Published in final edited form as:

Behav Brain Res. 2011 October 1; 223(2): 371–375. doi:10.1016/j.bbr.2011.05.004.

Age-Related Differences in the Anticipation of Future Rewards

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Abstract

The present study examined the anticipation of future reward in 7-month and 26-month-old Fischer 344/Brown Norway rats. Young and old rats were divided randomly and assigned into one of two conditions. In the Contrast Condition, subjects were given a water solution containing 2% sucrose for 3 minutes followed immediately by a water solution containing 32% sucrose for 3 minutes. In the No-Contrast Condition, subjects were given a water solution containing 2% sucrose for 3 minutes followed immediately by a water solution containing 2% sucrose for 3 minutes. Across 10 days of testing in the Contrast Condition, young rats showed significantly less intake of the less preferred 2% sucrose solution, whereas old rats showed increased intake of the 2% sucrose solution. Young rats showed a significant increase in intake of the preferred 32% sucrose solution compared to aged rats across the 10-day testing period with the exception of days 8–10 where intake did not differ between groups. In the No-Contrast Condition, there were no significant differences between young and old rats, with both groups consuming significantly more of the first 2% solution than the second 2% solution. Therefore, these data suggest that age-related changes may impair the ability to anticipate future rewards.

Keywords

Aging; Reward; Anticipation; Decision-Making; Prefrontal Cortex

1. Introduction

Appropriate decision-making is an important factor in determining the ability of older adults to maintain functional independence. Older adults are required to make important decisions on a daily basis regarding finances, health care, and activities of daily living. Although numerous studies have examined the effects of aging on traditional measures of executive functioning, few studies have examined age-related differences in the anticipation of rewards and how changes in this ability may affect decision-making. Some studies have suggested that age-related changes in decision-making may have substantial societal and public policy implications because impaired decision-making may contribute to older adults being more susceptible to, and often victimized by, misleading and fraudulent advertising [1,2].

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As reviewed by Denburg and colleagues [1], neuropsychological, neuroanatomical, and functional neuroimaging data indicate that the frontal cortices may be substantially affected by aging. Studies involving lesions in rodents [3,4], electrophysiological recordings in monkeys [5,6], and functional neuroimaging in humans [7,8] indicate that the orbitofrontal cortices may play a critical role in decision-making based on the anticipation of reward. A previous study found that patients with damage to the ventromedial region of the prefrontal cortex, who displayed no other cognitive or intellectual deficits, made less advantageous decisions on the Iowa Gambling Task, which is thought to require real-world decision-making by factoring in reward, punishment, and unpredictability [9]. It was found that ventromedial prefrontal cortex damage caused patients to be more likely than controls to make choices that result in high immediate reward, but a more severe delayed punishment. To test the hypothesis that aging may alter decision-making based on anticipated reward, researchers tested younger and older adults on the gambling task [1,2]. Otherwise cognitively normal older adults were found to make less advantageous decisions on the task compared to younger adults [1,2]. Therefore, age-related changes in ventromedial regions of the brain may contribute to impaired decision-making in older adults on the gambling task. However, other studies have not detected age-related impairment in advantageous decision-making [10]. One study argued that although age-related differences in advantageous decision-making were not detected, older adults were found to use different strategies than young adults when performing the task [11].

Since environmental factors and life experience in humans can render decision-making differences between young adults and older adults difficult to interpret, a study was conducted to examine choice behavior based on future rewards in a rodent model of aging where experimental factors such as prior learning and environmental history can be controlled to a greater extent [12]. The study tested young and aged rats on a two-choice delayed discounting task where one choice resulted in immediate delivery of a small reward, whereas the other resulted in a large reward delivered following a variable delay period. The study found that young rats chose the large rewards at short delays but shifted toward choosing the smaller rewards as the delays increased. In contrast, aged rats chose the large rewards regardless of delay. The data suggest that aged rats show an attenuated discounting of delayed rewards suggesting that age-related changes in the brain may affect decision-making, possibly contributing to the increased ability to delay gratification associated with aging. To further examine age-related changes in the anticipation of future rewards, the present study tested 7 mo and 26 mo rats on a paradigm similar to those used in previous studies [4,13,14]. The task was designed to assess anticipation of future reward by measuring the intake of a less preferred reward when followed immediately by a preferred reward across a 10-day period. Prior studies have shown that normal rats will decrease consumption of the less preferred reward across days in anticipation of the preferred reward [4,13,14].

2. Methods

2.1 Subjects

Forty Fischer 344/Brown Norway (F344BN) male rats (Harlan Laboratories) approximately 7 months ($n = 20$) and 26 months ($n = 20$) of age were used as subjects. The F344BN is a hybrid between a female Fisher 344 rat and male Brown Norway rat. One rat 26 mo of age assigned to the “Contrast Condition” (described below) and two rats 26 mo of age assigned to the “No-Contrast Condition” died during testing and were not included in the analyses. Subjects were housed in pairs in standard plastic containers prior to testing on the task. However, each rat was housed individually in a hanging cage during testing. Subjects were fed freely and were allowed continuous access to water except during testing on the task.

The colony room was kept on a 12hr: 12hr light: dark cycle and all testing was conducted during the light phase.

2.2 Testing Procedure

Each rat was tested on a paradigm similar to those used in previous studies [4,13,14]. The task was designed to assess anticipation of future reward by measuring the intake of a less preferred solution (2% sucrose) when followed by a preferred solution (32% sucrose). For one day prior to the 10-day testing period, subjects were placed on overnight water deprivation. The morning following overnight water restriction, subjects were given plain water (i.e. 0% sucrose) for 3-min and then following a 15 s interstimulus interval (ISI), the rats received water again for 3-min, in order to establish a baseline water drinking level using the same parameters as the experimental task (see below). Subjects also were given a 2% sucrose solution for 15 min to insure adequate habituation to the hanging cages and to negate any neophobia to the sucrose solution prior to testing. A prior pilot study in our lab found that aged rats demonstrated increased neophobia to a water solution containing sucrose. The water solutions were presented in 50 ml graduated cylinders with a standard drinking spigot that attached to the front of the cage and extended into the interior.

Prior to testing, the rats in each age group were equally divided and randomly assigned to either a Contrast Condition (2%–32%) or a No-Contrast Condition (2%-2%). Each day, the water bottles were removed from the home cages 30 min prior to testing. In the Contrast Condition (2%–32%), each rat was given a water solution containing 2% sucrose to drink for 3-min. Then following a 15 s ISI, the rat was given a water solution containing 32% sucrose for 3-min. This procedure was followed once daily for 10 consecutive days. In the No-Contrast Condition (2%-2%), each rat was given a water solution containing 2% sucrose to drink for 3-min followed by a second water solution containing 2% sucrose with a 15 s ISI between solutions. The sucrose solutions were presented in 50 ml graduated cylinders with a standard drinking spigot that attached to the front of the cage and extended into the interior. The rats were tested in small cohorts to maintain control over the timing of the stimulus presentation and ISI. Following testing, the amount consumed of each solution was recorded and used as the dependent measure.

2.3 Statistical Analyses

2.3.1 Water Baseline Trials—A 2×2 analysis of variance test (ANOVA) with group (7 mo, 26 mo) as a between group variable and session (first 3-min session, second 3-min session) as a within group variable was used to assess group differences in baseline water consumption. Newman-Keuls posthoc comparison tests were used to further analyze any statistically significant main effects or interactions involving more than two mean comparisons on this analysis and all ANOVAs described in the following sections.

2.3.2 Bottle 1 Consumption—A $2 \times 2 \times 4$ repeated measures ANOVA with age-group (7 mo, 26 mo) and condition (No-Contrast, Contrast) as between group variables and day (1, 2–4, 5–7, 8–10) as a within group variable was used to assess group differences in Bottle 1 consumption.

2.3.3 Bottle 2 Consumption—A $2 \times 2 \times 4$ repeated measures ANOVA with age-group (7 mo, 26 mo) and condition (No-Contrast, Contrast) as between group variables and day (1, 2–4, 5–7, 8–10) as a within group variable was used to assess group differences in Bottle 2 consumption.

2.3.4 Overall Consumption—A 2×4 analysis of variance (ANOVA) with age-group (7 mo, 26 mo) as a between group variable and day (1, 2–4, 5–7, 8–10) as a within group

variable was used to compare the total amount consumed each day of the 2% sucrose solution plus the 32% solution for 7-mo and 26-mo old rats on the Contrast Condition (2%–32%). This analysis was used to assess whether group differences on the Contrast Condition were due to age-related differences in motivation to drink.

3. Results

3.1 Water Baseline Trials

The ANOVA did not reveal a significant main effect of age-group [$F(1,35) = .01, p = .92$] indicating that young and old rats consumed comparable amounts of water during the baseline trial. Seven-month old rats consumed an average of 1.85 ml (SE = .21) and 26-mo old rats consumed an average of 1.88 ml (SE = .34). In addition, the analysis did not reveal a main effect of session [$F(1,35) = .61, p = .44$] or a significant age-group $\times$ session interaction [$F(1,35) < .01, p = .99$] indicating that there were no differences in consumption across sessions and the age-groups did not differ in consumption as a function of sessions.

3.2 Bottle 1 Consumption

The repeated measures ANOVA revealed a statistically significant age-group $\times$ day $\times$ condition interaction, [$F(3, 99) = 4.23, p < .01$]. As shown in Figure 1 (top), a Newman-Keuls posthoc comparison test of the age-group $\times$ day $\times$ condition interaction revealed no significant group differences in consumption of Bottle 1 in the Contrast Condition (2%–32%) on Day 1. However, the analysis revealed that 7-mo rats consumed significantly less ($p < .05$) of the 2% sucrose solution from Bottle 1 than 26-mo rats on Days 2–4, 5–7, and 8–10. In the No-Contrast Condition (2%–2%), there were no significant group differences in consumption of Bottle 1 as a function of day (Figure 1 bottom). The analysis also revealed statistically significant interactions for day $\times$ condition [$F(3, 99) = 3.64, p < .05$] and age-group $\times$ condition [$F(1, 33) = 13.01, p < .01$] with 7-mo old rats consuming less of the Bottle 1 solution compared to 26-mo old rats in the Contrast Condition but no age-related differences were found in the No-Contrast Condition. The ANOVA also revealed a significant main effect of age-group [$F(1, 33) = 19.29, p < .001$] with 7-mo old rats consuming less of Bottle 1 than 26-mo old rats and a significant main effect of day [$F(3, 99) = 7.70, p < .001$] with intake decreasing across days. However, the main effect of condition did not reach statistical significance [$F(1, 35) = .135, p = .72$].

3.3 Bottle 2 Consumption

The repeated measures ANOVA revealed a statistically significant age-group $\times$ condition [$F(1, 33) = 6.13, p < .05$] interaction. As shown in Figure 2 (top), a Newman-Keuls posthoc comparison test of the age-group $\times$ condition interaction revealed that 7-mo rats in the Contrast Condition (2%–32%) consumed significantly more ($p < .05$) of Bottle 2 (32% sucrose) than 26-mo rats. However, as shown in Figure 2 (bottom), 7-mo and 26-mo old rats did not differ significantly in consumption of Bottle 2 (2% sucrose) in the No-Contrast Condition (2%–2%). The ANOVA also revealed a significant main effect of age-group [$F(1, 33) = 8.26, p < .01$] with 7-mo old rats consuming more of Bottle 2 than 26-mo old rats. The analysis also revealed significant main effects of day [$F(3, 99) = 4.56, p < .01$] and condition [$F(1, 33) = 51.10, p < .001$] and a significant day $\times$ condition [$F(3, 99) = 21.52, p < .001$] interaction. However, the age-group $\times$ day $\times$ condition interaction failed to reach significance [$F(3, 99) = 2.07, p = .11$].

3.4 Overall Consumption

The repeated measures ANOVA did not reveal a significant main effect of age-group [$F(1,17) = 1.09, p = .31$] or an age-group $\times$ day interaction [$F(1,17) = 1.05, p = .31$],

suggesting that overall consumption of the 2% sucrose solution plus the 32% solution on the Contrast Condition (2%–32%) did not differ between 7-mo and 26-mo old rats. However, the analysis did reveal a significant main effect of day [$F(1,17) = 13.89, p < .01$] indicating that consumption increased across days.

4. Discussion

The results of the present study demonstrate that old rats show significant deficits compared to young rats in the ability to anticipate future rewards as measured by the present paradigm. When rats were presented with a less preferred 2% sucrose solution followed by a more preferred 32% sucrose solution (Contrast Condition), young rats showed decreased intake of the less preferred 2% sucrose solution across the 10 days of testing compared to the old rats (Figure 1 top). Old rats actually showed an increased intake of the 2% sucrose solution across testing, whereas intake decreased in young rats (Figure 1 top). In addition, young rats showed a significant increase in the intake of a preferred 32% sucrose solution compared to old rats across the 10-day testing period (Figure 2 top). These data indicate that young rats anticipate the presentation of the preferred stimulus, and therefore suppress their intake of the less preferred stimulus. The present findings suggest that age-related changes in the brain may impair the ability to anticipate future rewards.

When rats were tested on the task with no contrast difference between the first and second solution (2%-2%), there were no group differences in consumption of either solution on day 1 of testing. Across the 10 days of testing, both young and old rats consumed more of the initial 2% solution and less of the second 2% solution; there were no significant group (7 mo, 26 mo) differences on any day of testing (Figures 1 and 2 bottom). The results of the present study indicate that when the first solution is followed by one of equal reward value, rats do not show anticipatory behavior and choose to consume more of the first solution. These data suggest that this behavior is not affected by aging.

As noted by Van der Staay [15], age-related differences in motivation are a considerable concern for between group comparisons of young and aged rats on behavioral tasks. Therefore in the present study, it could be argued that age-related differences on the 2%-32% Contrast Condition may be due to decreased motivation to drink in the 26 mo rats. To ensure that consumption differences in the aged rats were not due to a change in motivation, the total amount of 2% sucrose solution plus the 32% sucrose solution was calculated for each animal in the Contrast Condition. The results indicated that the total amount consumed of the two solutions did not differ between 7 mo and 26 mo rats (Figure 3). This finding also shows that although aged rats appear to increase consumption of both the 2% and 32% sucrose solutions across days, the total intake of both solutions did not differ from young rats. In addition, it is important to note that there were no significant group differences in consumption of the 2% or 32% sucrose solutions on Day 1 of testing (Figures 1 and 2 top), offering further evidence that the group differences were not likely due to age-related changes in motivation to drink. The lack of a significant group difference on Day 1 also suggests that baseline differences in consumption did not contribute significantly to the age-related differences on Days 2–10 of testing. The aforementioned findings also are important because age-related changes in renal function could influence drinking behavior in aged rats.

In the present study, anticipatory behavior on the Contrast Condition (2%–32%) required that rats could perceive the sweet taste of sucrose and actually prefer a 32% sucrose solution over a 2% solution. A previous study from our laboratory using the same strain of aged rats demonstrated that both young and old rats show a significant preference for a 32% sucrose solution relative to a 2% sucrose solution when the two solutions were presented

simultaneously during a preference task [16]. In addition, young and old rats consumed roughly equal quantities of the 32% sucrose solution suggesting that this strain of aged rat can perceive the difference between a 2% and 32% solution and prefer the 32% solution, further indicating that the perceived incentive value of the 32% sucrose may be comparable between groups. This finding also suggests that increased neophobia to a 32% sucrose in aged rats did not contribute to the present age-related differences on the task. Additional support for intact sucrose perception in aged rats comes from studies that did not detect age-related differences in neurophysiological responses to sucrose between young and old rats [17]. In addition, studies have demonstrated that taste thresholds for sucrose, unlike thresholds for sodium chloride, do not increase with age in humans [18,19]. Lastly, studies also have shown that rats with lesions in regions of the brain shown to be involved in the present task, including the agranular insular cortex [4] and the amygdala [14], can discriminate between water solutions containing either 2% or 32% sucrose. Therefore, age-related differences in performance in the Contrast Condition (2%–32%) are not likely due to impaired taste perception for sucrose in aged rats.

As discussed previously, a recent study reported attenuated discounting of delayed rewards in aged Fischer 344 rats [12]. The findings from their study indicated that young rats chose large rewards at short delays, but shifted toward choosing smaller rewards as the delays increased; however, old rats chose large rewards over small rewards regardless of delay. Therefore, the findings from Simon and colleagues [12] report that aged rats show an attenuated discounting of delayed rewards, which is consistent with the findings in older humans who tend to demonstrate an increased ability to delay gratification. However, in the present study, aged rats did not delay drinking the less preferred 2% sucrose solution in anticipation of the preferred 32% solution, even with a short 15 s delay between the two solutions that was not manipulated. Although both studies suggest that the anticipation of rewards may differ between young and aged rats, the present findings may seem somewhat at odds with the findings from the study published by Simon and colleagues [12]. However, it is possible that differences in task demands may have differentially influenced decision-making behavior in the aged rats. For example, the delay between the 2% and 32% sucrose solutions was not manipulated in the present study. Therefore, the present study did not assess how anticipatory behavior changes as a function of increased delay, which is where the largest group differences were found in the study by Simon and colleagues [12]. As discussed by Simon et al. [12], research has consistently shown that individuals will virtually always choose a large reward over a small reward when the delay to delivery of the large reward is short; however, as the time interval to the larger reward increases, there will be a decrease in the subjective value of the larger reward, making the smaller reward more preferable. In the present study, the 2% sucrose solution was available to each rat for 3-min. So even though the delay between the two sucrose solutions was 15 s, a total of 3-min and 15 s elapsed between the initial presentation of the 2% sucrose solution and the presentation of the 32% sucrose solution (in the Contrast Condition; 2%–32%). Therefore, one may speculate that this could have influenced anticipatory behavior in the present study. In the present study, rats in the Contrast Condition (2%–32%) were presented with the 2% sucrose solution and regardless of whether or not they consumed the 2% solution, the 32% sucrose solution always followed. However, in the delayed discounting task [12], if the rat chose the smaller reward (one food pellet) the rat would forgo the ability to obtain the larger reward (four food pellets) following a delay. This reinforcement schedule was the most notable difference between the present study and the delayed discounting task [12], and may have been the contributing factor to the discrepancies found between the two studies. Additionally, the appetitive reinforcement (water containing sucrose vs. food pellets) was a secondary difference between the two studies that may have contributed to the differential findings. It also is possible that aged rats were slower to learn and subsequently use outcome expectancies to guide behavior in the present task. Similarly, aged rats may be slower to

discount future rewards as well. Therefore, age-related learning deficits also may have contributed to the findings in these two studies. Although differences in task demands make it difficult to directly compare the present findings with those of Simon et al. [12], both studies offer a unique perspective on age-related differences in the anticipation of rewards in a rodent model of aging. However, a recent study reported that aged rats developed a conditioned taste aversion following reinforcer devaluation suggesting that aging does not affect the ability to use outcome value to guide Pavlovian responding [20]. The present findings and the findings reported by Simon et al. [12] are consistent with human studies reporting that otherwise cognitively normal older adults were found to make less advantageous decisions on the Iowa Gambling Task compared to younger adults [1,2].

Although no neural correlates of age-related brain change were examined in the present study, the impaired ability of aged rats to decrease intake of a less preferred reward in anticipation of a preferred reward may be due to age-related changes in the orbitofrontal regions of the brain [4]. Kesner and Gilbert [4] tested rats with lesions in the agranular insular region of the orbitofrontal cortex using the present paradigm. The data indicated that lesioned rats exhibited significant deficits compared to controls in the anticipation of a larger reward. Therefore, age-related changes in this region of the brain may contribute to the deficits observed in 26 mo old rats in the present study. Similarly, Gilbert and Kesner [14] tested rats with basolateral amygdala lesions using this task [14]. The results indicated that lesioned rats matched the performance of controls when a 2% sucrose solution was followed by a 32% sucrose solution, suggesting that the amygdala may not be necessary for task performance. Amygdala lesions only resulted in deficits when the difference between the two solutions was reduced (e.g. a 2% sucrose solution followed by either an 8% or 16% sucrose solution). Therefore, the decreased ability of aged rats to anticipate a future reward on the present task may be the result of age-related changes in orbitofrontal cortex than the amygdala. However, changes in other regions of the brain also may contribute to the present findings.

Many previous behavioral studies involving aged rats have used 24 mo old Fisher 344 rats (F344). The present study was conducted using a Fischer 344/Brown Norway (F344/BN) hybrid strain, which is recommended for aging research by the National Institute on Aging. The F344/BN strain has been shown to live longer than F344 rats. The 50% survival age for F344/BN male rats is 34 mo, whereas the 50% survival age for F344 male rats is 24 mo (National Institute on Aging). Therefore, the rats in the present study showed significant memory impairments at 26 months of age despite having longer average longevity than other strains of rats used in prior behavioral experiments. Prior studies have reported significant deficits in F344/BN rats 24–26 months of age on a variety of cognitive tasks including: object reversal learning [21], olfactory reversal learning [21], temporal order memory [22], contextual memory [23], conditioned taste preference [16], spatial memory [24], and transverse patterning [24]. However, age-related impairment in F344/BN rats may occur at different ages depending on the type of task used to measure cognitive function [25].

Empirical and anecdotal evidence in older humans suggests that aging may alter the ability to make decisions based on the anticipation of future rewards. The present data, coupled with those from Simon et al. [12], support this evidence from human studies and also suggest that decision-making tasks can be implemented using rodent models of aging. Studies conducted using animal models may offer unique insight into the effects of aging on decision-making and reward anticipation, because greater experimental control is possible over environmental factors such as prior experience [12]. Therefore, these experiments may have important implications for future studies investigating the neurobiological underpinnings of age-related changes in reward anticipation and decision-making ability.

Driscoll et al. [24] reported that the observed pattern of age-related changes in F344/BN rats closely resembles the changes found in nondemented older adults. Therefore, this strain of rat may serve as a useful animal model to study the effects of aging on cognitive function.

Acknowledgments

The research was supported by NIH grant #AG026505 from NIA to Paul E. Gilbert. The authors would like to thank Karen Guzman for her assistance with data collection.

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Research Highlights

- The study investigated age-related changes in the ability to anticipate future rewards in rats.
- Young rats decreased intake of a less preferred stimulus in anticipation of a preferred stimulus.
- Old rats increased intake of a less preferred stimulus and did not anticipate a preferred stimulus.
- Old rats show significant deficits compared to young rats in the anticipation of future rewards.

Figure 1. Mean milliliters consumed of Bottle 1 containing a 2% sucrose water solution when followed by a water solution containing either: 32% sucrose (Top: Contrast Condition) or 2% sucrose (Bottom: No Contrast Condition) by 7- month-old and 26-month-old Fisher 344 – Brown Norway rats.

Figure 2. Mean milliliters consumed of Bottle 2 containing either a 32% sucrose water solution (Top: Contrast Condition) or a 2% sucrose water solution (Bottom: No Contrast Condition) when preceded by a water solution containing 2% sucrose by 7- month-old and 26-month-old Fisher 344 – Brown Norway rats.

Figure 3. Total Mean milliliters consumed of a water solution containing 2% sucrose and a water solution containing 32% sucrose presented (Contrast Condition) by 7- month-old and 26-month-old Fisher 344 – Brown Norway rats.