Neuropsychology
2010, Vol. 24, No. 4, 534–541

0894-4105/10/$12.00 DOI: 10.1037/a0018652

Adult Age Differences in Learning From Positive and Negative Probabilistic Feedback

Jessica R. Simon
Georgetown University

James H. Howard, Jr.
Georgetown University and Catholic University of America

Darlene V. Howard
Georgetown University

Objective: Past research has investigated age differences in frontal-based decision making, but few studies have focused on the behavioral effects of striatal-based changes in healthy aging. Feedback learning has been found to vary with dopamine levels; increases in dopamine facilitate learning from positive feedback, whereas decreases facilitate learning from negative feedback. Given previous evidence of striatal dopamine depletion in healthy aging, we investigated behavioral differences between college-aged and healthy older adults using a feedback learning task that is sensitive to both frontal and striatal processes. ***Method:*** Seventeen college-aged (M = 18.9 years) and 24 healthy, older adults (M = 70.3 years) completed the Probabilistic Selection task, in which participants are trained on probabilistic stimulus-outcome information and then tested to determine whether they learned more from positive or negative feedback. ***Results:*** As a group, the older adults learned equally well from positive and negative feedback, whereas the college-aged group learned more from positive than negative feedback, $F(1, 39) = 4.10$, $p < .05$, $r_{effect} = .3$. However, these group differences were not due to older *individuals* being more balanced learners. Most individuals of both ages were balanced learners, but while all of the remaining young learners had a positive bias, the remaining older learners were split between those with positive and negative learning biases ($\chi^2(2) = 6.12$, $p < .047$). ***Conclusions:*** These behavioral results are consistent with the dopamine theory of striatal aging, and suggest there might be adult age differences in the kinds of information people use when faced with a current choice.

Keywords: aging, decision making, probabilistic selection, dopamine hypothesis

Older adults make complex choices concerning finances, medical care, and estate planning. Given the personal and social implications of such choices, it is important to study age differences in decision making. Learning from feedback is an essential component of decision making because positive and negative outcomes of previously made decisions influence current choices. Such learning involves a number of brain regions, including the striatum and prefrontal cortex (Schultz, 2000), both of which undergo significant age-related changes.

One way feedback-based learning has been examined is through the Probabilistic Selection task (Frank, Seeberger, & O'Reilly, 2004), which we have adopted in the current study. In this paradigm, people learn stimulus-outcome information about stimuli presented in pairs. Participants select one stimulus, with probabilistic feedback indicating whether or not this choice was correct. One symbol in each pair is associated more often with positive feedback and the other with negative feedback. After training, the stimuli are presented again in novel pairings during a test phase without feedback. This test phase makes it possible to dissociate positive from negative feedback learning by comparing responses to novel pairs that involve either the most or the least rewarded stimuli. In other words, this task reveals which feedback event during training had been more influential in guiding behavior during novel test choices, and hence whether people learned to choose the option that led to a positive outcome or to avoid the option that led to a negative outcome, that is, the proverbial "carrot or stick" (Frank et al., 2004).

Dopamine levels have been found to influence positive versus negative feedback learning in the Probabilistic Selection task, such that increased dopamine is advantageous for learning from positive feedback via the direct pathway of the striatum and decreased dopamine is beneficial for learning from negative feedback via the indirect pathway (Frank, 2005; Frank, Moustafa, Haughey, Curran, & Hutchison, 2007a; Frank et al., 2004). For example, a Probabilistic Selection study of Parkinson's disease (PD) patients with and without dopamine-agonist medications revealed that PD patients off medications, with reduced dopamine, were more likely to avoid decisions associated with negative feedback than they were to choose those associated with positive feedback (Frank et al., 2004). The reverse was true when these same patients took do-

Jessica R. Simon and Darlene V. Howard, Department of Psychology, Georgetown University; James H. Howard, Jr., Department of Neurology, Georgetown University and Department of Psychology, Catholic University of America.

This research was supported by Grant R37 AG15450 from the National Institute on Aging/National Institutes of Health. The authors want to thank Dr. Michael Frank at the University of Arizona for providing the Probabilistic Selection program. Additional thanks to Alison Lenet and Meghan Shapiro for help in testing participants, and Ilana Bennett and Dr. Frank for helpful comments and discussion. Preliminary findings from this project were presented at the 12th Bienniel Meeting of the Cognitive Aging Conference, Atlanta, GA, April 2008.

Correspondence concerning this article should be addressed to Jessica R. Simon, Georgetown University, Department of Psychology, 301 N. White Gravenor Building, Washington, DC 20057. E-mail: jrs92@georgetown.edu

pamine-elevating medications. A second Probabilistic Selection study investigated polymorphisms of different dopamine-related genes among healthy young (18–35 years) adults (Frank et al., 2007a). Here, a polymorphism associated with increased activity (e.g., increased dopamine levels or increased postsynaptic dopamine receptors) in the direct pathway of the striatum (i.e., the rs907094 polymorphism of the DARPP-32 protein) predicted greater learning from positive feedback, whereas a different genetic polymorphism associated with increased activity in the indirect pathway (i.e., the C957T polymorphism within the DRD2 gene) predicted more learning from negative feedback. In contrast, a frontal dopaminergic gene (Catechol-*O*-methyl transferase [COMT]) was not predictive of either feedback learning bias. Instead, this gene predicted trial-to-trial adjustments made during training (i.e., win-stay vs. lose-shift), reflecting the ability to maintain reinforcement outcomes in working memory to adjust behavior on subsequent trials (Frank et al., 2007a; Waltz, Frank, Robinson, & Gold, 2007). These results provide evidence for striatal dopaminergic involvement in the Probabilistic Selection task, as well as a frontal-dependent component of reinforcement learning during initial acquisition.

Most aging studies of feedback learning and decision making have been limited to tasks that can only tap frontal-dependent decision making processes. For example, the Iowa Gambling task (Bechara, Damasio, Damasio, & Anderson, 1994) assesses working memory via trial-to-trial learning of reinforcement contingencies and has been used to investigate decision-making associated with the ventromedial prefrontal cortex in older adults (Denburg, Tranel, & Bechara, 2005; Kovalchik, Camerer, Grether, Plott, & Allman, 2005; Wood, Busemeyer, Koling, Cox, & Davis, 2005). This focus on frontal-based processes has been driven by the "frontal lobe hypothesis of aging" (West, 1996), which suggests that impairments on frontal-dependent cognitive tasks result from age-related structural changes in associated regions, such as disproportionate age-related loss of frontal brain volume (Head, Snyder, Girton, Morris, & Buckner, 2005; Raz, 2000).

Age-related differences in the striatum and their implications for learning and decision making have been largely ignored, despite consistent and robust findings of age differences in this region, including increases in iron deposits (Raz, 2000) and reductions in volume (Gunning-Dixon, Head, McQuain, Acker, & Raz, 1998; Raz et al., 2003) and dopamine receptor density (Larisch et al., 1998; Pohjalainen, Rinne, Nagren, Syvalahti, & Hietala, 1998; Rinne, 1987; Rinne, Lonnberg, & Marjamaki, 1990; Wang et al., 1996; Wong et al., 1984; Wong, Young, Wilson, Meltzer, & Gjedde, 1997). In fact, neuronal damage similar to PD has been observed in substantia nigra dopaminergic cells of healthy adults over 70 years of age, with similar findings expected within the neostriatum (Kraytsberg et al., 2006). It is likely that these age-related losses of dopamine in striatal networks affect the functional processes of feedback-based learning and ultimately, decision making in older adulthood, consistent with a dopamine hypothesis of cognitive aging (Backman, Nyberg, Lindenberger, Li, & Farde, 2006).

The few studies that have considered age-related striatal dysfunction or dopamine losses and feedback-based learning have reported age differences (Mell et al., 2005; Schmitt-Eliassen, Ferstl, Wiesner, Deuschl, & Witt, 2007; Weiler, Bellebaum, & Daum, 2008). For instance, preliminary functional imaging data mentioned in a review by Marschner et al. (2005) showed reduced ventral striatal activation among older adults with impaired reward processing during probabilistic reversal learning, suggesting that ventral striatum dysfunction plays a role in altering the reward system and decision making in older adults. Additionally, Frank and Kong (2008) found age-related behavioral differences in feedback learning in older adulthood, which they believed were the result of age-related striatal dopamine declines. When given the Probabilistic Selection task, a group in their upper 70s ($M = 77 \pm 3.0$) demonstrated a greater tendency to learn from negative feedback relative to positive feedback than adults just 10 years younger ($M = 67 \pm 3.5$). The latter young-old group actually demonstrated no specific bias toward learning from positive or negative feedback; as a group, these young-old adults learned equally well from both. Moreover, the old-old adults demonstrated a reduction in the frontal-based trial-to-trial learning from positive feedback during training when compared with the young-old adults. Overall, such findings suggest that feedback learning does change during the later years of life, perhaps because of changes in frontostriatal regions that accompany aging.

The current study extended previous work on feedback-based learning in two ways. First, we carried out a direct comparison of college-aged and young-old adults on the Probabilistic Selection task used by Frank and Kong (2008). Although healthy adults of various ages have been tested in separate studies, often serving as comparison groups for patient populations, we are aware of no data that enable a direct comparison of learning between these two age groups on this task. In fact, comparisons across existing studies might at first suggest that the age groups we tested would not differ. Frank and Kong's (2008) young-old group, as well as groups of similar ages in their other studies, have shown balanced learning from positive and negative feedback (Frank, Samanta, Moustafa, & Sherman, 2007b; Frank et al., 2004), while young adult groups in other studies have also shown this balanced pattern (Frank & O'Reilly, 2006; Frank, Woroch, & Curran, 2005). However, we reasoned that age differences might not be apparent in such cross-experiment comparisons because the young groups always included very wide age ranges, such as 18–29 (Frank et al., 2005) and 18–35 (Frank & O'Reilly, 2006). This is important because changes in striatal brain regions start in early adulthood, with monotonic dopamine declines beginning in the early 20s (see Reeves, Bench, & Howard, 2002 for a review; van Dyck et al., 2002; Volkow et al., 1996). Therefore, in the present study we tested young adults ranging in age from 18–20, before such dopamine decline is present. Based on a dopamine hypothesis of aging, we predicted an age by feedback bias interaction, such that college-aged adults would learn more from positive than negative feedback, but the healthy young-old group would not demonstrate a preference to either positive or negative feedback.

The second way in which we went beyond previous work is in investigating whether these group patterns of feedback learning hold at the individual level. In earlier reports it is not possible to tell the extent to which individuals display balanced versus biased learning because only group data are reported. For example, Frank's earlier results (Frank & Kong, 2008; Frank et al., 2004) which we expect to replicate, suggest that as a group, young-old adults of the age we are studying here are balanced learners, in that they learn equally well from both positive and negative outcomes. But, such group data could mean either that individual young-old

adults tend to be balanced learners, as previous studies claim, or that approximately equal numbers of individuals in the group show a positive feedback bias versus a negative bias. In the latter case, characterizing older people as balanced learners is misleading; group dynamics of aging may not apply at the individual level (Hofer & Sliwinski, 2001). The distinction is also important theoretically, given that there are large individual differences in dopamine levels in older adults (Backman et al., 2000) and in the rate of dopamine decline shown by individuals (see Reeves et al., 2002), the dopamine hypothesis of aging would predict that older people of a given age will differ from each other in the extent to which they show positive versus negative feedback learning biases.

In addition to these major aims, we also compared frontal-based training strategies between college-aged students and young-old adults, by assessing trial-to-trial learning of reinforcement contingencies early in training. Similarities between age groups on this measure would suggest that any age differences observed in learning from positive and negative outcomes are more likely because of differences in striatal based processes than frontal based strategies or overall impairment.

Methods

Participants

Participants were 17 Georgetown University students, ranging from 18–20 years of age (M = 18.9 years, SD = .8) and 24 healthy, community-dwelling older adults who had responded to advertisements in the *Washington Post* Health Section, ranging from 64–87 years of age (M = 70.3 years, SD = 5.3). All but four of these old individuals (aged 75, 77, 79, and 87) were 72 or younger, thus making our sample comparable in age to the young-old group from Frank and Kong (2008), which had a mean age of 67. Participants were given a brief health screening questionnaire with exclusionary criteria including having a neurological disease or disorder, using drugs known to influence cognitive functioning, having physical problems (e.g., visual impairments) or disabilities (e.g., arthritis or back problems) that prevent them from comfortably completing the computerized cognitive testing and/or meeting criteria for dementia (i.e., score below 27 on the Mini-Mental Status Exam). Two of the college-aged adults reported use of dopaminergic medications, but analyses conducted with and without them yielded identical patterns of results and statistical significance, so their data are included here.

Participants received either monetary compensation or course credit. The Georgetown University Institutional Review Board approved the experimental procedures, and all participants gave informed consent before their inclusion in this study in accordance with the principles set out in the Declaration of Helsinki. Demographic information and neuropsychological test results are in Table 1. All participants scored within the age-expected range for the neuropsychological measures, with the typical pattern of age-related deficits in measures of processing speed and memory, but not vocabulary. Mini-Mental State Examination scores were ≥27 for all participants, though scores were not obtained for the college-aged group or for two old adults.

Table 1
Demographics and Neuropsychological Test Results

	College-aged (n = 17)	Old (n = 24)
Demographics		
Age*	18.9 ± .8	70.3 ± 5.3
Men/women	6/11	6/18
Years of education*	13.6 ± 1.5	16.3 ± 3.1
Neuropsychological tests		
Mini-mental state examination[a]	N/A	29.3 ± 1.0
WAIS-III vocabulary[b,*]	61.7 ± 6.2	69.1 ± 6.1
WAIS-III digit symbol coding[c,*]	89.9 ± 9.7	62.9 ± 11.3
WAIS-III digit symbol pairing[d,*]	15.8 ± 2.8	10.6 ± 4.7
WAIS-III digit symbol recall[e,*]	8.2 ± 1.1	6.8 ± 1.5

Note. All scores are given as mean ± SD neuropsychological tests screened for dementia[a] and measured vocabulary[b], processing speed[c], cued recall[d], and free recall[e].
* Significant age difference, $p < .005$.

Materials and Procedure

The task, instructions and all stimuli were created by and taken from Frank et al. (2004). Stimuli for the Probabilistic Selection task consisted of six different Japanese Hiragana characters. These stimuli were chosen because they are not easily verbalized, minimizing explicit strategy use during the task (Frank et al., 2004). Hiragana character assignment to stimulus elements was counterbalanced across subjects.

Participants were asked to view pairs of visual stimuli presented on a computer monitor. They were told to select the stimulus they judged as correct from each pair by pressing the *z* (to select the left character) or / (to select the right character) on the keyboard. The position of the correct stimulus was randomized. Once a response was detected, participants received visual feedback of either "correct" or "incorrect." If no response was made, the words "no response detected" appeared after 4 s. Participants were told to make selections by trial and error initially, but that with practice, they would learn which figure is correct. Once participants had decided which symbol was more likely to be correct, they were instructed to stick with it for the rest of the experiment (unless they discovered they were initially wrong in this selection).

Participants completed a training phase followed by a test phase. During *training*, participants were required to select the most rewarded stimulus from three pairs (e.g., AB, CD, EF) that were presented in a random order. The feedback was probabilistic, such that choosing stimulus A, C, and E was correct 80, 70, and 60% of the time, respectively. Each pair was presented 20 times in a 60-trial block. Performance during training was evaluated after each block of 60 trials. Participants advanced to a test phase once they met a specified performance criterion for a given block (selection of A in at least 65% of AB pairs, C in 60% of CD pairs, and E in 50% of EF pairs) or after six blocks of training (360 trials). Like Frank and colleagues, we used the 50% criterion for pair EF because stimulus E is only correct 60% of the time and this is particularly difficult for participants to learn. This criterion ensures that participants with a preference for stimulus F from the outset learn that this choice is not consistently correct. At *test*, participants were tested without feedback on the three training

pairs and on all possible novel pair combinations. Participants viewed the 15 possible pairs four times each, making one 60-trial test block.

Results

Overall Learning Performance

To determine whether there were age differences in overall Probabilistic Selection learning, we examined blocks to criterion during the training phase and accuracy on novel pairs during the test phase. During training, a larger proportion of college-aged (16/17) than older adults (18/24) reached performance criterion. Of those who met it, the age groups did not differ significantly in their number of training blocks to criterion (College-aged adults: 2.31, $SE = .37$; Old adults: 2.78, $SE = .42$; $t(32) = .81$, $p > .42$, $r_{effect} = .14$). All analyses were conducted with and without those people who failed to meet criterion, but because the pattern of results and statistical significance did not change, all individuals were included in the subsequently reported analyses.

At test, the age groups did not differ significantly in their accuracy on novel pairs (College-aged adults: .71, $SE = .03$; Old adults: .66, $SE = .03$; $t(39) = -1.04$, $p > .30$, $r_{effect} = .14$).

Group Differences in Feedback-Based Learning Biases Assessed at Test

Following Frank et al. (2004), we investigated positive and negative feedback learning biases by comparing correct performance on the 8 novel test pairs that involved either the most rewarded (A) or least rewarded (B) stimulus. A participant who focused on the positive feedback from stimulus A during training would reliably choose A in the novel pairs in which it was present during test, whereas a participant who focused on the negative feedback from stimulus B would reliably avoid B when it was presented during test. Thus, greater accuracy on Choose A than Avoid B pairs indicates a preference to learn from positive feedback while the reverse pattern indicates a preference to learn from negative feedback.

The mean accuracy on Choose A and Avoid B pairs for both age groups is shown in Figure 1. A two-way ANOVA was conducted on these data, with Group (College-aged vs. Old) varying between-subjects and Bias Type (Choose A vs. Avoid B) varying within-subjects. There was no main effect of Group, $F(1, 39) = .38$, $p > .54$, $r_{effect} = .1$, indicating no overall age differences in accuracy on these novel pairs. There was also no main effect of Bias Type, $F(1, 39) = 1.42$, $p > .24$, $r_{effect} = .17$, showing no overall differences between performance on Choose A versus Avoid B pairs. Most important, there was a significant Group × Bias Type interaction, $F(1, 39) = 4.10$, $p < .05$, $r_{effect} = .3$. College-aged adults showed a positive learning bias in that they were significantly more accurate on Choose A than on Avoid B pairs, $t(16) = 2.27$, $p < .04$, $r_{effect} = .49$, whereas older adults were not, $t(23) = -.62$, $p > .54$, $r_{effect} = .14$.

Individual Learning Biases Assessed at Test

The analyses of older adults just reported replicate Frank and Kong (2008; Frank et al., 2007b; Frank et al., 2004) findings that at the group level, young-old adults show balanced learning. To determine whether this balanced learning is an individual or group phenomenon, we calculated a difference score for each subject that consisted of proportion correct on Choose A minus proportion correct on Avoid B, during the test phase. Figure 2 depicts these data, with each bar showing the difference score for a single participant and the participants being ordered within each age group by the magnitude of the difference score. Because individuals might get a nonzero difference score by chance, we computed individual chi square tests comparing the frequency correct on choose A versus avoid B pairs for each subject. We found that the smallest Choose A minus Avoid B difference score that consistently reached marginal significance ($p < .10$) was ±.25. Therefore (as depicted by dotted lines in Figure 2), we classified any subject with a difference score *greater than* or *equal to* .25 as having a positive bias and any subject with a difference score *less than* or *equal to* −.25 as having a negative bias. All others were considered balanced learners. Of the 17 college students, 6 showed a positive bias, 0 showed a negative bias, and the remaining 11 were balanced learners and of the 24 old adults, 5 showed a positive bias, 7 showed a negative bias, and the remaining 12 were balanced learners. Participants who did not meet performance criterion did not account for any one particular learning bias; hence, the fact that more old than college-aged adults failed to meet criterion cannot explain these results. A chi-square test to determine whether the distribution of learning biases differed between the age groups was significant, $\chi^2(2) = 6.12$, $p < .047$. At the individual level, most participants of both ages (65% of college-aged and 50% of older) were balanced learners; however, the age groups differed in that all of the remaining young learners had a positive bias, whereas the remaining older learners were approximately equally split between positive and negative learning biases. Interestingly, older adults categorized as having a positive bias ($n = 5$, $M = 68.2$ years, $SE = 1.6$) were marginally younger than those with a negative learning bias ($n = 7$, $M = 72.6$ years, $SE = 1.7$), $t(10) = 1.787$, $p = .052$, one-tailed, $r_{effect} = .24$, consistent with the findings from Frank and Kong (2008) who

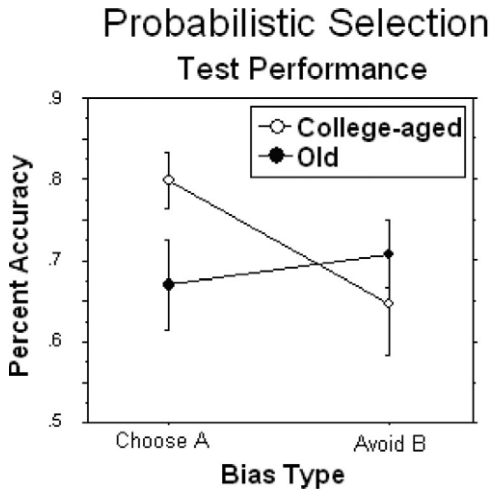

Figure 1. Accuracy on novel test pairs involving stimulus A (Choose A) versus stimulus B (Avoid B) for college-aged and old adults. Error bars reflect standard error of the mean.

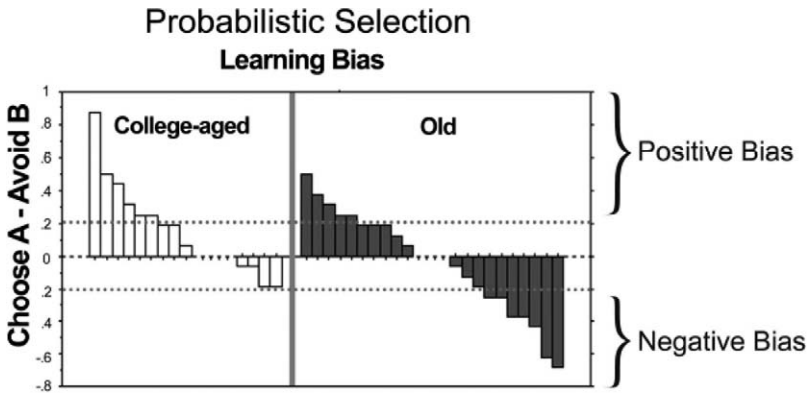

Figure 2. Individual participants' difference scores (Choose A accuracy minus Choose B accuracy) reflecting individual subjects' biases to learn from either positive (Choose A) or negative (Avoid B) feedback for college-aged and old adults. Each bar represents an individual subject, and within each age group, participants are ordered by the magnitude of their difference score. The blank spaces in the middle of each age group depict participants with difference scores of zero. The dotted lines represent the threshold for positive or negative learning biases; individuals with a difference score greater than or equal to the upper dotted line have a positive bias and those with a difference score less than or equal to lower dotted line have a negative bias.

reported negative feedback biases in a group of older-old adults relative to their young-old counterparts.

Win-Stay versus Lose-Shift Strategies During Training

To assess potential group differences in the prefrontal-dependent process of rapidly learning probabilistic contingencies (Frank et al., 2007a), we analyzed trial-to-trial strategies used during the first training block only. Following Frank, we restricted our analysis to the first block of training, when the effects of feedback from individual trials can be assessed more clearly, before learning of the probabilities across trials has occurred. This analysis assessed the performance adjustments participants made on each pair after receiving positive or negative feedback during training, reflecting the ability to keep reinforcement information online during intervening trials (Waltz, Frank, Robinson, & Gold, 2007). For example, if participants selected stimulus A in an AB trial and received positive feedback, they could use this feedback to guide their performance the next time this pair appeared by choosing A again. This "win-stay" strategy was calculated as the number of times that a participant stayed with the same selection after receipt of positive feedback divided by the total number of training trials that resulted in positive feedback. If, however, a participant selected stimulus B in the above example and received negative feedback, this feedback could be used to avoid selecting stimulus B in the next presentation of an AB pair. This "lose-shift" strategy was calculated as the proportion of negative feedback trials where a participant switched to the other stimulus in the pair.

A two-way ANOVA was conducted, with Group (College-aged vs. Old) as a between-subjects variable and Training Strategy (Win-Stay vs. Lose-Shift) as a within-subject variable. There was a main effect of Training Strategy, $F(1, 39) = 142.70$, $p < .0001$, $r_{effect} = .89$, with people being more likely to use a win-stay than lose-shift strategy, as is apparent in Figure 3. Although Figure 3 suggests that the college-aged group was slightly more likely to win-stay than the older group, neither the main effect of Group nor the Training Strategy by Group interaction approached significance, p's $> .11$. Thus, during the first training block, both groups used similar frontal-based strategies, in that both college-aged and old adults preferred the same training strategy (i.e., win-stay over lose-shift).

Discussion

This study used the Probabilistic Selection task to examine age differences in feedback-based learning and extended previous findings in two ways. First, as predicted, we found a significant interaction between age and feedback bias in the first direct com-

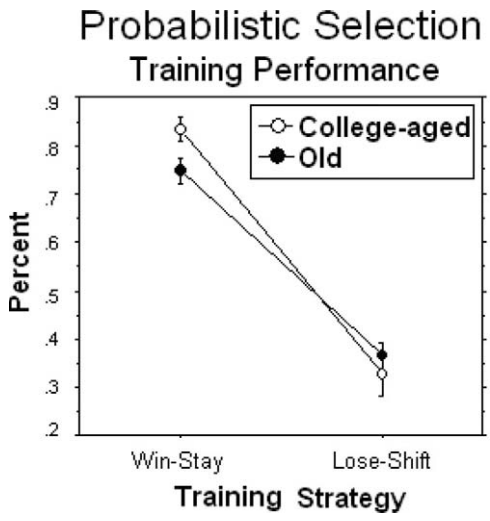

Figure 3. Trial-to-trial learning strategies from positive and negative feedback (win-stay vs. lose-shift) during training. Error bars reflect standard error of the mean.

parison of college-aged and young-old adults; as a group, the young-old adults learned equally well from positive and negative feedback, whereas the college-aged group learned more from positive than negative feedback. Second, examination of individual learning bias revealed that these group differences were not because of the older *individuals* being more balanced learners; 50% of the old and 65% of the college-aged were balanced learners. However, while the nonbalanced older individuals were equally divided between those with a positive and negative bias, all of the nonbalanced college-aged adults had a positive learning bias.

In the following, we first compare our results with existing studies and consider likely explanations for the age differences observed. We then outline three general implications of our results.

Age Group Differences in Feedback-Based Learning Biases

This study is the first to demonstrate an age difference in learning biases via a direct comparison of young-old and college-aged groups. Our finding that the young-old group learned equally well from positive and negative feedback replicates earlier results (Frank et al., 2007b; Frank et al., 2004). However, our data go beyond previous findings by showing that although half of the older individuals were balanced learners, the remainder was approximately equally divided between positive and negative learners. Consistent with Frank and Kong (2008), within our old group, the positive learners tended to be younger than the negative learners. This characterization of individual learning biases is not only important for revealing heterogeneity in individual learning and decision-making, but also for evaluating the dopamine theory of age-related differences as we discuss below.

Our finding of a positive learning bias in college-aged adults as a group is unique, in that earlier research with young adult groups in their 20s through early 30s had revealed balanced learning (Frank & O'Reilly, 2006; Frank et al., 2005). Methodological differences between studies are not the likely cause of these different findings; although the task used by Frank and colleagues (2005) had been adapted to measure event-related potentials, Frank and O'Reilly's (2006) task was identical to ours. It is possible that this discrepancy reflects some unknown factor such as genetic variation across studies (Frank et al., 2007a). Another possible reason that our young group revealed a positive feedback bias is that our sample was limited to 18- to 20-year-olds. In fact, individual analyses revealed that the majority of our young adults (65%) were balanced learners while the remaining 35% were all positive learners, which led the group as a whole to show a significant positive bias. If 30-year-olds are more likely to show a balanced or negative bias than 20-year-olds, then including a few 30-year-olds in our study might have removed the overall positive group bias we report here. Of course, this is speculative; because individual data on learning biases were not presented in earlier work, we cannot be sure that it is these few older "young" people who influenced the group data in earlier reports. This fact, combined with our relatively small and limiting sample size, suggests that definitive answers about feedback-based learning biases in young adulthood will require studies in which the relation between age and feedback biases is examined during the early adult years, with a particular focus on heterogeneity in learning biases.

We can rule out group differences in either overall performance or trial-by-trial learning strategies as an explanation for the age differences we observed. Regarding overall performance, although fewer older than younger adults reached criterion during training, the critical age group by bias type interaction persisted even after eliminating those participants who failed to meet criterion. Furthermore, the rate of learning, as measured by blocks to criterion, did not correlate significantly with either positive ($r(39) = -.25$, $p > .11$) or negative ($r(39) = -.09$, $p > .57$) feedback biases at test, and the age groups did not differ in their overall accuracy on novel test pairs. Age differences in frontal-based learning strategies can also be ruled out as an explanation because the age groups showed a similar preference for a win-stay over a lose-shift strategy.

Instead, we think that the presence of negative learners in the older but not the college-aged group is consistent with the dopamine hypothesis of cognitive aging that motivated this study. This hypothesis suggests that many cognitive changes associated with normal aging are related to simultaneous declines in dopamine availability (Backman et al., 2000; Volkow et al., 1998; Wang et al., 1998) which begin in early adulthood (Reeves et al., 2002). Our inference is based on previous literature which, as summarized in the Introduction, has shown that dopamine levels generally decline with age (e.g., Rinne, 1987) and that low dopamine leads to a bias to learn more from negative than positive feedback (Frank, 2005; Frank et al., 2007a; Frank & O'Reilly, 2006; Frank et al., 2007b; Frank et al., 2004; Klein et al., 2007).

We do not have the biological evidence here to substantiate this hypothesized role of dopamine in explaining our findings. Future research could more directly determine the cause for a risk avoidant, negative feedback bias in some older adults by capitalizing on the inter-individual variability in feedback-based learning biases in the older group reported here. For example, striatal dopamine levels could be correlated with learning scores to determine if individual feedback biases are linked to dopamine availability. In addition, future studies should investigate the extent to which feedback-based learning biases are because of tendency versus ability. That is, if a negative feedback bias is dopamine-related, then the older adults would have more trouble focusing on positive outcomes than college-aged adults even when instructed to do so.

General Implications

There are three more general implications of the current study. The first is that our findings highlight the need for more attention to the consequences of age-related striatal deficiency, because most studies of decision making in older adults have focused on frontal-lobe dysfunction. In fact, most of these studies have shown that the majority of old adults are successful at solving the frontal-dependent Iowa Gambling task (Kovalchik et al., 2005; Stout, Rodawalt, & Siemers, 2001; Wood et al., 2005), with only a small subset showing impairment (Denburg et al., 2005). Consistent with these findings, the current study found that the young-old and college student groups did not differ in frontal-dependent processes (i.e., win-stay vs. lose-shift strategies), also supporting Greenwood's (2000) argument that age-related changes are not limited to the frontal regions.

The second implication is that surface level similarities between college-aged and old adults often mask underlying age differences. Although measures of overall accuracy on novel pairs would suggest that our college students and old adults had learned successfully and equally, what and how they had learned differed. Fera et al. (2005) had also shown similar overall accuracy of probabilistic learning between young and older adults using a different task, but fMRI revealed deficient striatal activation among older adults. Similarly, Wood and colleagues (2005) demonstrated different decision strategies used by younger and older adults despite similar accuracy on the Iowa Gambling task.

Finally, the present study adds to evidence demonstrating an asymmetry between positive and negative emotional experiences across the life span (Carstensen & Mikels, 2005). Carstensen and colleagues have proposed a socioemotional selectivity theory of aging, and presented evidence that older adults place more emphasis on positive emotional experiences as they approach the end of life (Carstensen, 2006). One understudied aspect of this age-related optimization is how older adults respond to positive and negative *feedback* versus positive and negative *stimuli*. Previous studies found that older adults have an attentional bias to positive versus negative *stimuli*, because positive stimuli generate feelings of well-being (e.g., Charles, Mather, & Carstensen, 2003; Mather & Carstensen, 2003). Some older adults in the current study may have paradoxically focused on negative *feedback* to increase the well-being that results from avoiding mistakes. This hypothesis is supported by previous results showing that an age-related attempt to reduce negative arousal during anticipation of negative outcomes may have increased overall feelings of well-being (Samanez-Larkin et al., 2007). More research is needed to determine how feedback-learning relates to the socioemotional selectivity theory of aging.

In summary, our results show that most individuals of the ages studied here are balanced learners. However, the remaining nonbalanced college-aged adults all learn more from positive than negative outcomes of their decisions in a probabilistic task, while healthy young-old adults who are nonbalanced learners are approximately equally divided between those biased toward learning from positive versus negative outcomes. These findings may reflect age-related trajectories of striatal dopamine, though direct evidence for this link awaits future research. The implications of these biases for real-world decision making should also be a topic for future research, but our results suggest that old adults differ from young in the kinds of information from past experience they focus on when faced with a current choice.

References

Backman, L., Ginovart, N., Dixon, R. A., Wahlin, T. B., Wahlin, A., Halldin, C., & Farde, L. (2000). Age-related cognitive deficits mediated by changes in the striatal dopamine system. *American Journal of Psychiatry, 157,* 635–637.

Backman, L., Nyberg, L., Lindenberger, U., Li, S. C., & Farde, L. (2006). The correlative triad among aging, dopamine, and cognition: Current status and future prospects. *Neuroscience and Biobehavioral Reviews, 30,* 791–807.

Bechara, A., Damasio, A. R., Damasio, H., & Anderson, S. W. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition, 50,* 7–15.

Carstensen, L. L. (2006). The influence of a sense of time on human development. *Science, 312,* 1913–1915.

Carstensen, L. L., & Mikels, J. A. (2005). At the intersection of emotion and cognition: Aging and the positivity effect. *Current Directions in Psychological Science, 14,* 117–121.

Charles, S. T., Mather, M., & Carstensen, L. L. (2003). Aging and emotional memory: The forgettable nature of negative images for older adults. *Journal of Experimental Psychology: General, 132,* 310–324.

Denburg, N. L., Tranel, D., & Bechara, A. (2005). The ability to decide advantageously declines prematurely in some normal older persons. *Neuropsychologia, 43,* 1099–1106.

Fera, F., Weickert, T. W., Goldberg, T. E., Tessitore, A., Hariri, A., Das, S., . . . Mattay, V. S. (2005). Neural mechanisms underlying probabilistic category learning in normal aging. *Journal of Neuroscience, 25,* 11340–11348.

Frank, M. J. (2005). Dynamic dopamine modulation in the basal ganglia: A neurocomputational account of cognitive deficits in medicated and nonmedicated Parkinsonism. *Journal of Cognitive Neuroscience, 17,* 51–72.

Frank, M. J., & Kong, L. (2008). Learning to avoid in old age. *Psychology and Aging, 23,* 392–398.

Frank, M. J., Moustafa, A. A., Haughey, H. M., Curran, T., & Hutchison, K. E. (2007a). Genetic triple dissociation reveals multiple roles for dopamine in reinforcement learning. *Proceedings of the National Academy of Sciences, USA of the United States of America, 104,* 16311–16316.

Frank, M. J., & O'Reilly, R. C. (2006). A mechanistic account of striatal dopamine function in human cognition: Psychopharmacological studies with cabergoline and haloperidol. *Behavioral Neuroscience, 120,* 497–517.

Frank, M. J., Samanta, J., Moustafa, A. A., & Sherman, S. J. (2007b). Hold your horses: Impulsivity, deep brain stimulation, and medication in Parkinsonism. *Science, 318,* 1309–1312.

Frank, M. J., Seeberger, L. C., & O'Reilly, R. C. (2004). By carrot or by stick: Cognitive reinforcement learning in Parkinsonism. *Science, 306,* 1940–1943.

Frank, M. J., Woroch, B. S., & Curran, T. (2005). Error-related negativity predicts reinforcement learning and conflict biases. *Neuron, 47,* 495–501.

Greenwood, P. M. (2000). The frontal aging hypothesis evaluated. *Journal of the International Neuropsychological Society, 6,* 705–726.

Gunning-Dixon, F. M., Head, D., McQuain, J., Acker, J. D., & Raz, N. (1998). Differential aging of the human striatum: A prospective MR imaging study. *American Journal of Neuroradiology, 19,* 1501–1507.

Head, D., Snyder, A. Z., Girton, L. E., Morris, J. C., & Buckner, R. L. (2005). Frontal-hippocampal double dissociation between normal aging and Alzheimer's disease. *Cerebral Cortex, 15,* 732–739.

Hofer, S. M., & Sliwinski, M. J. (2001). Understanding Ageing. An evaluation of research designs for assessing the interdependence of ageing-related changes. *Gerontology, 47,* 341–352.

Klein, T. A., Neumann, J., Reuter, M., Hennig, J., von Cramon, D. Y., & Ullsperger, M. (2007). Genetically determined differences in learning from errors. *Science, 318,* 1642–1645.

Kovalchik, S., Camerer, C. F., Grether, D. M., Plott, C. R., & Allman, J. M. (2005). Aging and decision making: A comparison between neurologically healthy elderly and young individuals. *Journal of Economic Behavior and Organization, 58,* 79–94.

Kraytsberg, Y., Kudryavtseva, E., McKee, A. C., Geula, C., Kowall, N. W., & Khrapko, K. (2006). Mitochondrial DNA deletions are abundant and cause functional impairment in aged human substantia nigra neurons. *Nature Genetics, 38,* 518–520.

Larisch, R., Meyer, W., Klimke, A., Kehren, F., Vosberg, H., & Muller-Gartner, H. W. (1998). Left-right asymmetry of striatal dopamine D2 receptors. *Nuclear Medicine Communications, 19,* 781–787.

Marschner, A., Mell, T., Wartenburger, I., Villringer, A., Reischies, F. M., & Heekeren, H. R. (2005). Reward-based decision-making and aging. *Brain Research Bulletin, 67,* 382–390.

Mather, M., & Carstensen, L. L. (2003). Aging and attentional biases for emotional faces. *Psychological Science, 14,* 409–415.

Mell, T., Heekeren, H. R., Marschner, A., Wartenburger, I., Villringer, A., & Reischies, F. M. (2005). Effect of aging on stimulus-reward association learning. *Neuropsychologia, 43,* 554–563.

Pohjalainen, T., Rinne, J. O., Nagren, K., Syvalahti, E., & Hietala, J. (1998). Sex differences in the striatal dopamine D2 receptor binding characteristics in vivo. *The American Journal of Psychiatry, 155,* 768–773.

Raz, N. (2000). Aging of the brain and its impact on cognitive performance: Integration of structural and functional findings. In F. I. M. Craik & T. A. Salthouse (Eds.), *Handbook of aging and cognition* (pp. 1–90). Mahwah, NJ: Erlbaum Association.

Raz, N., Rodrigue, K. M., Kennedy, K. M., Head, D., Gunning-Dixon, F., & Acker, J. D. (2003). Differential aging of the human striatum: Longitudinal evidence. *American Journal of Neuroradiology, 24,* 1849–1856.

Reeves, S., Bench, C., & Howard, R. (2002). Ageing and the nigrostriatal dopaminergic system. *International Journal of Geriatric Psychiatry, 17,* 359–370.

Rinne, J. O. (1987). Muscarinic and dopaminergic receptors in the aging human brain. *Brain Research, 404,* 162–168.

Rinne, J. O., Lonnberg, P., & Marjamaki, P. (1990). Age-dependent decline in human brain dopamine D1 and D2 receptors. *Brain Research, 508,* 349–352.

Samanez-Larkin, G. R., Gibbs, S. E., Khanna, K., Nielsen, L., Carstensen, L. L., & Knutson, B. (2007). Anticipation of monetary gain but not loss in healthy older adults. *Nature Reviews Neuroscience, 10,* 787–791.

Schmitt-Eliassen, J., Ferstl, R., Wiesner, C., Deuschl, G., & Witt, K. (2007). Feedback-based versus observational classification learning in healthy aging and Parkinson's disease. *Brain Research, 1142,* 178–188.

Schultz, W. (2000). Multiple reward signals in the brain. *Nature Reviews Neuroscience, 1,* 199–207.

Stout, J. C., Rodawalt, W. C., & Siemers, E. R. (2001). Risky decision making in Huntington's disease. *Journal of the International Neuropsychological Society, 7,* 92–101.

van Dyck, C. H., Seibyl, J. P., Malison, R. T., Laruelle, M., Zoghbi, S. S., Baldwin, R. M., & Innis, R. B. (2002). Age-related decline in dopamine transporters: Analysis of striatal subregions, nonlinear effects, and hemispheric asymmetries. *American Journal of Geriatric Psychiatry, 10,* 36–43.

Volkow, N. D., Ding, Y. S., Fowler, J. S., Wang, G. J., Logan, J., Gatley, S. J., . . . Gur, R. (1996). Dopamine transporters decrease with age. *The Journal of Nuclear Medicine, 37,* 554–559.

Waltz, J. A., Frank, M. J., Robinson, B. M., & Gold, J. M. (2007). Selective reinforcement learning deficits in schizophrenia support predictions from computational models of striatal-cortical dysfunction. *Biological Psychiatry, 62,* 756–764.

Wang, G. J., Volkow, N. D., Fowler, J. S., Logan, J., Gur, R., Netusil, N., . . . Pappas, N. S. (1996). Age associated decrements in dopamine D2 receptors in thalamus and in temporal insula of human subjects. *Life Sciences, 59,* PL31–PL35.

Weiler, J. A., Bellebaum, C., & Daum, I. (2008). Aging affects acquisition and reversal of reward-based associative learning. *Learning & Memory, 15,* 190–197.

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin, 120,* 272–292.

Wong, D. F., Wagner, H. N., Jr., Dannals, R. F., Links, J. M., Frost, J. J., Ravert, H. T., . . . Kuhar, M. J. (1984). Effects of age on dopamine and serotonin receptors measured by positron tomography in the living human brain. *Science, 226,* 1393–1396.

Wong, D. F., Young, D., Wilson, P. D., Meltzer, C. C., & Gjedde, A. (1997). Quantification of neuroreceptors in the living human brain: III. D2-like dopamine receptors: Theory, validation, and changes during normal aging. *Journal of Cerebral Blood Flow & Metabolism: Clinical and Experimental, 17,* 316–330.

Wood, S., Busemeyer, J., Koling, A., Cox, C. R., & Davis, H. (2005). Older adults as adaptive decision makers: Evidence from the Iowa Gambling Task. *Psychology and Aging, 20,* 220–225.

Received March 15, 2009
Revision received October 13, 2009
Accepted November 23, 2009 ■