their intake and preference when housed with animals categorized as low drinkers. This evidence provides some explanation for the previously observed correlation of alcohol intake in voles housed together (Anacker et al., 2011). To the best of our knowledge, this is the first demonstration of a direct peer influence on alcohol consumption in a laboratory animal model, further demonstrating the utility of the prairie vole model for examining effects of specific social relationships on alcohol drinking.

Experiment 1 demonstrates the main finding of this study, showing that high alcohol drinkers paired with low drinkers decrease their drinking, and that this decrease persists even in the absence of a direct social influence. High drinking animals demonstrated average intakes over 12 g/kg/day. This is in agreement with our earlier observations that prairie voles in general drink high levels of alcohol, on average comparable to intake of C57BL/6J mice (Anacker et al., 2011). Interestingly, even the low drinkers consumed approximately 5 g/kg/day, which is still high enough to observe a reduction in drinking if one were to occur, making it clear that the only group change occurred in the high drinkers.

Although these intakes are extremely high, they are lower than average intakes observed in our previous published study (Anacker et al., 2011) at the same concentration of ethanol (about 15 g/kg). This difference is most likely due to the fact that voles here were exposed to 10% ethanol from the first day, while in the previous study they were introduced to gradually increasing concentrations of ethanol (3%, 6%, and only then 10%). Therefore, voles in the present experiment could have experienced aversive effects of ethanol if they “overdosed” on this drug, and so it was important to test whether the decrease in intake in the high drinkers in the present experiment could be due to a general tendency to decrease ethanol intake because of exposure to extremely high doses of ethanol. This possibility was addressed in Experiment 2. Should the high drinking animals have decreased alcohol intake due to potential general aversive effects of ethanol, we would have expected to observe a decrease in intake in high drinkers paired with high drinkers in this experiment. This effect was not observed. This finding is in agreement with the idea that the change in intake and preference in high drinkers in Experiment 1 is due to the social influence of their partners.

The results of Experiment 3 suggest that the peer-mediated change in drinking level to match a partner is specific to alcohol, in that the same behavioral change is not observed for consumption of saccharin, a rewarding sweet substance. Here, as in Experiment 2, the small difference between intakes in high saccharin drinkers in the paired versus isolated phase is in the direction of higher intakes in the paired condition, indicating that no decrease in intake occurs when animals are paired. This result agrees with our previous finding that only ethanol but not saccharin or water intake is correlated between members of vole pairs (Anacker et al., 2011). This finding is a further indication that access to any rewarding substance is insufficient to lead to coordinated drinking behavior.

In Experiment 1, we show that on average voles that start out as high drinkers in isolation decrease their alcohol preference and intake when they are paired with low drinkers, while the low drinkers do not change their alcohol preference or intake in the presence of high drinkers. However, we also observed a substantial degree of variability in individual behavioral changes. While the individual variability within each group was not frequent enough to lead to a bimodal distribution in each group, where some low drinkers increased their drinking while high drinkers remained high, in contrast to the opposite overall group

effects, it is still important to consider this phenomenon. The reason is that if all high drinkers decreased their drinking, one would presume that the drinking level itself was the predictive factor for which animals would alter their drinking. Since that is not the case in all pairs, there must be another explanation for which animal alters its drinking. Our preliminary experiments suggest that prairie voles exhibit dominant-subordinate relationships within their pairs. Future studies will examine whether social dominance plays a role in this behavior. One would hypothesize that, within a pair, the dominant animal tends to maintain its original drinking level while the subordinate animal changes its behavior to more closely match the dominant animal. The relation of this hypothesis to the present study is consistent with a number of reports of an inverse correlation between dominance rank and alcohol intake level in non-human primates and rodents (reviewed by Anacker and Ryabinin, 2010; Blanchard et al., 1987; Blanchard et al., 1993; Kaur et al., 2008; Kudryavtseva et al., 2006; Kudryavtseva et al., 1991; McKenzie-Quirk and Miczek, 2008; Wolffgramm and Heyne, 1991); if the same relationship holds for prairie voles, then one would expect that the low drinkers in the present study were more likely to be dominant, and the high drinkers subordinate, and therefore the high drinkers may be more likely to decrease their drinking to match the dominant low drinkers.

The main finding of this study is relevant to the understanding of establishment of alcohol drinking levels or patterns in social circumstances, as well as the effect that a social influence can have on changing alcohol intake. There is considerable literature examining peer influences on alcohol drinking in humans, including both social influences that increase drinking as well as those that are protective against high drinking or relapse (e.g., Andrews et al., 2002; Henry et al., 2009; Homish and Leonard, 2008; Litt et al., 2009), but the literature in animal models is relatively sparse. However, there are several studies showing effects of a social influence, or social learning, on alcohol intake levels. In modifications of Galef's demonstrator-observer paradigm (1985), young rats exposed to either an intoxicated sibling (Hunt et al., 2001) or an alcohol-drinking adult female (Honey et al., 2004) increased subsequent alcohol intake. In these studies, the rats increased their alcohol intake after observing olfactory cues from the demonstrator animal, as has been described for a number of other substances. However, if the presence of the alcohol odor on one animal is a cue for another that it is acceptable to drink the same substance, then the expected result in our study would be an increase in the low drinkers, or even in both groups. Since the opposite effect is observed here, another mechanism must be responsible for the changes in drinking observed in the present study.

We are aware of only one other series of studies in mice showing bidirectional effects relevant to the present investigation. Juvenile mice of a genetic background that normally do not prefer alcohol (DBA) will consume significantly more if they are raised to adulthood with adult C57BL mice, while C57BL mice decrease their drinking when housed from weaning with adult DBA mice (Randall and Lester, 1975). This study and the current study both show that not only can the social environment influence alcohol intake, but the direction of the effect may be dependent on individual predisposition as well as the specific social influences. Randall and Lester concluded that the most likely explanations for the alterations in drinking behavior were peer pressure and setting examples of behavior.

These studies in other animal models show that social influences can have important effects. However, they do not model human peer interactions in which people drink together at the same time. Although in Randall and Lester's (1975) study the mice were exposed to alcohol in groups, their drinking was only monitored during an eight-day isolation period, and so the proximal effects of peer drinking are not known. The prairie vole model used here is able to address this issue by examining drinking in each individual while they are together, drinking at the same time.

Interestingly, the observed lowered drinking level of high drinkers persists in a subsequent isolation period, even when the presence of the low drinker is no longer a direct influence. This finding suggests that social interactions during pair housing may lead to long-term modifications in drinking behaviors that could involve learning mechanisms. This phenomenon could be of great importance for the understanding of how establishment of drinking patterns with peers can extend into drinking alone or under other circumstances. Future studies in this animal model could examine the neural changes that occur and persist following drinking with a peer, in order to better understand these mechanisms and potential therapeutic targets.

In summary, these studies provide the basis for a novel animal model for examination of direct peer influences on alcohol intake, including their prolonged effect. Understanding specific behavioral mechanisms leading to social influences on alcohol intake akin to peer pressure could be very informative for psychotherapy of alcohol use disorders. The prairie vole animal model has led to fruitful mechanistic discoveries in the field of social neuroscience, and appears likely to provide important insights into the social neurobiology of alcoholism and addiction.

Acknowledgments

This work was supported by NIH grants AA016886 to AER, AA02013601 to AMJA, and institutional training grant AA007468.23. This material is the result of work supported with resources and the use of facilities at the Portland Veterans Affairs Medical Center. JML is supported by a career development award from the Department of Veterans Affairs, Veterans Health Administration, Office of Research and Development, and Clinical Sciences Research and Development.

This work was supported by NIH grants AA016886 to AER, AA02013601 to AMJA, institutional training grant AA007468.23, and the ARCS Foundation Portland Chapter M&M award to AMJA. The authors would also like to thank the PVAMC VMU staff for their contributions to the colony management and animal care. This material is the result of work supported with resources and the use of facilities at the Portland Veterans Affairs Medical Center. JML is supported by a career development award from the Department of Veterans Affairs, Veterans Health Administration, Office of Research and Development, and Clinical Sciences Research and Development.

References

- Advani T, Hensler JG, Koek W. Effect of early rearing conditions on alcohol drinking and 5-HT1A receptor function in C57BL/6J mice. *Int J Neuropsychopharmacol.* 2007; 10(5):595–607. [PubMed: 17134528]
- Anacker AMJ, Loftis JM, Kaur S, Ryabinin AE. Prairie voles as a novel model of socially facilitated excessive drinking. *Addict Biol.* 2011; 16(1):92–107. [PubMed: 20579002]
- Anacker AMJ, Ryabinin AE. Biological contribution to social influences on alcohol drinking: evidence from animal models. *Int J Environ Res Public Health.* 2010; 7(2):473–493. [PubMed: 20616986]
- Andrews JA, Tildesley E, Hops H, Li F. The influence of peers on young adult substance use. *Health Psychol.* 2002; 21(4):349–57. [PubMed: 12090677]
- Blanchard RJ, Hori K, Tom P, Blanchard DC. Social structure and ethanol consumption in the laboratory rat. *Pharmacol Biochem Behav.* 1987; 28(4):437–42. [PubMed: 3432310]
- Blanchard RJ, Yudko EB, Blanchard DC. Alcohol, aggression and the stress of subordination. *J Stud Alcohol Suppl.* 1993; 11:146–55. [PubMed: 8410956]
- Bot SM, Engels RC, Knibbe RA, Meeus WH. Friend's drinking behaviour and adolescent alcohol consumption: the moderating role of friendship characteristics. *Addict Behav.* 2005; 30(5):929–47. [PubMed: 15893090]
- Carter CS, Grippio AJ, Pournajafi-Nazarloo H, Ruscio MG, Porges SW. Oxytocin, vasopressin and sociality. *Prog Brain Res.* 2008; 170:331–6. [PubMed: 18655893]
- Galef BG Jr, Kennett DJ, Stein M. Demonstrator influence on observer diet preference: Effects of simple exposure and the presence of a demonstrator. *Animal Learning & Behavior.* 1985; 13:25–30.

- Getz LL, Carter CS, Gavish L. The mating system of the prairie vole *Microtus ochrogaster*: Field and laboratory evidence for pair-bonding. *Behav Ecol Sociobiol*. 1981; 8:189–194.
- Henry KL, Oetting ER, Slater MD. The Role of Attachment to Family, School, and Peers in Adolescents' Use of Alcohol: A Longitudinal Study of Within-Person and Between-Persons Effects. *J Couns Psychol*. 2009; 56(4):564–572. [PubMed: 20228876]
- Homish GG, Leonard KE. The social network and alcohol use. *J Stud Alcohol Drugs*. 2008; 69(6): 906–14. [PubMed: 18925349]
- Honey PL, Varley KR, Galef BG Jr. Effects of ethanol consumption by adult female rats on subsequent consumption by adolescents. *Appetite*. 2004; 42(3):299–306. [PubMed: 15183921]
- Hunt PS, Holloway JL, Scordalakes EM. Social interaction with an intoxicated sibling can result in increased intake of ethanol by periadolescent rats. *Dev Psychobiol*. 2001; 38(2):101–9. [PubMed: 11223802]
- Kaur, S.; Anacker, AMJ.; Kapasova, Z.; Loftis, JM.; Ryabinin, AE. Alcohol consumption in periadolescent voles. Program No. 847.3. 2008 Neuroscience Meeting Planner; Washington, DC: Society for Neuroscience; 2008. Online
- Kiuru N, Burk WJ, Laursen B, Salmela-Aro K, Nurmi JE. pressure to drink but not to smoke: disentangling selection and socialization in adolescent peer networks and peer groups. *J Adolesc*. 2010; 33(6):801–12. [PubMed: 20732711]
- Kleiman DG. Monogamy in mammals. *Q Rev Biol*. 1977; 52(1):39–69. [PubMed: 857268]
- Knecht AB, Burk WJ, Weesie J, Steglich C. Friendship and Alcohol Use in Early Adolescence: A Multi-level Social Network Approach *Journal of Research on Adolescence*. 2011 in press.
- Kudryavtseva N, Gerrits MA, Avgustinovich DF, Tenditnik MV, Van Ree JM. Anxiety and ethanol consumption in victorious and defeated mice; effect of kappa-opioid receptor activation. *Eur Neuropsychopharmacol*. 2006; 16(7):504–11. [PubMed: 16524701]
- Kudryavtseva NN, Madorskaya IA, Bakshtanovskaya IV. Social success and voluntary ethanol consumption in mice of C57BL/6J and CBA/Lac strains. *Physiol Behav*. 1991; 50(1):143–6. [PubMed: 1946707]
- Litt MD, Kadden RM, Kabela-Cormier E. Individualized assessment and treatment program for alcohol dependence: results of an initial study to train coping skills. *Addiction*. 2009; 104(11): 1837–8. [PubMed: 19712124]
- McKenzie-Quirk SD, Miczek KA. Social rank and social separation as determinants of alcohol drinking in squirrel monkeys. *Psychopharmacology (Berl)*. 2008; 201(1):137–45. [PubMed: 18641974]
- Needle R, McCubbin H, Wilson M, Reineck R, Lazar A, Mederer H. Interpersonal influences in adolescent drug use--the role of older siblings, parents, and peers. *Int J Addict*. 1986; 21(7):739–66. [PubMed: 3781689]
- Oostveen T, Knibbe R, de Vries H. Social influences on young adults' alcohol consumption: norms, modeling, pressure, socializing, and conformity. *Addict Behav*. 1996; 21(2):187–97. [PubMed: 8730520]
- Park A, Sher KJ, Krull JL. Selection and socialization of risky drinking during the college transition: The importance of microenvironments associated with specific living units. *Psychol Addict Behav*. 2009; 23(3):404–14. [PubMed: 19769425]
- Randall CL, Lester D. Social modification of alcohol consumption in inbred mice. *Science*. 1975; 189(4197):149–51. [PubMed: 1138373]
- Schenk S, Gorman K, Amit Z. Age-dependent effects of isolation housing on the self- administration of ethanol in laboratory rats. *Alcohol*. 1990; 7(4):321–6. [PubMed: 2390208]
- Thorsell A, Slawecki CJ, Khoury A, Mathe AA, Ehlers CL. Effect of social isolation on ethanol consumption and substance P/neurokinin expression in Wistar rats. *Alcohol*. 2005; 36(2):91–7. [PubMed: 16396742]
- Windle M, Spear LP, Fuligni AJ, Angold A, Brown JD, Pine D, Smith GT, Giedd J, Dahl RE. Transitions into underage and problem drinking: developmental processes and mechanisms between 10 and 15 years of age. *Pediatrics*. 2008; 121(Suppl 4):S273–89. [PubMed: 18381494]
- Wolffgramm J, Heyne A. Social behavior, dominance, and social deprivation of rats determine drug choice. *Pharmacol Biochem Behav*. 1991; 38(2):389–99. [PubMed: 2057508]

- Yanai J, Ginsburg BE. Increased sensitivity to chronic ethanol in isolated mice. *Psychopharmacologia*. 1976; 46(2):185–9. [PubMed: 986055]
- Young KA, Liu Y, Gobrogge KL, Dietz DM, Wang H, Kabbaj M, Wang Z. Amphetamine alters behavior and mesocorticolimbic dopamine receptor expression in the monogamous female prairie vole. *Brain Res*. 2011; 1367:213–22. [PubMed: 20933511]
- Young LJ, Murphy Young AZ, Hammock EA. Anatomy and neurochemistry of the pair bond. *J Comp Neurol*. 2005; 493(1):51–7. [PubMed: 16255009]

Figure 1. High drinkers paired with low drinkers decrease alcohol drinking

Compared to baseline drinking in isolation, high drinkers (black bars) decrease A) preference for alcohol, and B) intake of alcohol, when paired with low drinkers (white bars), and the decrease in drinking persists during a subsequent isolation. Values indicate mean + SEM. *Statistically significant post-hoc differences ($p < 0.01$).

Figure 2. Example of variation between pairs in intake level changes

Average alcohol intake (g/kg/day) across each four-day period is shown for individuals from two pairs. Pair 1 (open triangles) exhibits the alterations in alcohol drinking level corresponding to the group effects: the high drinker (upright triangle) decreases alcohol intake when paired with the low drinker, and the decrease persists in the subsequent isolation, while the low drinker (upside-down triangle) maintains its low drinking level. In contrast, Pair 2 (filled triangles) exhibits the opposite effect: the high drinker (upright triangle) maintains its high level of alcohol intake, even increasing when paired with the low drinker, while the low drinker (upside-down triangle) increases its intake to the level of the high drinker, and the increase persists in the subsequent isolation.

Figure 3. Matched drinkers exhibit no change in alcohol drinking

High drinkers (black bars) and low drinkers (white bars) do not alter their alcohol A) preference, or B) intake, when paired with same-level drinkers, or in a subsequent isolation. Values indicate mean + SEM.

Figure 4. Saccharin drinkers exhibit no change in drinking

High drinkers (black bars) and low drinkers (white bars) do not alter their saccharin A) preference, or B) intake, when paired with opposite-level drinkers, or in a subsequent isolation. Values indicate mean + SEM. *Statistically significant post-hoc differences ($p < 0.01$).

Table 1

Criteria for alcohol drinking level group assignment

Group	Alcohol Preference Ratio	Alcohol Dose (g/kg/day)
Low	< 0.5	< 5
Medium	0.5 – 0.749	5 – 8.999
High	≥ 0.75	≥ 9

Table 2

Criteria for saccharin drinking level group assignment

Group	Saccharin Preference Ratio	Saccharin Dose (g/kg/day)
Low	< 0.65	< 0.075
Medium	0.65 – 0.85	0.075 – 0.125
High	> 0.75	> 0.125