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DECISION MAKING ACROSS THE LIFE SPAN

Topic Editors Shu-Chen Li, K. Richard Ridderinkhof and Gregory R. Samanez-Larkin





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DECISION MAKING ACROSS THE LIFE SPAN

Topic Editors:

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Brain systems including the ventral striatum (shown here activated in red/ orange near the center of the brain) play a central role in computing and representing value signals used for making decisions. Image adapted by Gregory Samanez Larkin with permission from original photographer Leroy Skalstad. Learning to choose adaptively between different behavioral options in order to reach goals is a pervasive task in life for people of all ages. Individuals are often confronted with complex, uncertain situations that nonetheless require decisive actions that would facilitate the pursuit of short-term or long-term goals. Adaptive decision making as such entails interactions between processes that monitor the choice-outcome relations as well as processes that evaluate these relations with respect to goal relevance. These dynamics implicate close interplays between attention, learning, memory, motivation, and emotion, which are subserved by cortical-subcortical networks and are neurochemically regulated by transmitters, such as norepinephrine, dopamine, and serotonin. Across the life span, these functional brain circuits as well as neurotransmitter systems undergo basic biological maturation and senescence as well as plasticity due to the accumulation of experience or changes in motivational goals. Studying decision making across different adult life periods may shed light on how the very processes of decision making adapt to constraints on brain resources due to aging, how these processes benefit from experience, or how decision making is influenced by shifting goals.

The aim of this Research Topic in Frontiers in Decision Neuroscience is to open a forum for the subfield of decision science that focuses on comparing and contrasting decision making in people of different ages.

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Complementary approaches to the study of decision making across the adult life span

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Learning to choose adaptively between different behavioral options in order to reach goals is a pervasive task in life for people of all ages. Individuals are often confronted with complex, uncertain situations that nonetheless require decisive actions that would facilitate the pursuit of short-term or long-term goals. Adaptive decision making as such entails interactions between processes that monitor the choice-outcome relations as well as processes that evaluate these relations with respect to goal relevance. These dynamics implicate close interplays between attention, learning, memory, motivation, and emotion, which are subserved by cortical-subcortical networks and are neurochemically regulated by transmitters, such as norepinephrine, dopamine, and serotonin. Across the life span, these functional brain circuits as well as neurotransmitter systems undergo basic biological maturation and senescence as well as plasticity due to the accumulation of experience or changes in motivational goals (Braver and Barch, 2002; Li and Sikström, 2002; Düzel et al., 2010; Li et al., 2010; Mohr et al., 2010; Li, 2013). Studying decision making across different adult life periods may shed light on how the very processes of decision making adapt to constraints on brain resources due to aging, how these processes benefit from experience, or how decision making is influenced by shifting goals.

Multidisciplinary research on decision making and aging is growing at a rapid pace (Brown and Ridderinkhof, 2009; Eppinger et al., 2011; Samanez-Larkin, 2011; Hämmerer and Eppinger, 2012; Samanez-Larkin and Knutson, 2014). Given the increasing interest in work in this area, the aim of this research topic in Frontiers in Neuroscience is to open a forum for the subfield of decision science that focuses on comparing and contrasting decision making in people of different ages. In this series, we have highlighted the range of complementary methodological approaches that are currently being used.

Here we feature empirical work ranging from behavioral (Mather and Schoeke, 2011; Cavanagh et al., 2012; Shivapour et al., 2012; Spaniol and Wegier, 2012; Westbrook et al., 2012; Worthy and Maddox, 2012) and computational (Samanez-Larkin et al., 2011a; Cavanagh et al., 2012; Worthy and Maddox, 2012) to cognitive neuroscience (Samanez-Larkin et al., 2011a) and non-human animal research (Gilbert et al., 2011), investigating age similarities and differences in decision making, together with

theoretical perspectives (Mata et al., 2012) that integrate existing evidence and provides new insights. The papers also cover a broad range of topics including reward effects on learning and memory, risky decision making, intertemporal choice, strategy use, and financial decision making in healthy adults (Gilbert et al., 2011; Mather and Schoeke, 2011; Samanez-Larkin et al., 2011a; Cavanagh et al., 2012; Mata et al., 2012; Shivapour et al., 2012; Spaniol and Wegier, 2012; Westbrook et al., 2012; Worthy and Maddox, 2012) along with a complementary study on susceptibility to misleading advertisements in individuals with frontal cortical damage (Asp et al., 2012).

Despite stereotypes of old age as a life period characterized by global cognitive declines, there are many decision-related processes that remain intact or might even be enhanced in older adults. In this Research Topic, Mather and Schoeke (2011) and Cavanagh et al. (2012) provide evidence for reward effects on memory and risky decision making, respectively, in younger and older adults. In the past several years a growing literature on learning and decision making provides contradictory evidence for differential sensitivity to monetary rewards relative to losses across adulthood (Hämmerer and Eppinger, 2012; Samanez-Larkin and Knutson, 2014). These opposing findings stand in contrast to a larger, related, and more consistent literature on valence effects in attention and memory. These studies find that older adults pay increasingly more attention to and better remember positive relative to negative material (Carstensen and Mikels, 2005; Mather and Carstensen, 2005; Carstensen, 2006). The study by Mather and Schoeke (2011) lies at the intersection of these sets of findings by examining the impact of associating monetary gains and losses with pictures, and subsequently testing memory for these pictures. They observe similar effects in both age groups: Both younger and older adults better remember pictures that were associated with positive outcomes (monetary gains or loss avoidance) than negative outcomes (missed gains or realized losses). There were no age differences; both younger and older adults showed the same reward-enhancement of memory suggesting that the motivating effects of monetary rewards might be preserved across adulthood (Castel et al., 2011). Using a computational model of decision making in the BART task, Cavanagh et al. (2012) show that older adults are not only as sensitive to reward as younger adults but that they may be even more sensitive to reward

compared to young adults in some situations. However, in this task the reward effects lead to excessively risky behavior that may be detrimental to performance in some contexts.

The perspective piece by Mata et al. (2012) in this series provides an in-depth discussion of adaptation to different decision contexts suggesting that what may be an effective strategy in some contexts may be maladaptive in others. An example of this is highlighted in the paper by Worthy and Maddox (2012) that uses computational models of learning and decision making to identify strategy differences between younger and older adults. Consistent with previous studies of age differences in strategy use (Mata et al., 2007, 2010), Worthy and Maddox (2012) show that older adults use a simpler strategy (win-stay/lose-shift) compared to younger adults (who are better fit by a more traditional reinforcement learning model). Using two different decision environments, these authors show that such simpler strategies are adaptive in one context (where future performance is dependent on current choice behavior) but maladaptive in the other context (where future performance is independent of current choice behavior). Related to the issue of adaptation across contexts, Spaniol and Wegier (2012) in this series provide evidence that although older adults show reduced information search in a risky decision task compared to younger adults. Consistent with prior work (Mata and Nunes, 2010), both younger and older adults shift their information search strategies according to the relative probability of monetary gains providing evidence for some level of intact adaptation across adulthood.

Given the evidence for the adaptability of choice in old age, these findings might suggest that it would be beneficial to provide decision strategies to older adults in scenarios where they would be most vulnerable to making mistakes (Samanez-Larkin et al., 2011b). Westbrook et al. (2012) in this series attempt to do just that. They trained younger and older adults to use a specific strategy in a risky decision task to reduce excessive risk aversion. They found no age differences in risk aversion in the task at baseline, but they did observe differential effectiveness of the strategy training across age groups. The older adults tended to abandon the strategy over time and, as a result, the effect of strategy training was smaller overall in the older compared to younger adults. The authors suggest that the effects may be related to goal neglect deficits such that older adults have difficulty maintaining the strategy. However, it is also possible that they perceive the strategy to be less effective than their own baseline strategy and hence intentionally utilize it less and less over time. Independent of whether the age differences are due to cognitive constraints or personal preferences, the study suggests that instructional training or the encouragement of a specific strategy may be less effective in older adults.

Two of the papers in this series examine age differences in discounting of temporal delays (Samanez-Larkin et al., 2011a) and probability (Gilbert et al., 2011). A growing body of prior research has shown that older adults are often more likely to wait for larger, temporally delayed rewards (Löckenhoff, 2011). For the relatively short time delays (seconds to weeks) used in these studies, older adults show reduced discounting of time delays. Samanez-Larkin et al. (2011a,b) in this series provide evidence for similar ventral striatal sensitivity to non-delayed and delayed rewards suggesting that there is a lower temporal discount rate in striatal brain activity in old age. The enhanced sensitivity to immediacy in young adults seems to be reduced across adulthood. This age by delay interaction in the striatum subsequently replicated in another fMRI study with humans (Eppinger et al., 2012) and the same pattern was observed in the orbitofrontal cortex of older compared to younger rodents (Roesch et al., 2012). This increased delay cost tolerance with age may be viewed as adaptive in that larger rewards are obtained after longer delays, however, for some individuals a more general reduction in cost integration may lead to excessively risky choice behavior. Gilbert et al. (2011) in this series show that younger and older animals make similar choices in a probabilistic choice task overall, but that there are strong individual differences in the older animals. A subset of older rats showed a reduced sensitivity to probability, maintaining a preference for probabilistic over certain rewards even when the expected values were lower. These same animals showed a reduced sensitivity to time delays compared to younger animals in a prior study (Simon et al., 2010), demonstrating that there are a subset of older animals who may be overly focused on reward magnitude and are not integrating potential benefits with costs.

Older adults are not always more willing to wait. Shivapour et al. (2012) in this series show that older adults are more likely to make financial decisions without much deliberation compared to younger adults who are more likely to put off financial decisions for later. Although older adults showed higher levels of financial knowledge and reported being highly motivated to prevent financial losses (Shivapour et al., 2012), older individuals are often targets of financial fraud attempts. It is not clear whether they are more susceptible to fraud, but they are disproportionately targeted likely due to their greater financial assets compared to young adults. The age-related positivity effect in attention and memory mentioned above may be beneficial for the promotion of well being in everyday life (Carstensen et al., 2000, 2011), but to the extent that these affective biases are domain general they may also have negative consequences for some financial decisions. Recent evidence for reduced sensitivity in the anterior insula in older age to the prospect of financial loss (Samanez-Larkin et al., 2007), unfair offers in social decision making tasks (Harlé and Sanfey, 2012), and untrustworthy faces (Castle et al., 2012) suggests that older adults may be more vulnerable to making financial mistakes such as falling victim to fraudulent investments. Normal aging is characterized by gradual structural decline of the prefrontal cortex (Grady, 2012), but there are large individual differences in the rate of this decline. To test an extreme case of loss of frontal cortical systems, Asp et al. (2012) in this series show that individuals with frank damage to the prefrontal cortex were more influenced by misleading advertisements. The study suggests that individuals with steeper rates of frontal cortical decline may be the most vulnerable to making financial mistakes.

Overall the series of papers identifies areas of potential improvement, preservation, and decline in decision-related processes across adulthood. A potentially interesting area that we did not cover in this series but one that is gaining recent attention is the examination of differential effects of genetic variability on decision making across the life span (Hämmerer et al., 2013). This collection of papers highlights the range of approaches being used in this area, and the set together provides promising evidence that future discoveries and refinements of theoretical models of human aging will be more comprehensive through the increasing adoption of a multi-method, multidisciplinary approach.

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REFERENCES

- Asp, E., Manzel, K., Koestner, B., Cole, C. A., Denburg, N. L., and Tranel, D. (2012). A neuropsychological test of belief and doubt: damage to ventromedial prefrontal cortex increases credulity for misleading advertising. *Front. Neurosci.* 6:100. doi: 10.3389/fnins.2012.00100
- Braver, T. S., and Barch, D. M. (2002). A theory of cognitive control, aging cognition, and neuromodulation. *Neurosci. Biobehav. Rev.* 26, 809–817. doi: 10.1016/S0149-7634(02)00067-2
- Brown, S. B. R. E., and Ridderinkhof, K. R. (2009). Aging and the neuroeconomics of decision making: a review. *Cogn. Affect. Behav. Neurosci.* 9, 365–379. doi: 10.3758/CABN.9.4.365
- Carstensen, L. L. (2006). The influence of a sense of time on human development. *Science* 312, 1913–1915. doi: 10.1126/science.1127488
- Carstensen, L. L., and Mikels, J. A. (2005). At the intersection of emotion and cognition: aging and the positivity effect. *Curr. Dir. Psychol. Sci.* 14, 117–121. doi: 10.1111/j.0963-7214.2005.00348.x
- Carstensen, L. L., Pasupathi, M., Mayr, U., and Nesselroade, J. R. (2000). Emotional experience in everyday life across the adult life span. J. Pers. Soc. Psychol. 79, 644–655. doi: 10.1037/0022-3514.79.4.644
- Carstensen, L. L., Turan, B., Scheibe, S., Ram, N., Ersner-Hershfield, H., Samanez-Larkin, G. R., et al. (2011). Emotional experience improves with age: evidence based on over 10 years of experience sampling. *Psychol. Aging* 26, 21–33. doi: 10.1037/a0021285
- Castel, A. D., Humphreys, K. L., Lee, S. S., Galván, A., Balota, D. A., and McCabe, D. P. (2011). The development of memory efficiency and value-directed remembering across the life span: a cross-sectional study of memory and selectivity. *Dev. Psychol.* 47, 1553–1564. doi: 10.1037/ a0025623
- Castle, E., Eisenberger, N. I., Seeman, T. E., Moons, W. G., Boggero, I. A., Grinblatt, M. S., et al. (2012). Neural and behavioral bases of age differences in perceptions of trust. *Proc. Natl. Acad. Sci. U.S.A.* 109, 20848–20852. doi: 10.1073/pnas.1218518109
- Cavanagh, J. F., Neville, D., Cohen, M. X., Van de Vijver, I., Harsay, H., Watson, P., et al. (2012). Individual differences in risky decision-making among seniors reflect increased reward sensitivity. *Front. Neurosci.* 6:111. doi: 10.3389/fnins.2012.00111
- Düzel, E., Bunzeck, N., Guitart-Masip, M., and Düzel, S. (2010). NOveltyrelated motivation of anticipation and exploration by dopamine (NOMAD): implications for healthy aging. *Neurosci. Biobehav. Rev.* 34, 660–669. doi: 10.1016/j.neubiorev.2009.08.006
- Eppinger, B., Hämmerer, D., and Li, S.-C. (2011). Neuromodulation of rewardbased learning and decision making in human aging. *Ann. N.Y. Acad. Sci.* 1235, 1–17. doi: 10.1111/j.1749-6632.2011.06230.x
- Eppinger, B., Nystrom, L. E., and Cohen, J. D. (2012). Reduced sensitivity to immediate reward during decision-making in older than younger adults. *PLoS ONE* 7:e36953. doi: 10.1371/journal.pone.0036953
- Gilbert, R. J., Mitchell, M. R., Simon, N. W., Bañuelos, C., Setlow, B., and Bizon, J. L. (2011). Risk, reward, and decision-making in a rodent model of cognitive aging. *Front. Neurosci.* 5:144. doi: 10.3389/fnins.2011.00144
- Grady, C. (2012). The cognitive neuroscience of ageing. Nat. Rev. Neurosci. 13, 491–505. doi: 10.1038/nrn3256

- Hämmerer, D., Biele, G., Müller, V., Thiele, H., Nürnberg, P., Heekeren, H. R., et al. (2013). Effects of PPP1R1B (DARPP-32) polymorphism on feedbackrelated brain potentials across the life span. *Front. Psychol.* 4:89. doi: 10.3389/fpsyg.2013.00089
- Hämmerer, D., and Eppinger, B. (2012). Dopaminergic and prefrontal contributions to reward-based learning and outcome monitoring during child development and aging. *Dev. Psychol.* 48, 862–874. doi: 10.1037/ a0027342
- Harlé, K. M., and Sanfey, A. G. (2012). Social economic decision-making across the lifespan: an fMRI investigation. *Neuropsychologia* 50, 1416–1424. doi: 10.1016/j.neuropsychologia.2012.02.026
- Li, S.-C. (2013). Lifespan development of neuromodulation of adaptive control and motivation as an ontogenetic mechanism for developmental niche construction. *Dev. Sci.* 16, 317–319. doi: 10.1111/desc.12032
- Li, S.-C., Lindenberger, U., and Bäckman, L. (2010). Dopaminergic modulation of cognition across the life span. *Neurosci. Biobehav. Rev.* 34, 625–630. doi: 10.1016/j.neubiorev.2010.02.003
- Li, S.-C., and Sikström, S. (2002). Integrative neurocomputational perspectives on cognitive aging, neuromodulation, and representation. *Neurosci. Biobehav. Rev.* 26, 795–808. doi: 10.1016/S0149-7634(02)00066-0
- Löckenhoff, C. E. (2011). Age, time, and decision making: from processing speed to global time horizons. Ann. N.Y. Acad. Sci. 1235, 44–56. doi: 10.1111/j.1749-6632.2011.06209.x
- Mata, R., and Nunes, L. (2010). When less is enough: cognitive aging, information search, and decision quality in consumer choice. *Psychol. Aging* 25, 289–298. doi: 10.1037/a0017927
- Mata, R., Pachur, T., von Helversen, B., Hertwig, R., Rieskamp, J., and Schooler, L. (2012). Ecological rationality: a framework for understanding and aiding the aging decision maker. *Front. Neurosci.* 6:19. doi: 10.3389/fnins.2012. 00019
- Mata, R., Schooler, L., and Rieskamp, J. (2007). The aging decision maker: cognitive aging and the adaptive selection of decision strategies. *Psychol. Aging* 22, 796–810. doi: 10.1037/0882-7974.22.4.796
- Mata, R., von Helversen, B., and Rieskamp, J. (2010). Learning to choose: cognitive aging and strategy selection learning in decision making. *Psychol. Aging* 25, 299–309. doi: 10.1037/a0018923
- Mather, M., and Carstensen, L. L. (2005). Aging and motivated cognition: the positivity effect in attention and memory. *Trends Cogn. Sci.* 9, 496–502. doi: 10.1016/j.tics.2005.08.005
- Mather, M., and Schoeke, A. (2011). Positive outcomes enhance incidental learning for both younger and older adults. *Front. Neurosci.* 5:129. doi: 10.3389/fnins.2011.00129
- Mohr, P. N. C., Li, S.-C., and Heekeren, H. R. (2010). Neuroeconomics and aging: neuromodulation of economic decision making in old age. *Neurosci. Biobehav. Rev.* 34, 678–688. doi: 10.1016/j.neubiorev.2009.05.010
- Roesch, M. R., Bryden, D. W., Cerri, D. H., Haney, Z. R., and Schoenbaum, G. (2012). Willingness to wait and altered encoding of time-discounted reward in the orbitofrontal cortex with normal aging. J. Neurosci. 32, 5525–5533. doi: 10.1523/JNEUROSCI.0586-12.2012
- Samanez-Larkin, G. R. (2011). Decision Making Over the Life Span. New York, NY: Wiley-Blackwell.
- Samanez-Larkin, G. R., Gibbs, S. E. B., Khanna, K., Nielsen, L., Carstensen, L. L., and Knutson, B. (2007). Anticipation of monetary gain but not loss in healthy older adults. *Nat. Neurosci.* 10, 787–791. doi: 10.1038/nn1894
- Samanez-Larkin, G. R., and Knutson, B. (2014). "Reward processing and risky decision making in the aging brain," in *The Neuroscience of Risky Decision Making*, eds V. F. Reyna and V. Zayas (Washington DC: American Psychological Association).
- Samanez-Larkin, G. R., Mata, R., Radu, P. T., Ballard, I. C., Carstensen, L. L., and McClure, S. M. (2011a). Age differences in striatal delay sensitivity during intertemporal choice in healthy adults. *Front. Neurosci.* 5:126. doi: 10.3389/fnins.2011.00126
- Samanez-Larkin, G. R., Wagner, A. D., and Knutson, B. (2011b). Expected value information improves financial risk taking across the adult life span. Soc. Cogn. Affect. Neurosci. 6, 207–217. doi: 10.1093/scan/ nsq043
- Shivapour, S. K., Nguyen, C. M., Cole, C. A., and Denburg, N. L. (2012). Effects of age, sex, and neuropsychological performance on financial decision-making. *Front. Neurosci.* 6:82. doi: 10.3389/fnins.2012.00082

- Simon, N. W., Lasarge, C. L., Montgomery, K. S., Williams, M. T., Mendez, I. A., Setlow, B., et al. (2010). Good things come to those who wait: attenuated discounting of delayed rewards in aged Fischer 344 rats. *Neurobiol. Aging* 31, 853–862. doi: 10.1016/j.neurobiolaging.2008.06.004
- Spaniol, J., and Wegier, P. (2012). Decisions from experience: adaptive information search and choice in younger and older adults. *Front. Neurosci.* 6:36. doi: 10.3389/fnins.2012.00036
- Westbrook, A., Martins, B. S., Yarkoni, T., and Braver, T. S. (2012). Strategic insight and age-related goal-neglect influence risky decision-making. *Front. Neurosci.* 6:68. doi: 10.3389/fnins.2012.00068
- Worthy, D. A., and Maddox, W. T. (2012). Age-based differences in strategy use in choice tasks. *Front. Neurosci.* 5:145. doi: 10.3389/fnins.2011. 00145

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Positive outcomes enhance incidental learning for both younger and older adults

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Previous studies suggest that memory encoding is enhanced when people are anticipating a potential reward, consistent with the idea that dopaminergic systems that respond to motivationally relevant information also enhance memory for that information. In the current study, we examined how anticipating and receiving rewards versus losses affect incidental learning of information. In addition, we compared the modulatory effects of reward anticipation and outcome on memory for younger and older adults. Forty-two younger (aged 18-33 years) and 44 older (aged 66-92 years) adults played a game involving pressing a button as soon as they saw a target. Gain trials began with a cue that they would win \$0.25 if they pressed the button fast enough, loss trials began with a cue that they would avoid losing \$0.25 if they pressed the button fast enough, and no-outcome trials began with a cue indicating no monetary outcome. The target was a different photoobject on each trial (e.g., balloon, dolphin) and performance outcomes were displayed after the photo disappeared. Both younger and older adults recalled and recognized pictures from trials with positive outcomes (either rewarding or loss avoiding) better than from trials with negative outcomes. Positive outcomes were associated with not only enhanced memory for the picture just seen in that trial, but also with enhanced memory for the pictures shown in the next two trials. Although anticipating a reward also enhanced incidental memory, this effect was seen only in recognition memory of positive pictures and was a smaller effect than the outcome effect. The fact that older adults showed similar incidental memory effects of reward anticipation and outcome as younger adults suggests that reward-memory system interactions remain intact in older age.

Keywords: aging, reward outcome, incidental memory and learning, monetary incentive delay task, valence, picture recognition

INTRODUCTION

Most of what we experience everyday is quickly forgotten, if it is even encoded in the first place. Yet the human brain is remarkably effective at learning about things that matter. Our memory systems rely on a variety of signals to distinguish things that matter from things that do not, such as the probability of encountering information again given the pattern of previous exposure to that information (Anderson and Schooler, 2000; Kornell et al., 2010) or levels of arousal during learning (Mather and Sutherland, 2011). Recent work has started to examine whether receiving or anticipating a reward is another factor that modulates memory encoding and consolidation processes. Prioritizing memory encoding for information learned around the time of receiving a reward could have utility. For instance, it may be useful to remember what one did or saw just before obtaining a positive outcome in order to replicate the outcome in the future.

Several recent studies with humans suggest that anticipating rewards can enhance memory. For instance, participants who studied lists of items with some items promising high rewards if remembered later had better long-term memory for the highreward items (Adcock et al., 2006; Callan and Schweighofer, 2008). Greater activity in the midbrain, nucleus accumbens, and hippocampus during study predicted better memory performance later (Adcock et al., 2006). Such findings suggest that activating neural pathways involved in reward processing enhances memory – but it is also possible that this pattern of brain activity was not the critical factor enhancing memory – the enhanced memory may have resulted from the more effortful encoding for the items that would get a larger reward when remembered later, at the same time that reward regions activated at the prospect of a potential future reward.

However, other studies suggest that enhanced memory for information learned during reward anticipation can occur even when memory for the information itself is not tied with the future reward. For instance, a couple of studies showed objects as cues; whether the object was living or non-living was the signal indicating whether participants could expect a reward if they executed the upcoming task (indicating whether a target number was larger or smaller than five) fast enough (Wittmann et al., 2005; Bialleck et al., 2011). Although the object category was relevant to the reward, the specifics of the objects were irrelevant. In both studies, participants remembered the objects that had predicted reward better than those that had not. Activity in the midbrain (specifically, the substantia nigra) and hippocampus during the initial viewing of the rewarding object cues predicted subsequent memory for them, but midbrain activity did not predict memory for neutral object cues (Wittmann et al., 2005).

In another study using the same number comparison task (Wittmann et al., 2008a), memory was tested for pictures whose content was entirely irrelevant to the anticipated rewards. Positive, neutral, or negative pictures were placed behind a fixation point that was green to signal potential reward and yellow to signal no potential reward. Participants remembered positive pictures seen behind the green cues better than positive pictures seen behind the yellow cues, but reward anticipation did not affect incidental memory for negative or neutral pictures. Thus, positive emotional valence seems to interact with the reward system to enhance memory formation further.

One limitation of the previous studies showing enhanced incidental memory on rewarding trials (Wittmann et al., 2005, 2008b; Bialleck et al., 2011) is that they did not separate the effects of reward anticipation and reward delivery. In those studies, it was not clear whether memory enhancements were due to anticipating rewards or to retroactive enhancement of the initial cues once the reward was received later in the trial.

Another limitation of the studies described above is that they were all conducted with younger adults, leaving open the question of whether older adults show similar or different influences of reward processing on incidental memory encoding. Aging is associated with changes in neural systems and brain regions linked with reward processing (Marschner et al., 2005; Backman et al., 2010) as well as with changes in memory processes (Hedden and Gabrieli, 2004; Luo and Craik, 2008; Mather, 2010). Thus, one cannot assume that reward anticipation or delivery will affect memory encoding in the same way for older adults as for younger adults.

Although the question of whether there are age differences in how the process of anticipating or receiving a reward influences memory encoding of novel information has not been tackled directly in the literature, there are some related findings. For instance, previous studies have examined whether there are age differences in the ability to learn stimulus–reward contingencies. Such studies reveal that older adults take longer than younger adults to learn which letters or pictures are probabilistically associated with higher point outcomes (Mell et al., 2005, 2009; Eppinger et al., 2010; Eppinger and Kray, 2011). However, an important point to note is that findings that older adults are worse at learning associations between reward and certain cues may be driven by age-related impairments in associative memory (e.g., Mitchell et al., 2000; Naveh-Benjamin et al., 2004) rather than by age-related changes in how reward processing modulates memory.

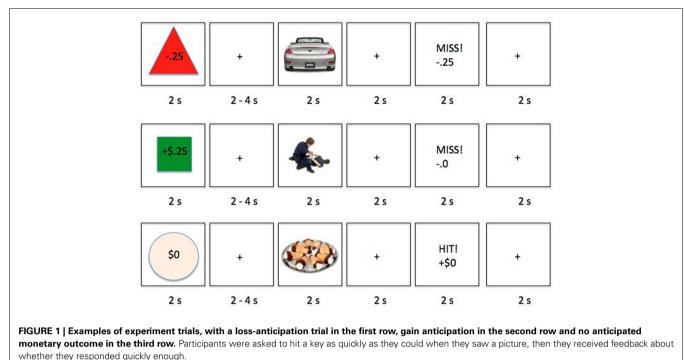
Indeed, there is some evidence that argues against the hypothesis that older adults show poorer stimulus-outcome learning because of decline in reward processing. One piece of evidence is that when reward modulation and stimulus-reward associative learning are measured separately, reward modulation of item learning is as strong among older adults as among younger adults, even when older adults show impaired stimulus-reward associative learning (Eppinger et al., 2010). In Eppinger et al.'s study, participants made two-choice decisions between two pictures of objects. Some of the objects were seen repeatedly in a positive learning task, in which feedback was either a gain of 50 cents or a gain of 0 cents. Other objects were seen repeatedly in a negative learning task, in which feedback was either a loss of 50 cents or a loss of 0 cents. Each object always was always associated with the same outcome (a gain, no monetary outcome, or a loss). After completing the learning task, participants were shown the objects from the positive and negative learning tasks intermixed with new objects and asked to identify which objects they had seen before. Although older adults showed impaired stimulus–outcome learning during the learning tasks (they were less likely to choose the objects that predicted better outcomes), both younger and older adults had better item recognition memory for the objects seen in the positive learning condition than those seen in the negative learning condition, and there was no age difference in the size of this advantage.

This finding that the type of reward outcome modulates memory similarly in younger and older adults is consistent with another study in which participants had to try to select the correct symbol–color association on each trial (Weiler et al., 2008). Participants slowly learned the correct associations across the trials and performance was better for the two symbols for which correct responses were rewarded with 20 cents than for the two symbols for which correct responses were rewarded with 5 cents. This rewardenhancement in symbol–color associative learning was similar in magnitude for younger and older adults.

Another relevant pattern from previous research is that older adults effectively prioritize their explicit memory to focus on high value information (Castel, 2008). For instance, when presented briefly with one word at a time together with the point value that remembering that word would yield, older adults were as likely as younger adults to recall the highest point value words despite having overall lower recall (Castel et al., 2002).

In summary, previous research with younger adults indicates that anticipating or receiving rewards can enhance concurrent memory encoding (Wittmann et al., 2005, 2008b; Bialleck et al., 2011), but these studies did not distinguish clearly between the effects of reward anticipation and delivery. In addition, two studies (Weiler et al., 2008; Eppinger et al., 2010) provide initial evidence that rewarding outcomes modulate memory for information seen just beforehand to a similar extent in younger and older adults. However, in both studies, the stimuli were each presented many times and learning the information helped to obtain the rewarding outcomes. In the current study, we were interested in whether rewarding outcomes modulate incidental memory encoding of novel information presented just once. In addition, we examined the independent contributions of reward anticipation and outcome.

To investigate these questions, we modified the Monetary Incentive Delay task (Knutson et al., 2001). In our version of the task (**Figure 1**), participants saw a cue on each trial that indicated whether they could earn money, avoid losing money, or have no monetary outcome from responding to the upcoming target quickly enough. The target was a novel object on each trial, and after they pressed the key in response to the target, participants received feedback about the outcome. After completing this response time task, participants then completed a surprise recognition memory test for the objects. We examined whether the anticipation or outcome type on each trial affected incidental



whether they responded quickly enough.

memory for the target object and whether such effects differed for younger versus older adults. In addition, because previous research suggests that reward anticipation has a larger benefit for memory encoding when the to-be-remembered information is emotionally positive than when it is negative (Wittmann et al., 2008a), we compared the effects of reward anticipation and outcome on memory for emotionally positive versus negative stimuli.

MATERIALS AND METHODS

PARTICIPANTS

Forty-two younger adults (aged 18–33 years; M = 21.6, SD = 3.4, 30 females and 12 males) and 44 older adults (aged 66-92 years; M = 74.5, SD = 5.7, 31 females and 13 males) completed the study. Participants were recruited through a list of research volunteers that was obtained via newspaper and online ads, fliers at senior centers and public places, and letters to University of Southern California (USC) alumni. Some younger adult participants were recruited through the USC Psychology participant pool. Participants received monetary compensation or course credit for their time as well as earnings received during the task. Younger adults had completed fewer years of education (M = 14.6, SD = 1.62)than the older adults (M = 17.34, SD = 3.12), t(84) = 4.99,p < 0.001, and also scored lower on the Nelson–Denny vocabulary test (Brown et al., 1993; M = 16.0, SD = 3.3) than the older adults (M = 20.1, SD = 2.6), t(84) = 6.3, p < 0.001. Scores on the 20item Center for Epidemiological Studies Depression Scale (CES-D; Radloff, 1977) indicated slightly more symptoms of depression among younger adults (M = 14.4, SD = 9.2) than among older adults (M = 10.6, SD = 8.5), t(84) = 2.01, p = 0.048. Mood scores on the Positive and Negative Affect Scale (PANAS; Watson et al., 1988) did not differ significantly for negative affect (M younger = 13.1, SD = 3.5; *M* older = 12.4, SD = 3.6), but positive

affect was lower among younger adults (M = 29.5, SD = 7.2) than among older adults (M = 33.8, SD = 6.8), t(84) = 2.83, p = 0.01. On a scale of 1 being "very poor health" and 9 being "excellent health," younger (M = 7.5, SD = 0.9) and older adults (M = 7.6, SD = 0.9) did not differ significantly. Self ratings of how "your stress level is today on a scale of 1-9" with 1 being very low and 9 very high also did not differ significantly by age group (Myounger = 4.3, SD = 2.0; M older = 4.2, SD = 2.4).

MATERIALS

Ninety-six photo-objects were used for target items and 40 photo-objects as filler new items on the recognition test, selected from photo-objects used in previous studies with older adults (Kensinger et al., 2007). Half of the items within each set were mildly positive (e.g., sports car, dessert) and half were mildly negative (police officer handcuffing someone, knife).

PROCEDURE

After giving informed consent, participants completed a practice section in which the response deadline for the task was calibrated so that they could respond quickly enough about two-third of the time. Next, in the actual experiment task, participants played 96 trials in a response speed game. Each trial involved a cue to let participants know whether responding fast enough to a target picture would lead to a gain, loss, or no monetary outcome (**Figure 1**). After the 2-s presentation of the cue, they saw a fixation cross for 2 s plus a random number between 0 and 2.5 s (for a total of 2–4.5 s) and then the target picture of a positive or negative photo-object for 2 s. Their task was to respond to the picture as quickly as they could before a beep indicating the response deadline (which was dynamically calibrated throughout the task based on performance on that type of trial). Regardless of the response

deadline, the picture remained visible for the full 2 s. After the picture disappeared, they were shown a fixation cross for 2 s, then feedback about their performance and any gain or loss (e.g., "Miss! -\$0.25") for 2 s. The trial ended with a fixation cross for 2 s.

After the response speed game, participants completed vocabulary, health, and other questionnaires for 10 min. They then were given a pen and paper and 5 min to recall and list descriptions of as many of the target pictures as they could. Next, in a recognition memory test, they were shown each of the photo-objects from the game as well as new photo-objects, in a random order and asked to indicate whether they saw each one during the response speed game or not with a simple yes/no judgment. Finally, they rated each picture for valence on a 1–9 scale (1 = very negative, 9 = very positive) and for arousal on a 1–9 scale (1 = not at all arousing or intense, 9 = very arousing or intense). At the end of the session, participants were paid their winnings in addition to their regular compensation or credit for the study session. Winnings ranged from \$5.25 to \$8.75 (M =\$7.44, SD = 0.80) and there was no significant difference in amounts for younger and older adults.

RECALL CODING

Two coders labeled each picture description to indicate which picture in the stimuli set it corresponded with, or whether it did not match any of the pictures seen. There was 89% agreement between the two coders on the exact pictures the descriptions matched. If the two coders disagreed, one of the coders reviewed the item and made a final judgment. The criterion for successful recall of a picture was that coders could identify a specific image that fit the participant's description. After coding was complete, for each participant, we linked each recalled item to the parameters of the original trial on which it was seen (i.e., was it a reward, loss, or no anticipation trial; did it have a hit or miss outcome).

RESULTS

Initial analyses revealed that one younger female failed to follow instructions (she called every new item old during the recognition test). Her data were excluded from the analyses below.

RESPONSE TIMES

There were two issues of interest for the response times. The first was whether our adaptive algorithm had equalized the proportion of responses during the MID task that were counted as having been made within the response deadline for each type of trial type. In other words, were younger and older participants equally likely to get positive feedback and was positive-feedback equally likely for each trial type? We confirmed that positive outcomes were equally distributed by analyzing the proportion of responses that yielded a "hit" feedback in a 3 (anticipation: loss, none, gain) $\times 2$ (item valence: negative, positive) $\times 2$ (age group: younger, older) ANOVA. As intended, on average, 67% of responses were made within each respective deadline and there were no significant main effects or interactions, indicating that about the same number of responses were counted as hits for each type of trial for younger and older adults.

The second question for the response times was whether they varied depending on what type of outcome was anticipated. Repeating the above ANOVA with mean MID task response time as the dependent measure revealed a significant effect of age group, F(1,83) = 23.94, MSE = 680782, p < 0.001, $\eta_p^2 = 0.22$, as younger adults responded faster (M = 266 ms, SE = 17) than older adults (M = 380 ms, SE = 16). In addition, there was a significant interaction of anticipation type and age group, F(2, 166) = 4.58, MSE = 3731, p = 0.01, $\eta_p^2 = 0.05$, as younger participants responded slower when there was no potential monetary outcome (M = 286 ms, SE = 17) than when there was a potential for loss (M = 254 ms, SE = 19) or a potential for gain (M = 259 ms, SE = 17), whereas older adults showed little difference between the no-outcome condition (M = 376 ms, SE = 16) and the loss (M = 380 ms, SE = 18) or gain conditions (M = 383 ms, SE = 16). There were no other significant effects.

RECALL

On average, participants recalled about 10 pictures, with no significant difference between age groups (younger M = 10.8, SE = 0.9; older M = 10.0, SE = 0.9). We examined how the context in which a particular picture was seen during the MID task affected later memory for it. The two context variables were anticipation type and response outcome from the trial in which that picture was originally seen. A 3 (anticipation: loss, none, gain) $\times 2$ (item valence: negative, positive) \times 2 (MID task outcome: hit, miss) \times 2 (age group: younger, older) ANOVA with the proportion of previously seen items that were recalled from each category revealed that participants were more likely to recall items from the MID task hit trials (M = 0.12, SE = 0.01) than from the response time miss trials (M = 0.09, SE = 0.01), F(1,83) = 11.21, MSE = 0.01,p = 0.001, $\eta_p^2 = 0.12^{-1}$. This enhanced recall for target items from hit trials was seen for both younger and older adults (Figure 2). Response outcome also showed a marginally significant interaction with anticipation type, such that the memorial benefit of a rewarding outcome was seen more on trials with anticipated monetary outcomes than on trials with no anticipated monetary outcome (effect shown separately for younger and older adults in Figure 3), F(2,166) = 2.91, MSE = 0.01, p = 0.06, $\eta_p^2 = 0.03$. There were no other significant effects.

RECOGNITION MEMORY

Because our hypotheses focused on comparing how different types of encoding contexts affect later memory for the pictures, we

¹To examine whether the feedback outcome effect could be accounted for by response time differences for trials receiving positive feedback versus negative feedback, we compared the effect of outcome on both slow and fast response times. For each participant, we computed the median response time separately for each type of anticipation (reward, none, loss). We then categorized each old item as having had a response during the MID task that was above or below the median response time in its anticipation type category and computed the proportion of slow and fast-response items were recalled. A 2 (response time: slow, fast) × 2 (MID task outcome: hit, miss) × 2 (age group: younger, older) ANOVA confirmed the main effect of task outcome seen in the other analysis, F(1,83) = 6.64, MSE = 0.005, p = 0.01, $\eta_p^2 = 0.07$ and revealed no interaction of task outcome and response time (p > 0.9) and no other significant effects. Post hoc t-tests showed that the enhancement for items followed by positive outcomes was independently significant for items from fast response trials (M hit = 0.12, SE = 0.01; M miss = 0.10, SE = 0.01), t(84) = 2.18, p = 0.03, and marginally significant for items from slow response trials (M hit = 0.11, SE = 0.01; M miss = 0.09, SE = 0.01), t(84) = 1.83, p = 0.07. Thus, the effect of feedback was similar across performance levels.

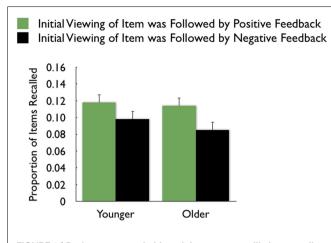
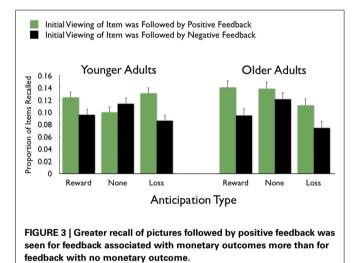


FIGURE 2 | Both younger and older adults were more likely to recall pictures that were followed by positive feedback than those followed by negative feedback.



could only include old pictures in our primary analyses (new pictures could not be categorized by encoding context). However, to get an indication of overall memory accuracy, we used a 2 (item valence: negative, positive) \times 2 (age group: younger, older) ANOVA with d' recognition accuracy measures as the dependent variable. There was a significant effect of valence, F(1,83) = 6.58, MSE = 0.27, p < 0.001, $\eta_p^2 = 0.27$, with d' higher for positive (M = 2.08, SE = 0.08) than for negative (M = 1.69, SE = 0.08)pictures. Neither the main effect of age group nor the interaction was significant (both F < 1). In contrast with the lack of age differences in accuracy, repeating the ANOVA using the response bias measure C (Macmillan and Creelman, 1991) as the dependent variable revealed that older adults were significantly more biased to call pictures old (M = 0.39, SE = 0.06) than younger adults were (M = 0.65, SE = 0.06), F(1,83) = 10.31, MSE = 0.28,p = 0.002, $\eta_p^2 = 0.11$. Overall, participants were more likely to call positive pictures old (M = 0.39, SE = 0.04) than to call negative pictures old (M = 0.66, SE = 0.05), F(1,83) = 46.30, MSE = 0.07,

p < 0.001, $\eta_p^2 = 0.36$, and there was not a significant interaction of age and valence $(F < 1)^2$.

Next, we turned to our main focus comparing the effects of reward anticipation and outcome on incidental memory. We conducted a 3 (anticipation: loss, none, gain) \times 2 (item valence: negative, positive) \times 2 (MID task outcome: hit, miss) \times 2 (age group: younger, older) ANOVA with the proportion of old target pictures correctly identified as old as the dependent measure. Consistent with the age difference in response bias reported above, older adults were more likely to identify the pictures as old (M = 0.68), SE = 0.02) than the younger adults were (M = 0.60, SE = 0.02), F(1,83) = 8.24, MSE = 0.22, p = 0.005, $\eta_p^2 = 0.09$. As in the recall data, there was a large effect of MID task outcome, F(1,83) = 24.99, MSE = 0.05, p < 0.001, $\eta_p^2 = 0.23$, with participants recognizing pictures from trials in which they got "hit" feedback (M = 0.67, SE = 0.02) better than pictures from trials in which they got "miss" feedback (M = 0.60, SE = 0.02; see Figure 4 for effect separately for younger and older adults)³.

There also was an interaction of item valence and anticipation, F(2,166) = 4.00, MSE = 0.03, p = 0.02, $\eta_p^2 = 0.05$. Participants remembered positive items best in the reward-anticipation condition (M = 0.65, SE = 0.02), followed by the no-outcome condition (M = 0.63, SE = 0.02) then by the loss-anticipation condition (M = 0.59, SE = 0.02). For the negative items, anticipation type had less effect ($M_{reward} = 0.64$, SE = 0.02, $M_{none} = 0.66$, SE = 0.02, $M_{loss} = 0.65$, SE = 0.02).

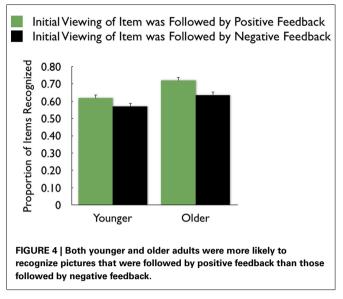
Thus, both anticipation of whether there was a potential reward or loss and actually getting positive or negative-feedback influenced incidental memory for the response time target items, although the anticipation effect was modulated by whether the items were negative or positive. The feedback effect was particularly strong.

LINGERING EFFECTS OF POSITIVE OUTCOMES

The analyses above revealed that getting positive feedback enhanced later memory for the item from that trial. In additional exploratory analyses, we compared the proportion of recognized pictures that had been seen on trials with positive feedback on the

²In terms of the raw hits (proportion of old items called old), older adults had significantly more (M = 0.69, SE = 0.02) than younger adults (M = 0.61, SE = 0.02), F(1,83) = 9.02, MSE = 0.04, p = 0.004, $\eta_p^2 = 0.10$. Consistent with their more lenient criterion to call pictures old, older adults also had more false alarms (M = 0.13, SE = 0.02) than younger adults (M = 0.09, SE = 0.02), F(1,83) = 3.68, MSE = 0.02, p = 0.058, $\eta_p^2 = 0.04$.

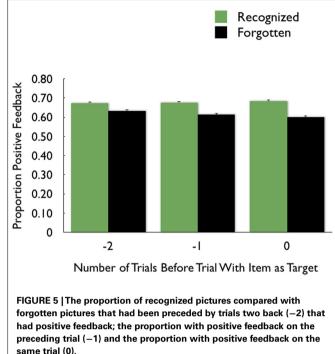
³As done with the recalled items (see footnote 1), we categorized each old item on the recognition test by whether it had been responded to faster or slower than the median response for items in the same type of trial (reward, none, or loss anticipation). A 2 (response time: slow, fast) × 2 (MID task outcome: hit, miss) × 2 (age group: younger, older) ANOVA revealed that, as in the previous analyses, participants were more likely to recognize items from trials with positive feedback (M = 0.67, SE = 0.02) than from trials with negative feedback (M = 0.61, SE = 0.02), F(1,84) = 12.91, MSE = 0.02, p = 0.001, $\eta_p^2 = 0.13$. Other than a significant main effect of age as in the main analysis, there were no significant effects (p > 0.6 for the interaction of outcome and response time). In addition, *t*-tests revealed that the effects of feedback were significant for both the slow (M hit = 0.66, SE = 0.02; M miss = 0.60, SE = 0.02), t(84) = 3.38, p = 0.001, and the fast responses (M hit = 0.68, SE = 0.02, M miss = 0.63, SE = 0.02), t(84) = 2.19, p = 0.03. Thus, feedback outcomes influenced whether the target would later be remembered both when response time performance was good and when it was poor.



preceding trial versus the proportion of non-recognized pictures that had been seen on trials with positive feedback on the preceding trial. As shown in the middle two bars of **Figure 5**, recognized pictures were more likely to have been preceded by trials with positive feedback than were forgotten pictures. There was a similar effect for the N - 2 trials, as well. These effects were significant in exploratory *t*-tests, whereas anticipation on one trial did not have lingering effects on subsequent trials⁴.

To follow up on these observations and examine whether the outcome on a preceding trial affected memory for the target in the current trial above and beyond the effects of outcomes from other preceding trials or from the current trial, we used hierarchical linear model (HLM) analyses. In these analyses, we examined whether getting positive feedback on one trial would have lingering enhancing effects on memory for items seen on subsequent trials. For each old item we categorized: (1) whether it was recognized or forgotten on the recognition memory test; (2) feedback outcome on the current trial; (3) feedback outcome on the previous trial; and (4) feedback outcome on the trial two back from the current trial. As all values were 1 or 0, we specified Bernoulli model distributions for the two-level HLM analyses. The outcome variable was the recognition (or recall) outcome for each item, age group was a level-1 predictor, and feedback outcomes (items 2-4 above) were level-2 predictor variables. We included interactions of each level-2 predictor with age group in the model.

The analyses revealed that, even when controlling for the current trial outcome and the other preceding trial outcome, recognized items were more likely to have trials one and two back with positive feedback than were forgotten items (see **Table 1** for statistics). Thus, positive feedback on one trial was associated with enhanced memory encoding for the unrelated target



item on the next trial, and even on the next trial after that. While there was a significant age group effect on the intercept (consistent with the greater likelihood of calling pictures old seen among older adults), there were no other significant age group interactions.

We repeated the above analyses for recalled versus non-recalled items. Although the pattern was similar (**Figure 6**) to that seen in recognition memory, outcomes on the two preceding trials did not significantly affect picture recall (in part perhaps because small numbers of recalled items for some participants led to greater variability). However, as in the earlier analyses, there was a significant effect of the outcome on the current trial on later memory for that picture.

PICTURE RATINGS⁵

Positive pictures were given higher valence ratings (M = 6.49, SE = 0.09) than negative pictures (M = 3.39, SE = 0.09), F(1,80) = 433.31, MSE = 2.34, p < 0.001, $\eta_p^2 = 0.84$. There were no significant effects of age group on the valence ratings. For the arousal ratings, there was not a significant main effect of picture valence, but there was an interaction of age group by valence category, F(1,81) = 7.72, MSE = 4.31, p = 0.007, $\eta_p^2 = 0.09$. Younger adults rated the negative pictures as more arousing (M = 4.06, SE = 0.25) than the positive pictures (M = 3.33, SE = 0.26), whereas the older adults rated the negative pictures as less arousing (M = 4.00, SE = 0.25) than the positive pictures (M = 4.31, SE = 0.26).

⁴We also did not find any significant relationships between subsequent memory for the target on trial *N* by reward anticipation type or feedback type on trial N + 1 or N + 2.

⁵Due to time constraints, three participants did not complete the post-experiment valence ratings of pictures. Of these, two did not complete the arousal ratings either.

Effect	β	SE	t	df	<i>p</i> value
(A) ANALYSIS FOR CURRENT AND	PRECEDING TRIALS F	OR RECOGNITION			
Intercept	0.65	0.01	45.85	82	<0.001
Intercept × age group	0.09	0.03	3.00	82	0.004
Outcome on current trial	0.06	0.03	4.514	7903	< 0.001
Current outcome × age	0.02	0.03	0.63	7903	0.53
Outcome on current – 1 trial	0.04	0.01	3.32	7903	<0.001
Current – 1 outcome × age	0.03	0.02	1.07	7903	0.29
Outcome on current – 2 trial	0.02	0.01	2.01	7903	0.045
Current – 1 outcome × age	-0.02	0.02	-0.93	7903	0.35
(B) ANALYSIS FOR CURRENT AND	PRECEDING TRIALS F	OR RECALL			
Intercept	0.11	0.01	16.36	82	<0.001
Intercept × age group	-0.01	0.01	-0.66	82	0.51
Outcome on current trial	0.02	0.01	2.76	7903	0.006
Current outcome × age	0.01	0.01	0.41	7903	0.68
Outcome on current – 1 trial	0.01	0.01	1.57	7903	0.12
Current – 1 outcome × age	-0.002	0.01	-0.14	7903	0.89
Outcome on current – 2 trial	0.005	0.01	0.59	7903	0.55
Current – 1 outcome × age	0.002	0.02	0.13	7903	0.90

Table 1 | Hierarchical linear model (HLM) analysis beta coefficients (β), robust standard errors (SE), *t* ratios (*t*), degrees of freedom (df), and *p* values using the outcome on the current and preceding two trials to predict recognition (A) and recall (B) of the current trial's target picture.

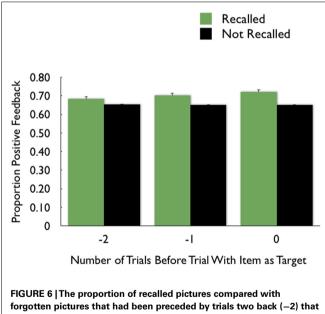


FIGURE 6 | The proportion of recalled pictures compared with forgotten pictures that had been preceded by trials two back (-2) tha had positive feedback; the proportion with positive feedback on the preceding trial (-1) and the proportion with positive feedback on the same trial (0).

DISCUSSION

EFFECTS OF ANTICIPATION AND OUTCOMES ON INCIDENTAL LEARNING

In this study, we examined the effects of reward and loss anticipation as well as the effects of positive and negative outcome feedback (reaction time "hit" versus "miss" feedback) on incidental memory for items shown as response time targets (**Figure 1**). We found that the most robust effects were from whether the feedback was positive or negative. In both the reward and lossanticipation conditions, targets from positive-feedback trials were remembered better than targets from negative-feedback trials. This similar effect across reward and loss conditions was seen despite the fact that the positive feedback was associated with monetary reward in the reward condition and with a lack of a monetary loss in the loss condition. Thus, it seems that the outcome being positive relative to expectations is what matters, rather than the absolute amount of the reward. In addition, the enhancement in memory due to positive feedback was seen for both recall and recognition memory.

In recognition memory, anticipation type also influenced incidental memory, but only for the positively valenced items. The positive items were remembered best from reward-anticipation trials and worst from loss-anticipation trials. Thus, while anticipating a reward did enhance memory, its influence was not seen across all item types and did not show up in recall. In contrast, positive feedback was associated with better memory than negativefeedback nearly across the board, with the exception of recall of pictures from trials with no monetary outcomes (Figure 3). From these results, it seems that both anticipating and receiving positive outcomes modulates memory, but that reward delivery has a larger impact. Previous studies have not distinguished the effects of reward anticipation and delivery (Wittmann et al., 2005, 2008b) and so effects from those studies that have been interpreted as being due to reward anticipation may actually have been influenced by reward delivery.

In addition to having a strong effect on memory for items previously seen in that trial, positive feedback on one trial was associated with better later recognition of the targets in the subsequent trial and even in the trial after that (**Figure 5**). HLM analyses revealed that the significant relationship between the outcomes on the preceding trials and later memory for the target picture on the current trial held up even when the influence of the current trial outcome was factored out. These findings suggest that positive outcomes can enhance memory-encoding processes in the period after the positive event (in this case, for the next 20 s or so).

EFFECTS OF ANTICIPATION AND OUTCOMES WERE SIMILAR FOR YOUNGER AND OLDER ADULTS

As reviewed above, our study revealed three main findings about how the reward/loss context affected incidental encoding. First, reward anticipation did not have much effect, but did enhance recognition memory for positive pictures compared with loss anticipation. Second, there were large effects of feedback outcome on both recognition and recall of the pictures. Third, feedback outcome was not only associated with memory enhancement of the picture seen just before on the same trial, but also with enhanced recognition of the pictures on the next trial or two. For all of these effects, older adults showed similar patterns of results and there were no significant age interactions. Our sample size provided good power to detect large effects (96% according to Cohen, 1988), therefore our results suggest there are not large age differences in how reward anticipation and outcome modulate memory. While previous research shows that older adults are impaired at learning associations between cues and rewards (Mell et al., 2005, 2009; Eppinger et al., 2010; Eppinger and Kray, 2011), our findings are consistent with previous studies that found that manipulating the reward value of outcomes modulated memory for other information similarly in younger and older adults (Weiler et al., 2008; Eppinger et al., 2010).

HOW CAN THE CURRENT FINDINGS BE RECONCILED WITH AGE-RELATED DECLINES IN DOPAMINE?

These results are especially intriguing when considered against the backdrop of age-related declines in dopamine-related systems in the brain. Consistent with the idea that receiving rewards may signal the presence of worthwhile information for learning, there is growing evidence that midbrain dopamine regions that respond to motivationally relevant information interact with the hippocampus to enhance memory for that information (Shohamy and Adcock, 2010). Research with animals reveals that dopamine facilitates encoding novel information and increases the persistence of memory for that information (Jay, 2003; O'Carroll et al., 2006; Rossato et al., 2009; Bethus et al., 2010). In the rat hippocampus, blocking dopamine (D1/D5) receptors prevented exposure to a novel environment from facilitating long-term potentiation (Li et al., 2003). Furthermore, in healthy people as well as in Alzheimer's disease patients, D2 receptor binding in the hippocampus is positively correlated with memory function (Kemppainen et al., 2003; Takahashi et al., 2008; MacDonald et al., 2009).

There is abundant research demonstrating age-related declines in various aspects of dopaminergic systems in the brain (Bäckman et al., 2006; Backman et al., 2010). These declines are seen in particular in the striatal regions (Suhara et al., 1991; Wang et al., 1998), for instance, striatal dopamine levels decrease by more than threefold from those in their 30s to those in their late 80s (Haycock et al., 2003).

However, the behavioral consequences of age-related declines in dopamine systems are not yet well understood. One challenge is that dopamine synthesis is affected differentially by age in different brain regions. For instance, in a study in which uptake of L-DOPA decreased 4.2% per decade in the putamen and 5.4% in the caudate nucleus, no age-related differences were found in the midbrain (Ota et al., 2006). However, larger declines were found in prefrontal, parietal, and medial temporal cortices, with as high as 16.4% decline per decade seen in the dorsolateral prefrontal cortex (Ota et al., 2006). D2 and D3 receptor subtypes also decline at different rates in different brain regions (Kaasinen et al., 2000, 2002). In addition to these regional differences in age-related decline in dopamine, there are also differences in how the various components of the dopaminergic brain systems are affected by age. For instance, a study that compared levels of six different presynaptic dopaminergic markers in postmortem striatum in people aged 1 day to 103 years old found that striatal dopamine levels decreased during adult aging but that the proteins involved in its biosynthesis and compartmentation were relatively preserved (Haycock et al., 2003).

While our study provides no direct evidence about dopaminergic processing, one candidate mechanism for the reward-related memory modulations shown by our participants are fluctuations in dopamine elicited by reward anticipation and outcomes that modulate hippocampal encoding. With this mechanism, for older adults to show effective reward-related modulation of memory encoding, they would need to have: (A) modulations in phasic dopamine activity during reward anticipation or outcomes and (B) maintained effectiveness of dopamine to modulate new memory encoding.

There is little direct evidence yet in the literature to indicate whether older adults do or do not have these necessary preconditions. However, some functional neuroimaging studies have examined brain activity in the striatum, a target region for midbrain dopaminergic neurons (Lyndbalta and Haber, 1994). Such studies have found that older adults show robust responses in ventral and/or dorsal striatum to positive outcomes (Schott et al., 2007; Cox et al., 2008; Mell et al., 2009; Samanez-Larkin et al., 2010). Results from studies examining reward anticipation are more mixed, with older adults showing less ventral striatal activation than younger adults in some cases (Schott et al., 2007; Dreher et al., 2008) but not in all studies (Samanez-Larkin et al., 2007). There are also age differences in whether stronger responses to outcomes are seen early or late in the learning phase of a probabilistic learning task (Mell et al., 2009). Thus, although there may be age differences in the conditions or types of stimuli that evoke striatal activation, evidence suggests there is some degree of intact functional signaling of reward in dopaminergic pathways among older adults.

In terms of the second precondition – dopamine modulated memory encoding – a recent study found that older participants showed reliable memory impairments/enhancements from a D2 antagonist/agonist manipulation whereas younger adults did not show significant memory modulation from the D2 manipulation (Morcom et al., 2010). In addition, administration of levadopa improved older adults' encoding of a motor memory more than it did for younger adults (who were already at a high level; Floel et al., 2005). Thus, there is evidence that dopaminergic agents modulate memory-encoding processes for older adults.

In summary, previous evidence indicates that older adults show robust responses to reward outcomes and also show robust dopaminergic modulation of memory encoding. These findings suggesting intact aspects of reward processing and dopamine function may help explain our behavioral findings that reward processing can modulate incidental memory encoding as effectively for older adults as for younger adults.

FUTURE DIRECTIONS

Future research should explore the neural mechanisms underlying these effects, as well as further delineating the nature of the behavioral effects. For instance, are the effects driven more by positive outcomes enhancing memory or by negative outcomes impairing memory? Do outcomes modulate memory more or less for representations that are initially weak? In our study, encoding was incidental; would an intentional memory encoding task also yield significant modulation by outcomes? Addressing

REFERENCES

- Adcock, R. A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., and Gabrieli, J. D. E. (2006). Rewardmotivated learning: mesolimbic activation precedes memory formation. *Neuron* 50, 507–517.
- Anderson, J. R., and Schooler, L. J. (2000). "The adaptive nature of memory," in Oxford Handbook of Memory, eds E. Tulving and F. I. M. Craik (London: Oxford University Press), 557–570.
- Backman, L., Lindenberger, U., Li, S. C., and Nyberg, L. (2010). Linking cognitive aging to alterations in dopamine neurotransmitter functioning: recent data and future avenues. *Neurosci. Biobehav. Rev.* 34, 670–677.
- Bäckman, L., Nyberg, L., Linderiberger, U., Li, S. C., and Farde, L. (2006). The correlative triad among aging, dopamine, and cognition: current status and future prospects. *Neurosci. Biobehav. Rev.* 30, 791–807.
- Bethus, I., Tse, D., and Morris, R. G. M. (2010). Dopamine and memory: modulation of the persistence of memory for novel hippocampal NMDA receptor-dependent paired associates. *J. Neurosci.* 30, 1610–1618.
- Bialleck, K. A., Schaal, H. P., Kranz, T. A., Fell, J., Elger, C. E., and Axmacher, N. (2011). Ventromedial prefrontal cortex activation is associated with memory formation for predictable rewards. *PLoS ONE* 6, e16695. doi:10.1371/journal.pone.0016695
- Brown, J. I., Fishco, V. V. and Hanna, G. (1993). Nelson-Denny Reading Test: Manual for Scoring and Interpretation. Itasca, IL: Riverside.

- Callan, D. E., and Schweighofer, N. (2008). Positive and negative modulation of word learning by reward anticipation. *Hum. Brain Mapp.* 29, 237–249.
- Castel, A. D. (2008). The adaptive and strategic use of memory by older adults: evaluative processing and value-directed remembering. *Psychol. Learn. Motiv.* 48, 225–270.
- Castel, A. D., Benjamin, A. S., Craik, F. I. M., and Watkins, M. J. (2002). The effects of aging on selectivity and control in short-term recall. *Mem. Cognit.* 30, 1078–1085.
- Cohen, J. (1988). Statistical Power Analysis for the Behavioral Sciences. Hillsdale, NJ: Lawrence Erlbaum.
- Cox, K. M., Aizenstein, H. J., and Fiez, J. A. (2008). Striatal outcome processing in healthy aging. *Cogn. Affect. Behav. Neurosci.* 8, 304–317.
- Dreher, J. C., Meyer-Lindenberg, A., Kohn, P., and Berman, K. F. (2008). Age-related changes in midbrain dopaminergic regulation of the human reward system. *Proc. Natl. Acad. Sci. U.S.A.* 105, 15106–15111.
- Eppinger, B., Herbert, M., and Kray, J. (2010). We remember the good things: age differences in learning and memory. *Neurobiol. Learn. Mem.* 93, 515–521.
- Eppinger, B., and Kray, J. (2011). To choose or to avoid: age differences in learning from positive and negative feedback. *J. Cogn. Neurosci.* 23, 41–52.
- Floel, A., Breitenstein, C., Hummel, F., Celnik, P., Gingert, C., Sawaki, L., Knecht, S., and Cohen, L. G. (2005). Dopaminergic influences on formation of a motor memory. *Ann. Neurol.* 58, 121–130.

such issues would further clarify the specific mechanisms of this outcome-modulated memory effect.

CONCLUSION

This study revealed strong associations between outcomes on each trial and incidental memory for the target on that trial, as well as for incidental memory for the next target. This relationship between outcomes and memory was not dependent on response time performance and so suggests that receiving a good outcome creates a brief window of enhanced memory encoding. This association between good outcomes and memory was as strong for older adults as it was for younger adults, suggesting that the ability of reward processing to modulate memory remains robust in older age.

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- Haycock, J. W., Becker, L., Ang, L., Furukawa, Y., Hornykiewicz, O., and Kish, S. J. (2003). Marked disparity between age-related changes in dopamine and other presynaptic dopaminergic markers in human striatum. J. Neurochem. 87, 574–585.
- Hedden, T., and Gabrieli, J. D. E. (2004). Insights into the ageing mind: a view from cognitive neuroscience. *Nat. Rev. Neurosci.* 5, 87–96.
- Jay, T. M. (2003). Dopamine: a potential substrate for synaptic plasticity and memory mechanisms. *Prog. Neurobiol.* 69, 375–390.
- Kaasinen, V., Kemppainen, N., Nagren, K., Helenius, H., Kurki, T., and Rinne, J. O. (2002). Age-related loss of extrastriatal dopamine D2-like receptors in women. *J. Neurochem.* 81, 1005–1010.
- Kaasinen, V., Vilkman, H., Hietala, J., Nagren, K., Helenius, H., Olsson, H., Farde, L., and Rinne, J. (2000). Agerelated dopamine D2/D3 receptor loss in extrastriatal regions of the human brain. *Neurobiol. Aging* 21, 683–688.
- Kemppainen, N., Laine, M., Laakso, M. P., Kaasinen, V., Nagren, K., Vahlberg, T., Kurki, T., and Rinne, J. O. (2003).
 Hippocampal dopamine D2 receptors correlate with memory functions in Alzheimer's disease. *Eur. J. Neurosci.* 18, 149–154.
- Kensinger, E. A., Garoff-Eaton, R. J., and Schacter, D. L. (2007). Effects of emotion on memory specificity in young and older adults. J. Gerontol. B Psychol. Sci. Soc. Sci. 62, 208–215.
- Knutson, B., Adams, C. M., Fong, G. W., and Hommer, D. (2001).

Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *J. Neurosci.* 21, RC159.

- Kornell, N., Castel, A. D., Eich, T. S., and Bjork, R. A. (2010). Spacing as the friend of both memory and induction in young and older adults. *Psychol. Aging* 25, 498–503.
- Li, S. M., Cullen, W. K., Anwyl, R., and Rowan, M. J. (2003). Dopaminedependent facilitation of LTP induction in hippocampal CA1 by exposure to spatial novelty. *Nat. Neurosci.* 6, 526–531.
- Luo, L., and Craik, F. I. M. (2008). Aging and memory: a cognitive approach. *Can. J. Psychiatry* 53, 346–353.
- Lyndbalta, E., and Haber, S. N. (1994). The organization of midbrain projections to the striatum in the primate: sensorimotor-related striatum versus ventral striatum. *Neuroscience* 59, 625–640.
- MacDonald, S. W. S., Cervenka, S., Farde, L., Nyberg, L., and Backman, L. (2009). Extrastriatal dopamine D2 receptor binding modulates intraindividual variability in episodic recognition and executive functioning. *Neuropsychologia* 47, 2299–2304.
- Macmillan, N. A., and Creelman, C. D. (1991). *Detection Theory: A User's Guide*. New York: Cambridge University Press.
- Marschner, A., Mell, T., Wartenburger, I., Villringer, A., Reischies, F. M., and Heekeren, H. R. (2005). Rewardbased decision-making and aging. *Brain Res. Bull.* 67, 382–390.
- Mather, M. (2010). Aging and cognition. Wiley Interdiscip. Rev. Cogn. Sci. 1, 346–362.

- Mather, M., and Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspect. Psychol. Sci.* 6, 114–133.
- Mell, T., Heekeren, H. R., Marschner, A., Wartenburger, I., Villringer, A., and Reischies, F. M. (2005). Effect of aging on stimulus-reward association learning. *Neuropsychologia* 43, 554–563.
- Mell, T., Wartenburger, I., Marschner, A., Villringer, A., Reischies, F. M., and Heekeren, H. R. (2009). Altered function of ventral striatum during reward-based decision making in old age. *Front. Hum. Neurosci.* 3:34. doi:10.3389/neuro.09.034.2009
- Mitchell, K. J., Johnson, M. K., Raye, C. L., Mather, M., and D'Esposito, M. (2000). Aging and reflective processes of working memory: binding and test load deficits. *Psychol. Aging* 15, 527–541.
- Morcom, A. M., Bullmore, E. T., Huppert, F. A., Lennox, B., Praseedom, A., Linnington, H., and Fletcher, P. C. (2010). Memory encoding and dopamine in the aging brain: a psychopharmacological neuroimaging study. *Cereb. Cortex* 3, 743–757.
- Naveh-Benjamin, M., Guez, J., Kilb, A., and Reedy, S. (2004). The associative memory deficit of older adults: further support using face-name associations. *Psychol. Aging* 19, 541–546.
- O'Carroll, C. M., Martin, S. J., Sandin, J., Frenguelli, B., and Morris, R. G. M. (2006). Dopaminergic modulation of the persistence of one-trial

hippocampus-dependent memory. *Learn. Mem.* 13, 760–769.

- Ota, M., Yasuno, F., Ito, H., Seki, C., Nozaki, S., Asada, T., and Suhara, T. (2006). Age-related decline of dopamine synthesis in the living human brain measured by positron emission tomography with L-[beta-C-11]DOPA. *Life Sci.* 79, 730–736.
- Radloff, L. S. (1977). The CES-D Scale: a self-report depression scale for research in the general population. *Appl. Psychol. Meas.* 1, 385–401.
- Rossato, J. I., Bevilaqua, L. R. M., Izquierdo, I., Medina, J. H., and Cammarota, M. (2009). Dopamine controls persistence of long-term memory storage. *Science* 325, 1017–1020.
- Samanez-Larkin, G. R., Gibbs, S. E. B., Khanna, K., Nielsen, L., Carstensen, L. L., and Knutson, B. (2007). Anticipation of monetary gain but not loss in healthy older adults. *Nat. Neurosci.* 10, 787–791.
- Samanez-Larkin, G. R., Kuhnen, C. M., Yoo, D. J., and Knutson, B. (2010). Variability in nucleus accumbens activity mediates age-related suboptimal financial risk taking. *J. Neurosci.* 30, 1426–1434.
- Schott, B. H., Niehaus, L., Wittmann, B. C., Schutze, H., Seidenbecher, C. I., Heinze, H. J., and Düzel, E. (2007). Ageing and early-stage Parkinson's disease affect separable neural mechanisms of mesolimbic reward processing. *Brain* 130, 2412–2424.
- Shohamy, D., and Adcock, R. A. (2010). Dopamine and adaptive memory.

Trends Cogn. Sci. (Regul. Ed.) 14, 464–472.

- Suhara, T., Fukuda, H., Inoue, O., Itoh, T., Suzuki, K., Yamasaki, T., and Tateno, Y. (1991). Age-related changes in human D1-dopamine receptors measured by positron emission tomography. *Psychopharmacology (Berl.)* 103, 41–45.
- Takahashi, H., Kato, M., Takano, H., Arakawa, R., Okumura, M., Otsuka, T., Kodaka, F., Hayashi, M., Okubo, Y., Ito, H., and Suhara, T. (2008). Differential contributions of prefrontal and hippocampal dopamine D-1 and D-2 receptors in human cognitive functions. *J. Neurosci.* 28, 12032–12038.
- Wang, Y., Chan, G. L. Y., Holden, J. E., Dobko, T., Mak, E., Schulzer, M., Huser, J. M., Snow, B. J., Ruth, T. J., Calne, D. B., and Stoessl, A. J. (1998).
 Age-dependent decline of dopamine D1 receptors in human brain: a PET study. *Synapse* 30, 56–61.
- Watson, D., Clark, L. A., and Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: the PANAS scales. J. Pers. Soc. Psychol. 54, 1063–1070.
- Weiler, J. A., Bellebaum, C., and Daum, I. (2008). Aging affects acquisition and reversal of reward-based associative learning. *Learn. Mem.* 15, 190–197.
- Wittmann, B. C., Daw, N. D., Seymour, B., and Dolan, R. J. (2008a). Striatal activity underlies noveltybased choice in humans. *Neuron* 58, 967–973.
- Wittmann, B. C., Schiltz, K., Boehler, C. N., and Duzel, E. (2008b).

Mesolimbic interaction of emotional valence and reward improves memory formation. *Neuropsychologia* 46, 1000–1008.

Wittmann, B. C., Schott, B. H., Guderian, S., Frey, J. U., Heinze, H. J., and Duzel, E. (2005). Reward-related fMRI activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent long-term memory formation. *Neuron* 45, 459–467.

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Individual differences in risky decision-making among seniors reflect increased reward sensitivity

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Increasing age is associated with subtle but meaningful changes in decision-making. It is unknown, however, to what degree these psychological changes are reflective of agerelated changes in decision quality. Here, we investigated the effect of age on latent cognitive processes associated with risky decision-making on the Balloon Analog Risk Task (BART). In the BART, participants repetitively inflate a balloon in order to increase potential reward. At any point, participants can decide to cash-out to harvest the reward, or they can continue, risking a balloon pop that erases all earnings. We found that among seniors, increasing age was associated with greater reward-related risk taking when the balloon has a higher probability of popping (i.e., a "high risk" condition). Cognitive modeling results from hierarchical Bayesian estimation suggested that performance differences were due to increased reward sensitivity in high risk conditions in seniors.

Keywords: aging, BART, impulsivity, cognitive modeling, reward

INTRODUCTION

The trajectory of cognitive change associated with aging suggests that some presumably stable cognitive traits can actually vary across the lifespan. The prevalence and predictability of these late life changes suggest that common underlying factors may contribute to these effects, yet it is difficult to identify and differentiate such latent cognitive constructs. A recent meta-analysis has suggested that age-related change in decision quality varies when learning is involved (Mata et al., 2011). When task dynamics are explicitly understood, differing decision strategies between age groups are less likely. In contrast, more ambiguous circumstances are characterized by potentially maladaptive decisions in seniors - specifically in risky situations. Here, we investigated the effect of age on risky decision-making as assessed by the Balloon Analog Risk Task (BART; Lejuez et al., 2002). We sought to determine what cognitive factors specifically contribute to performance differences using computational methods that facilitate an understanding of complex performance patterns. Cognitive modeling offers a promising method for objectively uncovering such latent parameters (Busemeyer and Stout, 2002), which may provide closer reflections of the unobservable computations that contribute to observable behavior (Yechiam et al., 2005; O'Doherty et al., 2007).

In the BART, participants repetitively inflate or pump a balloon in order to increase potential reward. At any point, participants can decide to cash-out to harvest the reward, or they can continue, risking a balloon pop that erases all earnings. The BART has good reliability (White et al., 2008) and generalizability to real life impulsive behaviors, as demonstrated by correlations between BART pumps/pops and self-reported psychopathy, sensation seeking,

impulsivity, drug and alcohol use, gambling, and unprotected sex (Lejuez et al., 2003; Hunt et al., 2005; Wallsten et al., 2005). Previous findings have detailed how seniors are characterized by risk aversive behavior on the BART (Henninger et al., 2010; Rolison et al., 2011). Intriguingly, these findings stand in contrast to results from the meta-analysis that found that seniors were usually characterized by risk-seeking behavior when optimal performance had to be learned (Mata et al., 2011). While BART performance is clear to interpret, it is difficult to determine what motivates different performance styles, especially when learning is involved. For example, an increased number of pumps could reflect impulsive risky decision-making, yet it could also reflect a more optimal decision strategy since participants often overestimate risk (Lejuez et al., 2002; Rao et al., 2008). Moreover, either of these motivations could be orthogonal to accurate learning.

In light of recent findings that age-related deficits in executive control may be unspecific and inaccurate (Verhaeghen, 2011), cognitive process models offer an opportunity to parse variance in performance to relevant latent constructs related to decisionmaking. For example, cognitive modeling has revealed how agerelated variability in response times may be due to a benign impact of generalized slowing, not task-specific manipulations that purportedly measure executive control (Ratcliff et al., 2006). More germane to the current investigation, Wood et al. (2005) have demonstrated that in the Iowa gambling task, young adults integrate reward expectations across a prolonged trial history, whereas seniors focus more on the most recent trials and are therefore more sensitive to incidental violations of probabilistic contingencies. Such cognitive process models offer a method for identifying candidate underlying processes that occur behind the scenes of observable behavior.

Capitalizing on a previously published cognitive model of BART performance (Wallsten et al., 2005; van Ravenzwaaij et al., 2011), here we aim to decompose observable behaviors to latent components reflecting reward sensitivity, behavioral consistency, and learning-related estimation of task probabilities. These latent parameters can offer a more specific explanation of the cognitive processes underlying observable behaviors.

MATERIALS AND METHODS

PARTICIPANTS

Young participants (aged 18-30) were recruited from the University of Amsterdam campus. Senior participants (above age 60) were recruited from the SeniorLab database (www.seniorlab.nl) of healthy self-selected older adults. Subjects received course credits or financial compensation for participation. They gave written informed consent before experimentation. All procedures were executed in compliance with relevant laws and institutional guidelines and were approved by the local ethics committee. The demographics of the final participant groups are as follows. Young participants: N = 23, female = 12, mean age = 21, age range = 18-26; senior participants: N = 29, female = 22, mean age = 73, age range = 63-87. Young and senior participants did not differ in their verbal intelligence, as assessed with the Nederlandse Leesvaardigheidstest voor Volwassenen (Dutch Reading test for Adults; Schmand et al., 1991) or in their working memory, as assessed with the O-span (Turner and Engle, 1989) scored using the partial-credit unit scoring system (Conway et al., 2005), ts < 1.5, ps < 15.

BALLOON ANALOG RISK TASK

Participants performed an adjusted version of the BART. A red balloon was presented in the center of a computer screen (see **Figure 1**). Participants could inflate the balloon by pressing the space bar, or cash the current virtual value of the balloon into a virtual bank by pressing the right shift button. On every pump the balloon could also explode; the probability of explosion was varied in two different risk conditions described below. If a balloon popped, the value of that balloon was lost to the participant, but the total amount that was previously cashed to the virtual bank was unaffected. The current value of the balloon was presented on the balloon in green digits, and in a separate box on the left side of the balloon. Two boxes on the right side indicated how much virtual money was earned with the previous-balloon, and how much virtual money the participant had collected on the virtual bank.

The starting radius of the balloon was 150 pixels; the starting value was $\in 0.00$. On every pump the radius of the balloon increased with 1.2 pixels and the value of the balloon with $\in 0.05$. The adjustment of the size and current value (on the balloon and in the left box) was accompanied by the sound of air entering the balloon for 100 ms. On every pop a picture of an exploded balloon was presented for 1000 ms, accompanied by the sound of an explosion. The current value of the balloon and the value in the previous-balloon box were set to $\in 0.00$ and a new balloon was presented. On every cash moment a yellow dollar sign was presented in the middle of the screen for 1000 ms, accompanied by

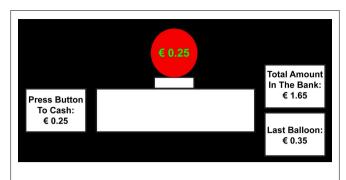


FIGURE 1 | Balloon Analog Risk Task (BART). Participants inflated a balloon until they decided to cash-out or until it popped and the accrued earnings on that trial were lost. Participants completed both high and low risk blocks of the BART.

the sound of an old cash register. The amount of money in the bank box and the previous-balloon box were adjusted to include the current earning, the current value of the balloon was set to \notin 0.00, and a new balloon was presented. The response window for the participant was unlimited.

Participants first received two short blocks of training. The first block consisted of five balloons. In this block participants could only pump the balloon until it popped; they could not cash-out yet. The five balloons would pop on the 7th, 18th, 28th, 42nd, and 56th pumps (in random order). The second practice block consisted of 10 balloons and was similar to the real task, but with an explosion probability of 3.75% (average of the two real blocks). In the test phase, participants were presented with two blocks of 40 balloons. The chance that the balloon would explode was 2.5 and 5% within each block. Although this constant probability is different than the increasing probability schedule used in most studies of the BART, this manipulation allowed us to explicitly assess performance during low (2.5%) and high (5%) risk conditions.

The order of the blocks was randomized between participants. Participants were informed about the risk prior to beginning each block, and they were instructed to try to maximize the amount of virtual money in the bank. To encourage this, 5% of the virtual money in the bank was paid to the participants in addition to the payment for participation. Outcome variables for each block included the average number of pumps on cash trials, the number of popped balloons, as well as the amount of virtual money earned at the end of the block. In addition, the ratio of the number of pumps following a cash-out to the number of pumps following a pop was included as a measure of reward-based risk taking. The evolution of performance across time was investigated by splitting each block of 40 trials into four bins of 10 trials each. This analysis was performed to investigate if age-related differences were specific to early trials (as in Rolison et al., 2011), which might suggest differences in initial learning about task contingencies.

COMPUTATIONAL MODELING

To decompose observable behavior into separable latent elements we used a hierarchical Bayesian extension of the best-fitting Wallsten et al. (2005) model, as detailed by van Ravenzwaaij et al. (2011). In hierarchical modeling, individual participants are nested within group (young and senior) and condition (low and high risk) categories, facilitating simultaneous parameter estimation for each condition for each participant. Wallsten et al. (2005) tested a variety of cognitive process models to distil latent factors influencing BART task performance. The best-fitting model (#3 in Wallsten et al., 2005) assumed that the decision maker updates the probability of explosion after each balloon, and slowly learns to estimate the explosion probability. Four free parameters were fit that describe variability between decision-making styles: two learning-related parameters alpha (α) and mu (μ), a reward sensitivity parameter gamma (γ^+), and a behavioral consistency parameter beta (β). These parameters are referred to with Greek letters for the description of computational algorithms; text will be used otherwise.

The model for each decision maker begins with the assumption that the probability of the balloon bursting on each trial k is constant: p_k^{belief} . This means that the balloon is equally likely to explode on the first pump as in the fourth, for example. The first trial starts with an *a priori* belief of the probability of explosion captured by a beta distribution with free scaling parameters α_0 and μ_0 . This prior belief is then updated according to Bayes' rule to calculate an updated belief of bursting. The probability of explosion for the balloon on any given trial is:

$$p_k^{\text{belief}} = 1 - \frac{\alpha_0 + \sum_{K=0}^{k-1} n_K^{\text{success}}}{\mu_0 + \sum_{K=1}^{k-1} n_K^{\text{pumps}}} \text{ with } \alpha < \mu$$

The prior belief is represented by the ratio $1 - \alpha_0/\mu_0$. This value then is updated by adding for the numerator the sum of all successful pumps so far (excluding the current trial), $\sum_{K=0}^{k-1} n_K^{\text{success}}$, and for the denominator by adding the sum of all pumps so far, $\sum_{K}^{k-1} n_K^{\text{pumps}}$.

The next component in the model specifies the number of pumps considered optimal. The free parameter γ^+ influences the assessment of the optimal number of pumps by weighting the estimated belief of a pop p_k^{belief} . Note that larger γ^+ values leads to more pumps. Notably, larger estimated γ^+ parameters have been correlated with a greater propensity for real world risky behaviors, including drug use, unprotected sex, and stealing as reported in Wallsten et al. (2005). For trial *k* the optimal number of pumps ω_k , is as follows:

$$\omega_k = \frac{-y^+}{\ln\left(1 - p_k^{\text{belief}}\right)} \text{ with } y^+ \ge 0$$

The actual probability of pumping the balloon on any opportunity *l* for trial *k* depends on both the optimal number of pumps ω_k , and on the free parameter β which reflects behavioral consistency. A larger β parameter reflects a sharper, more deterministic response strategy. For example, if $\beta = 0$, then the $p_{kl}^{pump} = 0.5$ and the decision maker will choose randomly between pumping and cashing. As β increases, behavior becomes more and more deterministic as defined by the optimal number of pumps $(l - \omega_k)$. A logistic equation is used to estimate response choices with free parameter β :

$$p_{kl}^{pump} = \frac{1}{1+e^{\beta(l-\omega_k)}}$$
 with $\beta \geq 0$

In the context of Bayesian statistics, van Ravenzwaaij et al. (2011) extended previous modeling work on the BART task by introducing a hierarchical extension for the BART models. The Bayesian approach combined with hierarchical modeling has several advantages over standard approaches (i.e., maximum likelihood estimation), primarily by providing more precise parametric estimates while simultaneously estimating both subject and group level effects (Wagenmakers et al., 2008; Wetzels et al., 2010; Lee, 2011).

The hierarchical extension draws individual parameters γ^+ and β from normal distributions around estimated group level parameters γ^{+*} and β^* . The learning parameters α and μ were kept as subject level parameters since they present a high degree of correlation and do not significantly affect the precision of γ^+ and β estimates (van Ravenzwaaij et al., 2011). Whereas a standard maximum likelihood approach to model estimation would estimate parameter values which maximize the (log) likelihood of the model predicting the data, Bayesian models instead follow a different approach. Each model parameter is estimated by a probability function with a unique mean and variance. These functions are initially set to a uniform or uninformative distribution and are updated with experience according to Bayes' rule.

A suitable numerical routine to sample from the posterior distributions is offered by the Gibbs Sampling algorithm and Markov Chain Monte Carlo (MCMC) simulations. MCMC relies on simulating one or more chains of random values sampled from the posterior distribution until all the chains have converged. Once convergence has been reached, successive samples can be assumed to be drawn from the posterior distribution representing the belief of the decision maker after experience. It is common procedure to discard initial samples (burn-in) to assure independence of the final samples from the starting chain values.

In all of the reported simulations the estimates are based on 15,000 iterations after 10,000 iterations of burn-in. For the parameters α and μ , uniform distributions were used as uninformative priors. For the parameters γ^+ and β , Gaussian distributions centered on their group level means, γ^{+*} and β^* were used. For these group level parameters γ^{+*} and β^* , uniform distribution were once again used as uninformative priors. Three chains were used in all simulations with random starting values. MCMC sampling was implemented via the open package OpenBugs (Lunn et al., 2009) interfaced through the statistical program R. Chain convergence was assessed by means of the Rhat statistic, a scaling factor which approaches a value of 1 under chain convergence.

Note that the size of the learning rate parameters alpha and mu were scaled to the specific task used here (due to the constant probability of explosion) and thus are different from previous studies that used a larger range (c.f. Rolison et al., 2011). To facilitate comparison across studies, probability density functions were computed based on the alpha and mu parameters. The mean and variance of these functions were computed for each participant in each risk condition; these variables were then compared to examine potential differences in learning that would affect beliefs in the chance the balloon would not pop (the prior).

To summarize, like van Ravenzwaaij et al. (2011), we used a hierarchical estimation procedure to estimate gamma (γ^+) and

beta (β) parameters in the best-fitting Wallsten et al. (2005) model. However, the two learning rate parameters alpha (α) and mu (μ) remained subject level, since hierarchical estimates provided worse fits to the data (i.e., there did not appear to be any group level regularities in these variables). Therefore our model assumed group level variance for risk sensitivity and behavioral consistency, and individual differences only for learning through experience. This hybrid hierarchical procedure created the best model given that: (1) it fit better than a baseline model which assumed no learning (Wallsten et al., 2005) as assessed by Deviance Information Criteria (all DIC learning < baseline, learning mean = 137, baseline mean = 179), (2) it had full convergence where only gamma and beta parameters from the fully hierarchical van Ravenzwaaij et al. (2011) model converged, and (3) the hierarchical fits improved on the single-subject level estimation used by Wallsten et al. (2005).

RESULTS

PERFORMANCE

Given that the focus of this paper is on aging, only main or interactive effects with age are described. There were no main or interaction effects for age group on the average number of pumps on cash-out trials (Fs < 1). However, there was a significant interaction between risk and age group for number of popped balloons [F(1, 50) = 4.56, p = 0.038], without a main effect of age [F(1, 50) = 4.56, p = 0.038], without a main effect of age [F(1, 50) = 4.56, p = 0.038], without a main effect of age [F(1, 50) = 4.56, p = 0.038], without a main effect of age [F(1, 50) = 4.56, p = 0.038], without a main effect of age [F(1, 50) = 4.56, p = 0.038], without a main effect of age [F(1, 50) = 4.56, p = 0.038], without a main effect of age [F(1, 50) = 4.56, p = 0.038], without a main effect of age [F(1, 50) = 4.56, p = 0.038], without a main effect of age [F(1, 50) = 4.56, p = 0.038]. 50 = 2.21, p = 0.14], see Figure 2. Contrasts revealed that seniors differed in the number of pops between high and low risk conditions (p < 0.01) and age groups differed in the high risk condition (p = 0.015). To investigate how performance changed over time, data from each condition was split into four consecutive 10-block bins. In the low risk condition, there was a significant interaction between age group and time [F(3, 50) = 3.80, p = 0.02], where seniors had more pumps in the third (p = 0.07) and fourth (p = 0.05) blocks. In the high risk condition, there was a significant interaction between age group and time [F(3, 50) = 4.087,p < 0.01], where contrasts revealed that seniors had more pumps in the last two blocks specifically (ps < 0.01). These performance differences occurred in the absence of a difference in the amount of virtual money earned (Fs < 1.9).

Figure 3 demonstrates how in the senior group, age was correlated with the number of pops in the high risk condition [r(29) = 0.44, p = 0.02] and with the difference in pops between high and low risk conditions [r(29) = 0.50, p < 0.01]. Age also correlated with an increased ratio of the number of pumps after a cash-out compared to number of pumps after a pop in the high risk condition [r(29) = 0.44, p = 0.02] and with the difference in ratios between the high and low risk conditions [r(29) = 0.53, p < 0.01]. However, after removal of the largest outlying value only this difference measure remained significant (high risk p = 0.09). This integrated set of findings suggests that increasing age is associated with greater reward-based risk taking.

MODEL RESULTS

The cognitive model fit four parameters for each participant during each condition: learning rate parameters alpha and mu, reward sensitivity parameter gamma, and behavioral consistency parameter beta. The reported parameter estimates were all drawn after convergence of chains (Rhat = 1). The young and senior groups were drawn from the same posterior distributions in low and high risk conditions. This suggests that the individual estimates of the probability of non-explosion (calculated as a beta distribution from the alpha and mu parameters) would be the same between age groups for each condition. When comparing the means of the distributions there was a significant effect of risk, with the high risk condition having lower estimated probabilities of non-explosion [F(1, 50) = 40.30, p < 0.01], yet there were no main or interactive effects with group, and no effects for the variance of the distributions.

To check whether learning changed over the course of the hard condition, the means of these distributions for each of the four blocks of 10 trials were estimated. There were no significant differences between age groups in the estimated probability of non-explosion over time (all ps > 0.11). In fact, the young group actually had marginally higher estimates of non-explosion in three out of four bins, providing evidence that differential performance in seniors was not due to a more optimistic learned belief. In conjunction with the finding of increased pops late in the high risk condition, these null effects suggest that the age groups were not characterized by differential learning of explosion probabilities during task performance.

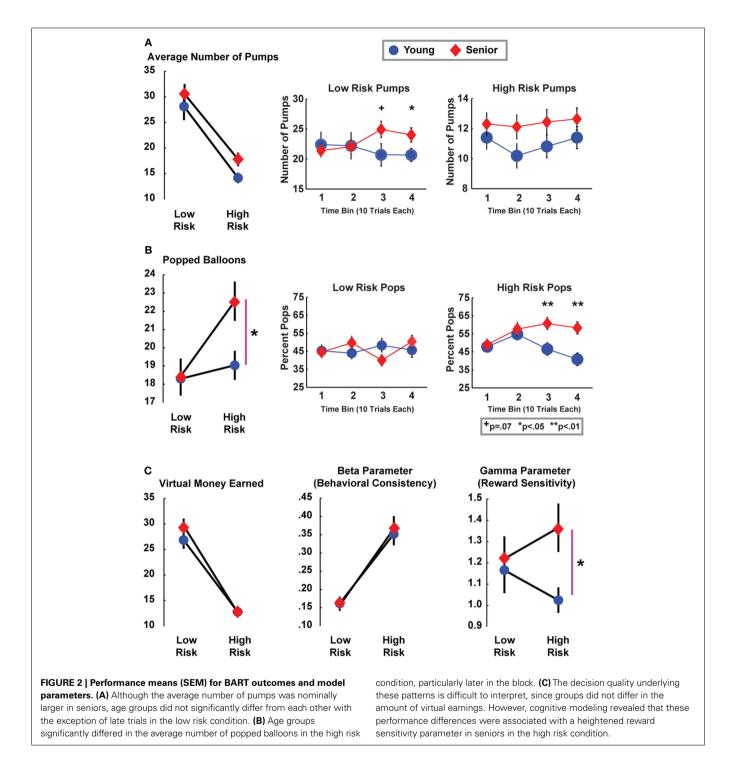
There were no main or interactive effects with age for the beta (behavioral consistency) parameter (Fs < 1). However, there was a significant interaction between risk and age group for the gamma (reward sensitivity) parameter [F(1, 50) = 4.79, p = 0.033], with no main effects (**Figure 2C**). The only significant contrast was between age groups in the high risk condition, where seniors were characterized by greater reward sensitivity [t(51) = 2.46, p = 0.017]. Condition-specific gamma parameters did not significantly correlate with age, pumps, pops, virtual earnings, or the post-cash:post-pop ratio in either age group. Thus, this model parameter reflects a distinct measure of reward-related decision-making.

DISCUSSION

This investigation revealed that increased age was associated with altered BART performance reflective of greater reward sensitivity during high risk decisions. In fact, age directly correlated with both pops and post-reward risk taking in the high risk condition without an increase in earnings. This performance style did not appear to depend on differences in learning: seniors had greater high risk reward sensitivity in the context of similar estimation of reward probabilities.

AGE-RELATED ALTERATION OF PERFORMANCE

Seniors did not differ from the young group in the overall amount of virtual money earned in either risk condition, and the number of pumps on cash-out trials was not significantly different from the young group. While seniors were characterized by a greater number of popped balloons than young adults, and increasing age amongst seniors predicted a greater number of pops, it is difficult to determine whether these performance features reflect a behavioral indicator of poor decision-making. In short, it is difficult to know if seniors were suboptimal impulsive performers or if they

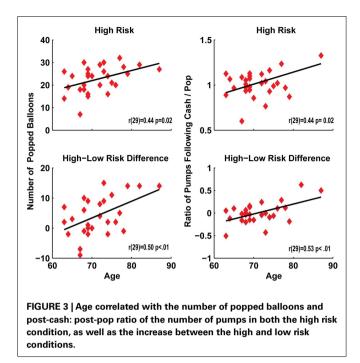


were simply following a different strategy – there was no ultimate difference in earnings between the groups.

The review of Mata et al. (2011) concluded that age-related decision changes appear to be due to impairments in learning. These age-related changes were most often associated with an increase in risk-seeking behaviors, with the specific exception of two previous findings from the BART. These studies described how seniors were more risk averse (fewer pumps) when tested with only

ten trials (Henninger et al., 2010; Rolison et al., 2011), yet behavioral trends converged with younger participants over a greater number of trials (Rolison et al., 2011). As shown in **Figure 2**, age-related differences in this investigation did not appear to be due to early task performance or learning. Rather, the age-related differences reported here were most prevalent late in each task.

The probabilistic task structure used here may have contributed to different findings between the current investigation and two



previous investigations. As opposed to other studies of the BART, the probability of a pop in the current investigation did not increase with each pump; rather it remained a constant value over time. While this modification facilitated the comparison of two discrete levels of risk, it may also contribute to differences in replication across studies. These current findings broadly converge with the conclusion of Mata et al. (2011) that learning-related change in cognitive capacities may lead to poorer decision-making. However, the current findings suggest that seniors may still be characterized by risky decision-making even when learning abilities are comparable with younger subjects.

COGNITIVE MODELING SUGGESTS AGE-RELATED ALTERATION OF REWARD SENSITIVITY

Cognitive modeling is useful for revealing latent parameters that underlie complicated patterns of behavior, especially when some behaviors (pops) but not others (pumps, earnings) significantly differ between groups. Hierarchical Bayesian estimation revealed that group level performance differences were reflective of variance in a latent reward sensitivity parameter, and did not relate to a change in behavioral consistency. This dissociation between reward sensitivity and response variability processes is supported by a rat study that demonstrated how inactivation of different cortical structures (mPFC and OFC, respectively) selectively alters these two performance features (Jentsch et al., 2010). Critically, participants had a similar estimation of the task structure and probability of explosions, suggesting that apparent increases in reward sensitivity were not due to poorer learning of risky probabilities.

A larger reward sensitivity parameter will directly scale with an increased probability of inflating the balloon on each trial. While the ANOVA was non-significant for a group difference in pumps, it can be seen in **Figure 2A** that seniors had a larger number of

pumps in the high risk condition compared to young participants [in fact, this difference was nearly statistically significant in the high risk condition: t(51) = 1.95, p = 0.056, but not in the low risk condition: t < 1]. Convergent with this trend, increasing age predicted riskier decision-making following successes (**Figure 3**). Behavioral findings were suggestive of riskier decision-making in the high risk condition, but the statistical evidence did not support a strong conclusion from performance differences. Cognitive modeling provided strong support for a determination of altered decision-making, revealing an increased sensitivity to reward in seniors during high risk trials. In sum, an increased sensitivity to reward in high risk trials led seniors to pump more often, leading to both greater pops and higher cash-out earnings on a smaller number of trials; these outcomes equated over trials to similar virtual earnings between age groups.

POTENTIAL NEURAL SYSTEMS INVOLVED IN ALTERED DECISION-MAKING IN OLD AGE

There are tremendous individual differences in performance on reward-based decision-making tasks amongst seniors. These differences likely implicate a host of differentially contributing mechanisms that underlie altered decision-making. For example, while many seniors still perform comparably well to young participants on the Iowa Gambling Task, a much larger percentage of seniors perform poorly (Denburg et al., 2005). Poor-performing seniors also fail to show anticipatory skin conductance increases prior to advantageous choices (Denburg et al., 2006). Other investigations have described how seniors have reduced neural activity and diminished affective tone during loss anticipation (Wood et al., 2005; Samanez-Larkin et al., 2007). These previous findings suggest that a decoupled neuro-visceral response may contribute to an alteration in risky decision-making.

In line with other studies of risk and reward (Kuhnen and Knutson, 2005; Wrase et al., 2007), neuroimaging investigations have detailed how a wide range of frontal cortical and striatal areas are increasingly active in the BART task in conjunction with riskier decisions (Rao et al., 2008, 2010). Parkinson's patients with impulse control disorders have lower resting blood flow and lower blood flow reactivity in the striatum during the BART (Rao et al., 2010). This specific type of Parkinsonian patient is also influenced by dopamine agonists to increase the number of pumps (Claassen et al., 2011). These imaging and pharmacological findings clearly implicate increased cortico-striatal activity with impulsive risk taking during the BART task. Both decreased neuro-visceral integration during risk and increased cortico-striatal reactivity to reward offer plausible hypotheses for age-related neural changes that could underlie the pattern of effects observed here.

CONCLUSION

This investigation revealed that increased age was associated with altered behavioral performance reflective of greater reward sensitivity during high risk decisions. Age-related structural or functional change in neural systems underlying neurovisceral integration and reward responsiveness are plausible candidates for this specific developmental change in decision quality.

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REFERENCES

- Busemeyer, J. R., and Stout, J. C. (2002). A contribution of cognitive decision models to clinical assessment: decomposing performance on the Bechara gambling task. *Psychol. Assess.* 14, 253–262.
- Claassen, D. O., van den Wildenberg, W. P., Ridderinkhof, K. R., Jessup, C. K., Harrison, M. B., Wooten, G. F., and Wylie, S. A. (2011). The risky business of dopamine agonists in Parkinson disease and impulse control disorders. *Behav. Neurosci.* 125, 492–500.
- Conway, A. R., Kane, M. J., Bunting, M. F., Hambrick, D. Z., Wilhelm, O., and Engle, R. W. (2005). Working memory span tasks: a methodological review and user's guide. *Psychon. Bull. Rev.* 12, 769–786.
- Denburg, N. L., Recknor, E. C., Bechara, A., and Tranel, D. (2006). Psychophysiological anticipation of positive outcomes promotes advantageous decision-making in normal older persons. *Int. J. Psychophysiol.* 61, 19–25.
- Denburg, N. L., Tranel, D., and Bechara, A. (2005). The ability to decide advantageously declines prematurely in some normal older persons. *Neuropsychologia* 43, 1099–1106.
- Henninger, D. E., Madden, D. J., and Huettel, S. A. (2010). Processing speed and memory mediate agerelated differences in decision making. *Psychol. Aging* 25, 262–270.
- Hunt, M. K., Hopko, D. R., Bare, R., Lejuez, C. W., and Robinson, E. V. (2005). Construct validity of the Balloon Analog Risk Task (BART): associations with psychopathy and impulsivity. Assessment 12, 416–428.
- Jentsch, J. D., Woods, J. A., Groman, S. M., and Seu, E. (2010). Behavioral characteristics and neural mechanisms mediating performance in a rodent version of the Balloon Analog Risk Task. *Neuropsychopharmacology* 35, 1797–1806.

- Kuhnen, C. M., and Knutson, B. (2005). The neural basis of financial risk taking. *Neuron* 47, 763–770.
- Lee, M. (2011). How cognitive modeling can benefit from hierarchical Bayesian models. J. Math. Psychol. 55, 1–7.
- Lejuez, C. W., Aklin, W. M., Zvolensky, M. J., and Pedulla, C. M. (2003). Evaluation of the Balloon Analogue Risk Task (BART) as a predictor of adolescent real-world risktaking behaviours. J. Adolesc. 26, 475–479.
- Lejuez, C. W., Read, J. P., Kahler, C. W., Richards, J. B., Ramsey, S. E., Stuart, G. L., Strong, D. R., and Brown, R. A. (2002). Evaluation of a behavioral measure of risk taking: the Balloon Analogue Risk Task (BART). J. Exp. Psychol. Appl. 8, 75–84.
- Lunn, D., Spiegelhalter, D., Thomas, A., and Best, N. (2009). The BUGS project: evolution, critique and future directions. *Stat. Med.* 28, 3049–3067.
- Mata, R., Josef, A. K., Samanez-Larkin, G. R., and Hertwig, R. (2011). Age differences in risky choice: a metaanalysis. *Ann. N. Y. Acad. Sci.* 1235, 18–29.
- O'Doherty, J. P., Hampton, A., and Kim, H. (2007). Model-based fMRI and its application to reward learning and decision making. *Ann. N. Y. Acad. Sci.* 1104, 35–53.
- Rao, H., Korczykowski, M., Pluta, J., Hoang, A., and Detre, J. A. (2008). Neural correlates of voluntary and involuntary risk taking in the human brain: an fMRI Study of the Balloon Analog Risk Task (BART). *Neuroimage* 42, 902–910.
- Rao, H., Mamikonyan, E., Detre, J. A., Siderowf, A. D., Stern, M. B., Potenza, M. N., and Weintraub, D. (2010). Decreased ventral striatal activity with impulse control disorders in Parkinson's disease. *Mov. Disord.* 25, 1660–1669.
- Ratcliff, R., Thapar, A., and Mckoon, G. (2006). Aging and individual differences in rapid two-choice

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decisions. Psychon. Bull. Rev. 13, 626–635.

- Rolison, J. J., Hanoch, Y., and Wood, S. (2011). Risky decision making in younger and older adults: the role of learning. *Psychol. Aging* 129–140.
- Samanez-Larkin, G. R., Gibbs, S. E., Khanna, K., Nielsen, L., Carstensen, L. L., and Knutson, B. (2007). Anticipation of monetary gain but not loss in healthy older adults. *Nat. Neurosci.* 10, 787–791.
- Schmand, B. A., Bakker, D., Saan, R. J., and Louman, J. (1991). De Nederlandse Leestest voor Volwassenen: een maat voor het premorbide intelligentieniveau./The Dutch Adult Reading Test: a measure of premorbid intelligence. *Tijdschr. Gerontol. Geriatr.* 22, 15–19.
- Turner, M. L., and Engle, R. W. (1989). Is working memory capacity task dependent? *J. Mem. Lang.* 28, 127–154.
- van Ravenzwaaij, D., Dutilh, G., and Wagenmakers, E. J. (2011). Cognitive model decomposition of the BART: assessment and application. J. Math. Psychol. 55, 94–105.
- Verhaeghen, P. (2011). Aging and executive control: reports of a demise greatly exaggerated. *Curr. Dir. Psychol. Sci.* 20, 174–180.
- Wagenmakers, E., Lee, M., Lodewyckx, T., and Iverson, G. (2008). "Bayesian versus frequentist inference," in *Bayesian Evaluation of Informative Hypotheses in Psychology*, eds H. Hoijtink, I. Klugkist, and P. Boelen (New York: Springer), 181–210.
- Wallsten, T. S., Pleskac, T. J., and Lejuez, C. W. (2005). Modeling behavior in a clinically diagnostic sequential risk-taking task. *Psychol. Rev.* 112, 862–880.
- Wetzels, R., Vandekerckhove, J., Tuerlinckx, F., and Wagenmakers, E. (2010). Bayesian parameter estimation in the expectancy valence model of the Iowa gambling task. *J. Math. Psychol.* 54, 14–27.
- White, T. L., Lejuez, C. W., and de Wit, H. (2008). Test-retest characteristics

of the Balloon Analogue Risk Task (BART). Exp. Clin. Psychopharmacol. 16, 565–570.

- Wood, S., Busemeyer, J., Koling, A., Cox, C. R., and Davis, H. (2005). Older adults as adaptive decision makers: evidence from the Iowa Gambling Task. *Psychol. Aging* 20, 220–225.
- Wrase, J., Kahnt, T., Schlagenhauf, F., Beck, A., Cohen, M. X., Knutson, B., and Heinz, A. (2007). Different neural systems adjust motor behavior in response to reward and punishment. *Neuroimage* 36, 1253–1262.
- Yechiam, E., Busemeyer, J. R., Stout, J. C., and Bechara, A. (2005). Using cognitive models to map relations between neuropsychological disorders and human decisionmaking deficits. *Psychol. Sci.* 16, 973–978.

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Decisions from experience: adaptive information search and choice in younger and older adults

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In real-world decision making, choice outcomes, and their probabilities are often not known a priori but must be learned from experience. The dopamine hypothesis of cognitive aging predicts that component processes of experience-based decision making (information search and stimulus-reward association learning) decline with age. Many existing studies in this domain have used complex neuropsychological tasks that are not optimal for testing predictions about specific cognitive processes. Here we used an experimental sampling paradigm with real monetary payoffs that provided separate measures of information search and choice for gains and losses. Compared with younger adults, older adults sought less information about uncertain risky options. However, like younger adults, older participants also showed evidence of adaptive decision making. When the desirable outcome of the risky option was rare (p = 0.10 or 0.20), both age groups engaged in more information search and made fewer risky choices, compared with when the desirable outcome of the risky option was frequent (p = 0.80 or 0.90). Furthermore, loss options elicited more sampling and greater modulation of risk taking, compared with gain options. Overall, these findings support predictions of the dopamine hypothesis of cognitive aging, but they also highlight the need for additional research into the interaction of age and valence (gain vs. loss) on experience-based choice.

Keywords: aging, dopamine, financial decisions, choice, sampling paradigm

INTRODUCTION

Decision making in everyday life often involves choosing among options that vary with respect to potential payoffs and outcome probabilities. Typically, payoffs and risks are not known *a priori* but must be inferred from past experience (e.g., Hertwig et al., 2004). For example, a commuter may have to choose between alternate routes to work. One route may be more direct (high payoff) but carry a larger risk of delays, whereas another route may be longer (low payoff) but carry no risk of delays. In this scenario, a poor decision may cost the decision maker no more than a few minutes of commuting time. In high-stakes domains such as healthcare, financial planning, and consumer choice, however, the costs associated with maladaptive decisions can be considerable.

What characterizes adaptive decision making in the context of experience-based risky choice? One aspect is *predecisional information search*, or the extent to which the decision maker explores the available options prior to making a choice. In the commuting example, the decision maker's chances of choosing the optimal route are likely to increase as a function of the number of times that she has used each route before. A second aspect is *stimulus–reward learning*, or the ability to learn from positive and negative feedback. If the decision maker is insensitive to successes (short commutes) and failures (long commutes), her choices are unlikely to change as a function of past experience. A third aspect of adaptive decision making is adaptive *choice*. This refers to the degree to which the decision maker modulates her choices according to the level of risk, risk being defined by the probability or the variability of

the possible outcomes of a choice (Glimcher, 2008). For example, other things being equal, routes with a small probability of delays should be chosen more often than routes with a high probability of delays.

The effects of aging on decision making have recently moved to the forefront of research in psychology and neuroeconomics. This trend has been partly motivated by evidence of age-related decline in dopaminergic neurotransmission in the brain (e.g., Wang et al., 1998; Kaasinen et al., 2000). According to the "dopamine hypothesis" of cognitive aging (e.g., Li et al., 2001; Braver and Barch, 2002; Bäckman et al., 2006, 2010), deficient dopaminergic neuromodulation is one of the causes of age-related cognitive decline. In younger adults, dopaminergically innervated brain structures such as the ventral striatum and the ventromedial prefrontal cortex have been linked to decision-relevant functions such as information search and exploration (e.g., Düzel et al., 2010), stimulus-reward learning (e.g., Schultz, 2000), as well as the coding of uncertainty (e.g., Fiorillo et al., 2003; Fiorillo, 2011). According to the dopamine hypothesis of aging, each of these aspects of experiencebased choice should therefore show age-related decline. However, the evidence from extant behavioral and neuroimaging studies is mixed.

Behavioral studies in domains such as consumer choice and medical decision making suggest that compared with younger adults, older adults prefer to have fewer choice options (Reed et al., 2008), seek less variety (Novak and Mather, 2007), and, critically, seek less information about choice options (for reviews, see Mather, 2006; Mata and Nunes, 2010). At least two studies indicate, however, that age-related decline in information seeking may be limited to situations in which choice options have negative features (Mather et al., 2005; Lockenhoff and Carstensen, 2007). This finding has been explained in terms of socioemotional selectivity theory (Carstensen et al., 1999), which postulates that age-related reductions in time perspective lead older adults to prioritize emotion-regulation goals at the expense of information-seeking goals. By this account, older adults may avoid seeking out negative information about choice options in order to protect their emotional well-being.

Stimulus-reward learning in younger and older adults has been investigated with a number of different neuropsychological and neuroimaging tasks. Studies using variants of the Probabilistic Object Reversal Task (Heekeren et al., 2007), which requires flexible adjustment to changes in stimulus-reward contingencies, have revealed age-related decline in learning from positive feedback (Mell et al., 2005), as well as under-activation of the ventral striatum in response to reward cues (Mell et al., 2009). In the Iowa gambling task (IGT; Bechara et al., 1994), participants make repeated draws from decks of cards that differ with respect to their expected value. To maximize their scores, participants must learn to choose "good decks" over "bad decks," an ability that is impaired in patients with damage in the ventromedial prefrontal cortex (e.g., Bechara et al., 2000). Successful performance requires learning of outcome contingencies, but likely also taps other cognitiveaffective processes (e.g., Wood et al., 2005). Findings with healthy older adults have been mixed, with some studies showing agerelated deficits (Denburg et al., 2005; Fein et al., 2007; Zamarian et al., 2008), and others reporting no age differences (Kovalchik et al., 2005; Wood et al., 2005; see also Hosseini et al., 2010). There is also no consistent evidence for age-by-valence effects on learning (but see Wood et al., 2005; Denburg et al., 2006). In the Probabilistic Selection Task (Frank et al., 2004), participants have to acquire positive and negative outcome contingencies, and there are separate learning measures for both. One study using this task with "younger-old" and "older-old" participants suggested that negative feedback may be more effective than positive feedback in the second group, possibly due to low tonic dopamine levels in advanced old age (Frank and Kong, 2008). In a more recent study with younger and older adults (Hämmerer et al., 2011), there was evidence of age-related decline in stimulus-reward learning, as well as a negative learning bias in older adults. There are also data suggesting that the proportion of individuals with a negative learning bias may increase with age (Simon et al., 2010). However, Samanez-Larkin et al., 2007, supplementary materials) found no age-by-valence interaction in a probabilistic learning task. Finally, neuroimaging studies with the monetary incentive delay (MID) task (Knutson et al., 2001), designed to separate brain activations related to anticipation and receipt of monetary gains and losses, have shown age-related reductions in anticipatory brain signals (Schott et al., 2007; Dreher et al., 2008). These findings have added to the evidence that reward-based learning is impaired in older adults. However, in one study with the MID task, older adults showed anticipatory responses similar to those observed in younger adults, at least during gain anticipation (Samanez-Larkin et al., 2007). Striatal activity associated with outcome processing also appears to be normal in older adults (Cox et al., 2008). In summary, the literature on stimulus–reward learning is mixed. There is a fair amount of evidence for an age-related learning deficit, but to what extent this deficit is modulated by valence is as yet unclear.

A final aspect of experience-based decision making is risk preference. Given two options of identical expected value, a risk-averse decision maker prefers low-risk to high-risk options (for a full definition of the term, see Glimcher, 2008). The idea that older adults are more risk-averse than younger adults has a long history in psychology (for an early review, see Okun, 1976), but empirical support for it is surprisingly scant. Studies of risky choice in real-world domains such as financial planning and gambling have often failed to show age-related increases in risk aversion (for a review, see Mather, 2006). A recent quantitative meta-analysis of the experimental literature (Mata et al., 2011) indicates that the size and direction of age differences in risk preference depends strongly on the task, with no evidence for task-general age-related changes. This heterogeneity is also illustrated by the two existing neuroimaging studies of aging and risky choice. In one of these studies (Lee et al., 2008), older adults made more risk-averse gambling decisions. They also showed greater activation in the right insula when choosing risky options, perhaps reflecting a stronger negative anticipatory response to risk. However, in another study (Samanez-Larkin et al., 2010) using a financial investment task, older adults were more risk-seeking than younger adults. Interestingly, this effect was shown to be associated with increased variability in subcortical brain activity, consistent with Li et al.'s (2001) proposal that age-related dopaminergic decline leads to increased "neural noise" and reduced sensitivity to outcome probabilities. Overall, there is no clear evidence for a systematic age-related shift in risk preferences. Instead, age differences in task-specific risk preferences may reflect differences in the learning demands of the tasks (Mata et al., 2011).

In summary, the dopamine hypothesis of cognitive aging predicts that critical aspects of experience-based decision making (information search and stimulus-reward learning) undergo agerelated decline. While this prediction has received support in some studies, there are many inconsistent findings, perhaps partly due to the diversity and complexity of the paradigms used (e.g., the IGT). Few studies have systematically compared younger and older adults on multiple components of experience-based risky choice within the same experimental setting (but see Deakin et al., 2004). Furthermore, only about half of the existing studies have used monetary incentives (Mata et al., 2011). There is a dearth of studies comparing gain- and loss-related decisions (Mata et al., 2011), even though several lines of evidence suggest that aging may affect the two types of choices differently (e.g., Mather et al., 2005; Samanez-Larkin et al., 2007; Frank and Kong, 2008). Finally, we noted a lack of theoretical integration between the neuropsychological and aging literatures, on the one hand, and the growing field on experience-based choice research in the behavioral economics literature, on the other (for reviews, see Hertwig and Erev, 2009; Rakow and Newell, 2010). Together, these observations provided the rationale for the current study.

Younger and older adults completed a computerized sampling task (Hau et al., 2010). Participants were presented with a series of financial choice problems requiring a choice between a certain

option (e.g., \$3 for sure) and a risky option (e.g., \$4 with a probability of 0.80, else nothing). The certain option was described explicitly, whereas the risky option had to be explored through active sampling. Because each choice problem features only one uncertain option, the task is less complex than the otherwise similar IGT, in which participants must track outcomes for multiple decks of cards. The sampling task provides separate measures of information search and choice, and it allows for a direct comparison of gain-related and loss-related decisions. It also involves manipulation of two aspects of risk: outcome probability and payoff variability (i.e., the SD of the outcomes of the risky option; Hau et al., 2010), neither of which has been systematically investigated in the aging literature.

We tested the following hypotheses:

- 1. In line with the idea that age-related dopaminergic decline leads to reduced information seeking (Düzel et al., 2010), we hypothesized that older adults would sample less than younger adults before making choices.
- 2. We predicted that participants would show adaptive decision making by modulating their choices according to objective outcome probabilities ("adaptive choice"; see also Deakin et al., 2004). On the assumption that information search and choice behavior reflect similar dopaminergic influences (Düzel et al., 2010), we made the novel prediction that sampling would also be sensitive to variations in outcome probabilities ("adaptive sampling").
- 3. Based on the idea that age-related dopaminergic decline results in noisy memory representations (Li et al., 2001; Samanez-Larkin et al., 2010), as well as prior evidence of impaired stimulus-reward learning in older adults (for a review, see Mohr et al., 2010), we hypothesized that adaptive sampling and adaptive choice would show age-related decline.

Additional questions for which the prior literature provided no clear hypotheses were (1) how the valence of the choice options (gain vs. loss) would affect age differences in experience-based decision making; (2) whether younger and older adults would differ with respect to overall risk preference; and (3) how payoff variability would affect age differences in experience-based decision making.

MATERIALS AND METHODS PARTICIPANTS

All participants gave written informed consent for the study, which was approved by the Research Ethics Board at Ryerson University. Participants in the final sample included 40 younger adults (35 women) who were students at Ryerson University and received course credit for their participation, as well as 41 communitydwelling older adults (32 women) who received a \$10 travel reimbursement. Participants in both groups also had the opportunity to win monetary rewards for their performance in the experimental task. Eight additional younger adults were excluded for failing to meet one or more of the criteria for inclusion: absence of major health problems (e.g., history of neurological or psychiatric illness, cancer, cardiovascular disease), normal, or corrected-to-normal vision and hearing, and a score of 27 or higher on the Mini-Mental Status Examination (Folstein et al., 1975). Two additional older adults were excluded for failing to follow the experimental instructions. Characteristics of the final sample are shown in **Table 1**. Compared with younger adults, older adults had significantly more years of education, t(79) = 5.86, p < 0.01 and scored higher on the Mill-Hill Vocabulary Scale (Raven, 1982), t(77) = 8.59, p < 0.01. Scores on a numeracy questionnaire (Reyna and Brainerd, 2008) showed no significant age difference.

DESIGN

The study employed a mixed factorial design that included the between-subjects factor age group (younger, older) and two within-subjects factors: (1) valence (gain, loss), (2) the probability of the desirable outcome of the risky option ($p_{desirable}$: 0.10, 0.20, 0.80, 0.90), and (3) the payoff variability of the risky option (\$1.6, \$4.5, \$9.6). Dependent variables were the sampling frequency, which provided a measure of information search, and the proportion of risky choices, which provided an index of risk taking.

STIMULI AND APPARATUS

We used the 12 choice problems (Hau et al., 2010; Experiment 1) shown in **Table 2**. In each problem, participants chose between a risky option (winning X with probability $p_{non-zero}$, or 0 with probability $1 - p_{non-zero}$) and a certain option (winning Y with probability 1.0). Y was either slightly below or slightly above the expected value of the risky option. For example, in Problem 1, the expected value of the risky option was \$0.53, and Y was either \$0.30 or \$0.70. For each participant, half of the problems used the smaller value of Y and half used the larger value of Y. The assignment of specific problems to the first group (small Y) and the second group (large Y), respectively, was counterbalanced across participants.

In Hau et al.'s (2010) protocol, all problems involved choosing between risky and certain *gains* (i.e., *X* and *Y* were always positive numbers). In contrast, we presented participants with both gain and loss problems. To this end, we created a loss version of each problem. For example, the loss version of Problem 1 required participants to choose between a 10% chance of *losing* \$5.30 (risky option) and a 100% chance of *losing* \$0.30/\$0.70 (certain option).

For the purpose of data analysis, the variable $p_{\text{non-zero}}$ (probability of the non-zero outcome) was recoded into $p_{\text{desirable}}$ (probability of the desirable outcome), with the following

Characteristic	Younger adults ($N = 40$)	Older adults ($N = 41$)
Age (years)	20.8 (5.3)	68.2 (6.8)
Age range	17–41	60–89
Education (years)	13.6 (1.3)	16.3 (2.64)
MMSE	29.63 (0.70)	29.33 (1.10)
Mill-Hill vocabulary	14.62 (3.44)	22.83 (4.91)
Numeracy	7.98 (1.91)	8.07 (1.79)

MMSE, Mini-Mental State Exam (Folstein et al., 1975). See text for additional information. SD are shown in parentheses.

rationale. Adaptive decision making involves maximizing desirable outcomes. On gain trials, it is adaptive to choose the risky option when $p_{non-zero}$ (the probability of a gain) is *high*. On loss trials, it is adaptive to choose the risky option when $p_{non-zero}$ (the probability of a loss) is *low*. To conduct meaningful comparisons between gain and loss trials, $p_{desirable}$ is therefore more useful than $p_{non-zero}$. For gain trials, $p_{desirable}$ equaled $p_{non-zero}$. For loss trials, $p_{desirable}$ was the probability of a non-loss, or $1 - p_{non-zero}$.

E-Prime 2.0 (Psychology Software Tools, Inc.) was used for stimulus presentation and response collection on an Intel Core 2 Duo 2.40 GHz laptop with 4 GB of RAM and a 16.0" LCD display running 32-bit Windows 7 Enterprise Edition. Viewing distance was approximately 50 cm. All text appeared in black 18-point Calibri font against a white background. Participants pressed the "X" and "," keys with their left and right index fingers to give their responses.

Table 2 | Twelve choice problems (Hau et al., 2010).

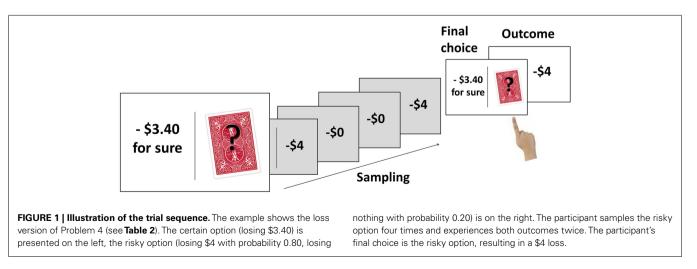
Problem	Risky option:	Risky option:	Payoff	Certain option:
	p _{non-zero}	X (in CAD)	variability	Y (in CAD)
1	0.10	5.30	1.60	0.30/0.70
2	0.20	4	1.60	0.60/1.00
3	0.80	4	1.60	3.00/3.40
4	0.90	5.30	1.60	4.60/5.00
5	0.10	15	4.50	1.30/1.70
6	0.20	11.30	4.50	2.10/2.50
7	0.80	11.30	4.50	8.80/9.20
8	0.90	15	4.50	13.30/13.70
9	0.10	32	9.60	3.00/3.40
10	0.20	24	9.60	11.80/12.20
11	0.80	24	9.60	19.00/19.40
12	0.90	32	9.60	28.60/29.00

 $p_{non-zero}$, probability of the non-zero outcome in the risky option. X, non-zero outcome of the risky option. CAD, Canadian dollars. Payoff variability is the SD of the risky option. Y, outcome of the certain option. Only the gain version of each problem is shown; the loss version was identical except that X and Y had a negative sign.

PROCEDURE

Participants were tested individually in a quiet testing room. After signing a consent form, participants received instructions for the choice task and completed four practice problems. After the practice, the experimenter repeated the instructions and provided clarification if necessary. Participants were informed that they would start with a balance of \$0, and that the computer would keep track of their gains and losses throughout the study. Participants were also told that they would receive their final balance in cash, if it was greater than 0. Older adults were reassured that the experimental rewards would be paid *in addition to* the compensation they would receive for participating in the study.

The 24 trials of the choice task included 12 gain and 12 loss problems, presented in random order. At the beginning of each trial, an on-screen message informed participants of the number of the upcoming trial (1-24). The message also indicated whether the upcoming trial was a gain trial ("you should try to maximize your gains") or a loss trial ("you should try to minimize your losses"). The risky option and the certain option were then presented sideby-side on the screen, separated by a central black vertical line (Figure 1). The left/right assignment of the two options was counterbalanced across trials for each participant. The outcome of the certain option was presented explicitly, whereas the risky option (symbolized by the playing card with a question mark) had to be explored through sampling. Participants were told that their balance would not be affected by the sample outcomes, and that they should sample the risky option until they felt that they knew which option they preferred. Participants sampled by pressing a key and immediately saw the outcome of the sample superimposed on the playing card. Each sample outcome was a random draw from the probability distribution of the risky option. After each sample, participants indicated, again via button press, whether they wished to continue sampling or to make their final choice. After they had finished sampling and made their final choice of either the certain or the risky option, a feedback screen indicated the trial outcome. If the participant had chosen the risky option, the outcome was again determined by a random draw from the probability distribution of the risky option. All aspects of the trials were participant-paced, and there was no upper limit on the number of samples drawn on



a given trial. After the last trial, the final balance was shown on the screen.

At the end of the session, participants completed a set of paperand-pencil questionnaires, including the Numeracy scale (Reyna and Brainerd, 2008), an 11-item questionnaire measuring proficiency with fractions, proportions, decimals, and percentages, and the Mill-Hill Vocabulary Scale, a 33-item vocabulary test in multiple-choice format (Raven, 1982). The experimenter also administered the Mini-Mental State Exam (Folstein et al., 1975). Afterward, participant were paid (if applicable) and debriefed about the goals of the study.

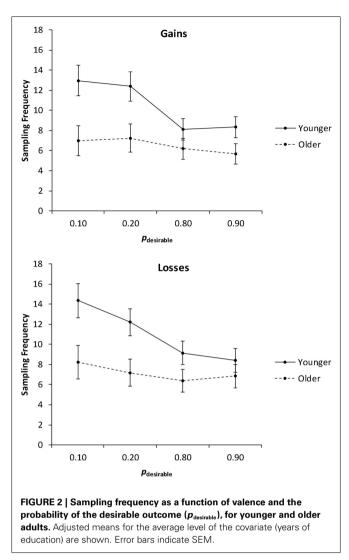
RESULTS

The analyses focused on two aspects of experience-based decision making: information search, operationalized as the sampling frequency, and choice, operationalized as the proportion of risky final choices. Analyzing the effects of all independent variables in a single step was not possible due to the small item set (see **Table 2**). We thus conducted two sets of analyses for each dependent variable. Because of the significant age-group difference in educational attainment (see Participants), the variable "years of education" was mean-centered and included as a covariate in the analyses below (Delaney and Maxwell, 1981). Vocabulary, which also showed an age difference, was not included as an additional covariate because it was significantly correlated with education (r = 0.43, p < 0.01).

INFORMATION SEARCH: SAMPLING FREQUENCY

In the first analysis, we collapsed the sampling frequencies across the levels of the payoff variability factor (Figure 2) and conducted a 2 (age group: younger, older) × 2 (valence: gain, loss) × 4 ($p_{desirable}$: 0.10, 0.20, 0.80, 0.90) mixed analysis of covariance (ANCOVA) with education as a covariate. Consistent with Hypothesis 1 (age-related reduction in overall sampling frequency), the main effect of age group was significant, F(1, 78) = 5.08, p = 0.03, partial $\eta^2 = 0.06$, with older adults (M = 6.84) sampling less than younger adults (M = 10.73). The main effect of valence was significant, F(1, 78) = 4.11, p = 0.05, partial $\eta^2 = 0.05$, reflecting the fact that loss trials elicited more sampling (M = 9.09) than gain trials (M = 8.47). A significant main effect of $p_{\text{desirable}}$, F(3, 234) = 19.37, p < 0.01, partial $\eta^2 = 0.20$, was qualified by a significant interaction of age group and $p_{\text{desirable}}$, F(3, 234) = 4.72, p < 0.01, partial $\eta^2 = 0.06$. Consistent with Hypothesis 2 (adaptive sampling), planned linear contrasts indicated that younger adults sampled more as p_{desirable} decreased, F(1, 38) = 14.03, p < 0.01, partial $\eta^2 = 0.27$. Consistent with Hypothesis 3 (age-related reduction in adaptive sampling), the effect was only marginally significant in older adults, F(1), 39) = 3.63, p = 0.06, partial $\eta^2 = 0.09$. There was no significant interaction of age and valence on sampling frequencies.

In the second analysis, we collapsed the sampling frequencies across the levels of $p_{\text{desirable}}$ (**Figure 3**) and conducted a 2 (age group) × 2 (valence) × 3 (payoff variability: 1.6, \$4.5, \$9.6) mixed ANCOVA with education as a covariate. In addition to the significant main effects of age group and valence, reported in the previous analysis, there was a significant interaction of valence and payoff variability, F(2, 156) = 3.18, p = 0.04, partial $\eta^2 = 0.04$. Follow-up linear contrasts indicated that payoff variability had no effect

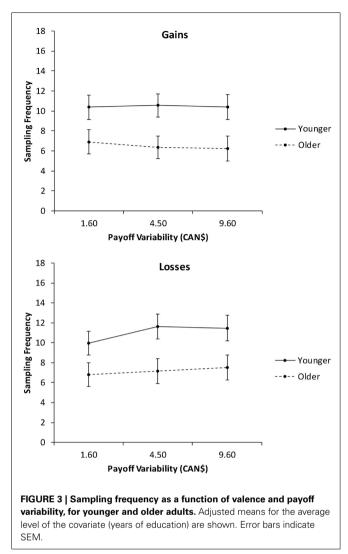


on sampling frequency for gain trials. For loss trials, increases in payoff variability were associated with increased sampling, F(1, 78) = 6.47, p = 0.01, partial $\eta^2 = 0.08$.

RISK TAKING: PROPORTION OF RISKY CHOICES

In the first analysis, we collapsed the proportions of risky choices across the levels of the payoff variability factor (**Figure 4**) and conducted a 2 (age group) × 2 (valence) × 4 ($p_{desirable}$) mixed ANCOVA with education as a covariate. The main effect of $p_{desirable}$ was significant, F(3, 234) = 49.06, p < 0.01, partial $\eta^2 = 0.39$. It was qualified by a significant Valence × $p_{desirable}$ interaction, F(3, 234) = 6.84, p < 0.01, partial $\eta^2 = 0.08$. Consistent with Hypothesis 2 (adaptive risk taking), planned linear contrasts indicated that risk taking increased as $p_{desirable}$ increased, suggesting that both age groups engaged in adaptive risk taking. This was the case for both gain trials, F(1, 78) = 24.16, p < 0.01, partial $\eta^2 = 0.24$, and loss trials, F(1, 78) = 78.81, p < 0.01, partial $\eta^2 = 0.50$, but the effect was more pronounced for loss trials than for gain trials (**Figure 4**). There was no significant interaction of age group and $p_{desirable}$, contrary to Hypothesis 3 (age-related



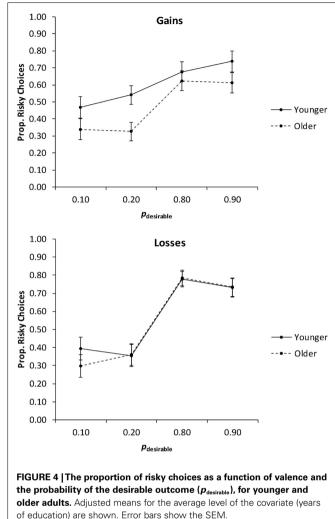


reduction in adaptive risk taking). Age group and valence also did not interact significantly.

In the second analysis, we collapsed the proportions of risky choices across the levels of $p_{\text{desirable}}$ (Figure 5) and conducted a 2 (age group) × 2 (valence) × 3 (payoff variability) mixed ANCOVA with education as a covariate. The only significant effect was the interaction of valence and payoff variability, F(2, 156) = 8.03, p < 0.01, partial $\eta^2 = 0.09$. Follow-up contrasts showed a significant quadratic effect of payoff variability on the proportion of risky choices for gain trials, F(1, 78) = 5.94, p = 0.02, partial $\eta^2 = 0.07$, with the medium level of payoff variability producing the highest proportion of risky choices. For loss trials, there was a significant linear effect of payoff variability, F(1, 78) = 15.82, p < 0.01, partial $\eta^2 = 0.17$, reflecting a linear increase in the proportion of risky choices with increasing payoff variability.

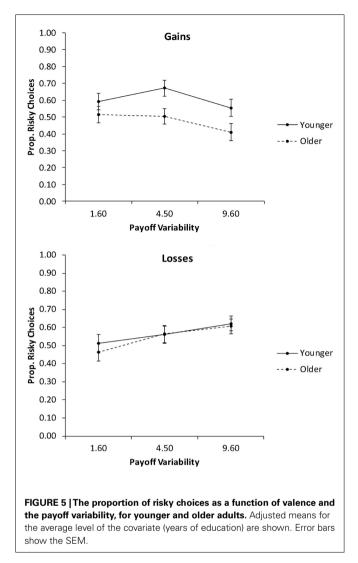
DISCUSSION

In this experiment, younger and older adults completed a series of decision problems involving choices between certain and risky financial options. In each problem, the risky option was not



explicitly described, but had to be explored through sampling. To test a set of predictions derived from the literature on dopamine, aging, and cognition (Li et al., 2001; Frank and Kong, 2008; Düzel et al., 2010), we analyzed the effects of age, valence, the probability of the desirable outcome in the risky option, and payoff variability on two dependent measures: sampling frequency, which provided an index of information search, and the proportion of risky choices, which provided an index of risk taking.

As predicted (Hypothesis 1), older adults overall sampled less than younger adults. This finding is consistent with the proposal that aging is associated with reduced exploratory drive due to dopaminergic decline (Düzel et al., 2010). Alternatively, it is possible that sampling frequency is constrained by working-memory capacity (e.g., Rakow et al., 2010), and that the reduced sampling in older adults is a consequence of age-related decline in working memory (e.g., Hasher and Zacks, 1988). Working memory is closely tied to the dorsolateral prefrontal cortex (e.g., D'Esposito et al., 1995; Cohen et al., 1997), a region that receives dopaminergic input and undergoes significant structural change in aging (e.g., Grady et al., 1994; Raz et al., 2005). We did not obtain a measure of working-memory capacity and thus could not test this



hypothesis directly. However, the young-adult literature suggests that access to explicit memory representations may not be critical for experience-based choice. In one study, memory demands were lifted entirely by providing participants with a visual record of their sampling histories (Hau et al., 2010, Experiment 1). Choice patterns in the visual-record condition did not differ significantly from those in the standard sampling condition - even when participants were forced to sample as many as 50 times. Furthermore, lower animals (e.g., worker bees) show experience-based choice patterns that resemble those of humans (Weber et al., 2004). These findings suggest that implicit, rather than explicit, memory representations may drive experience-based choice, and that working memory may not play a major role. Indeed, in one recent study, decision quality in an experience-based investment task was unaffected by the addition of a secondary task, for both younger and older adults (Samanez-Larkin et al., 2011). Even so, it is possible that older adults use working-memory load as a metacognitive heuristic for terminating their information search. One strategy for testing these possibilities in future research would be to adopt the visual-record method of Hau et al. (2010; see also

Samanez-Larkin et al., 2011). If the age-related difference in sampling frequency results from working-memory limitations rather than from reduced exploratory drive, then providing participants with a visual record of their sampling histories should eliminate age differences in sampling.

In line with Hypothesis 2, both younger and older adults showed adaptive decision making by adjusting their sampling and choice behavior in response to variation in the probability of the desirable outcome of the risky option. Adaptive choice of this kind has been demonstrated previously (e.g., Deakin et al., 2004; Hau et al., 2010), but we are not aware of previous reports of adaptive sampling. At a mechanistic level, the effect can be parsimoniously explained in terms of dopaminergic modulation of *both* information search/exploration and risk taking. At the subjective level, the increased sampling when the desirable outcome is rare (p = 0.10 or 0.20) may be associated with increased curiosity (i.e., anticipation of epistemic reward; e.g., Kang et al., 2009). In future research, think-aloud protocols during the sampling phase could help to shed light on the association between the subjective experience of curiosity and predecisional information search.

Based on theoretical models of "noisy processing" due to reduced dopaminergic neuromodulation in older adults (Li et al., 2001), as well as empirical evidence for impaired feedback learning in older adults (for a review, see Mohr et al., 2010), we had predicted that adaptive decision making would show age-related decline (Hypothesis 3). This hypothesis was supported for sampling, where older adults showed significantly flatter functions than younger adults (Figure 2). However, there was no evidence for an age-related deficit in adaptive choice (Figure 4). This dissociation indicates that age-related dopaminergic decline may affect information search more strongly than choice. Incidentally, the dissociation also suggests that sampling frequency had little effect on choice, at least within the range of sampling frequencies that we observed. To further explore this issue, we examined the relationship between sampling frequencies and the proportions of risky choices in both age groups, and found no significant correlations. This is consistent with findings in the behavioral decision-making literature which suggest that the impact of additional experience on choice is modest, and that participants' default strategy is to rely on small samples despite the fact that small samples are more susceptible to sampling error (e.g., Hau et al., 2010; Hertwig and Pleskac, 2010).

In addition to testing specific hypotheses, the study also allowed us to address a set of exploratory research questions. The first of these questions concerned valence effects on experience-based decision making. To our knowledge, the current study was the first to systematically compare experience-based choice for gains and losses using the same choice problems. Both age groups sampled more in the face of losses than they did in the face of gains. Regardless of age, loss anticipation thus appears to energize predecisional information search more strongly than gain anticipation, consistent with Kahneman and Tversky's (1979) influential loss-aversion hypothesis. Both age groups also showed greater adaptive modulation of risk taking for losses than for gains. Overall, these findings suggest that experience-based choice is affected by the valence of the choice options, but they offer no evidence to suggest that the nature of this modulation changes with age. The second exploratory question concerned age differences in overall risk preference. Across both the gain and loss domains, the average proportion of risky choices was similar for younger and older adults, contrary to the widely held notion that aging is associated with increased risk aversion. Mata et al. (2011) suggested that age differences in risk preference are a by-product of age-related learning impairments, which can manifest differently in different tasks. In the current study, there was no evidence for an age-related learning deficit, as both age groups showed similar sensitivity to variation in outcome probabilities. The lack of an age effect on overall risk preference is thus consistent with Mata et al.'s (2011) view.

The third exploratory question concerned payoff variability, an aspect of risk that combines the probability and magnitude of outcomes. Consistent with a previous study with younger adults (Hau et al., 2010, Experiment 1), the effects of payoff variability on experience-based decision making were relatively subtle. The most notable finding here was that, for both age groups, increased payoff variability led to modest linear increases in both sampling and risky choice on loss trials, but not on gain trials. This finding further highlights the impact of valence on experiential decision making.

In conclusion, the current findings add to the growing literature on aging and neuroeconomics by (a) providing novel

REFERENCES

- Bäckman, L., Lindenberger, U., Li, S. C., and Nyberg, L. (2010). Linking cognitive aging to alterations in dopamine neurotransmitter functioning: recent data and future avenues. *Neurosci. Biobehav. Rev.* 34, 670–677.
- Bäckman, L., Nyberg, L., Lindenberger, U., Li, S. C., and Farde, L. (2006). The correlative triad among aging, dopamine, and cognition: current status and future prospects. *Neurosci. Biobehav. Rev.* 30, 791–807.
- Bechara, A., Damasio, A. R., Damasio, H., and Anderson, S. W. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition* 50, 7–15.
- Bechara, A., Tranel, D., and Damasio, H. (2000). Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. *Brain* 123, 2189–2202.
- Braver, T. S., and Barch, D. A. (2002). A theory of cognitive control, aging cognition, and neuromodulation. *Neurosci. Biobehav. Rev.* 26, 809–817.
- Carstensen, L. L., Isaacowitz, D. M., and Charles, S. T. (1999). Taking time seriously – a theory of socioemotional selectivity. *Am. Psychol.* 54, 165–181.
- Cohen, J. D., Perlstein, W. M., Braver, T. S., Nystrom, L. E., Noll, D. C., Jonides, J., and Smith, E. E. (1997). Temporal dynamics of brain

activation during a working memory task. *Nature* 386, 604–608.

- Cox, K. M., Aizenstein, H. J., and Fiez, J. A. (2008). Striatal outcome processing in healthy aging. *Cogn. Affect. Behav. Neurosci.* 8, 304–317.
- Deakin, J., Aitken, M., Robbins, T., and Sahakian, B. J. (2004). Risk taking during decision-making in normal volunteers changes with age. J. Int. Neuropsychol. Soc. 10, 590–598.
- Delaney, H. D., and Maxwell, S. E. (1981). On using analysis of covariance in repeated measures designs. *Multivariate Behav. Res.* 16, 105–123.
- Denburg, N. L., Recknor, E. C., Bechara, A., and Tranel, D. (2006). Psychophysiological anticipation of positive outcomes promotes advantageous decision-making in normal older persons. *Int. J. Psychophysiol.* 61, 19–25.
- Denburg, N. L., Tranel, D., and Bechara, A. (2005). The ability to decide advantageously declines prematurely in some normal older persons. *Neuropsychologia* 43, 1099–1106.
- D'Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., and Grossman, M. (1995). The neural basis of the central executive system of workingmemory. *Nature* 378, 279–281.
- Dreher, J. C., Meyer-Lindenberg, A., Kohn, P., and Berman, K. F. (2008). Age-related changes in midbrain dopaminergic regulation of the human reward system. *Proc. Natl. Acad. Sci. U.S.A.* 105, 15106–15111.

empirical observations of age differences in experience-based choice, (b) on the basis of the dopamine hypothesis of cognitive aging, testing hypotheses about specific cognitive processes involved in experience-based choice, and (c) demonstrating the need for greater integration of research in aging, neuroeconomics, and behavioral economics. An obvious limitation of the study was that we used behavioral methods to test predictions derived from a neurobiological hypothesis. However, behavioral data are valuable, indeed necessary, for testing and constraining models of neurocognitive age-related change (e.g., Frank and Kong, 2008; Simon et al., 2010). In future work, a multimodal approach that combines behavioral assessment with measurement (or pharmacological manipulation) of dopamine biomarkers will be the method of choice for testing causal influences of dopamine on experience-based choice in younger and older adults.

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- Düzel, E., Bunzeck, N., Guitart-Masip, M., and Düzel, S. (2010). Noveltyrelated motivation of anticipation and exploration by dopamine (NOMAD): implications for healthy aging. *Neurosci. Biobehav. Rev.* 34, 660–669.
- Fein, G., McGillivray, S., and Finn, P. (2007). Older adults make less advantageous decisions than younger adults: cognitive and psychological correlates. J. Int. Neuropsychol. Soc. 13, 480–489.
- Fiorillo, C. D. (2011). Transient activation of midbrain dopamine neurons by reward risk. *Neuroscience* 197, 162–171.
- Fiorillo, C. D., Tobler, P. N., and Schultz, W. (2003). Discrete coding of reward probability and uncertainty by dopamine neurons. *Science* 299, 1898–1902.
- Folstein, M. F., Folstein, S. E., and McHugh, P. R. (1975). Mini-mental state – practical method for grading cognitive state of patients for clinician. J. Psychiatr. Res. 12, 189–198.
- Frank, M. J., and Kong, L. (2008). Learning to avoid in older age. *Psychol. Aging* 23, 392–398.
- Frank, M. J., Seeberger, L. C., and O'Reilly, R. C. (2004). By carrot or by stick: cognitive reinforcement learning in Parkinsonism. *Science* 306, 1940–1943.
- Glimcher, P. W. (2008). Understanding risk: a guide for the perplexed. *Cogn. Affect. Behav. Neurosci.* 8, 348–354.

- Grady, C. L., Maisog, J. M., Horwitz, B., Ungerleider, L. G., Mentis, M. J., Salerno, J. A., Pietrini, P., Wagner, E., and Haxby, J. V. (1994). Age-related changes in cortical blood flow activation during visual processing of faces and location. *J. Neurosci.* 14, 1450–1462.
- Hämmerer, D., Li, S. C., Müller, V., and Lindenberger, U. (2011). Life span differences in electrophysiological correlates of monitoring gains and losses during probabilistic reinforcement learning. *J. Cogn. Neurosci.* 23, 579–592.
- Hasher, L., and Zacks, R. T. (1988). "Working memory, comprehension, and aging: a review and a new view," in *The Psychology of Learning and Motivation*, ed. G. H. Bower (New York: Academic Press), 193–225.
- Hau, R., Pleskac, T. J., and Hertwig, R. (2010). Decisions from experience and statistical probabilities: why they trigger different choices than a priori probabilities. *J. Behav. Decis. Mak.* 23, 48–68.
- Heekeren, H. R., Wartenburger, I., Marschner, A., Mell, T., Villringer, A., and Reischies, F. M. (2007). Role of ventral striatum in reward-based decision making. *Neuroreport* 18, 951–955.
- Hertwig, R., Barron, G., Weber, E. U., and Erev, I. (2004). Decisions from experience and the effect of rare events in risky choice. *Psychol. Sci.* 15, 534–539.

- Hertwig, R., and Erev, I. (2009). The description-experience gap in risky choice. *Trends Cogn. Sci. (Regul. Ed.)* 13, 517–523.
- Hertwig, R., and Pleskac, T. J. (2010). Decisions from experience: why small samples? *Cognition* 115, 225–237.
- Hosseini, S. M. H., Rostami, M., Yomogida, Y., Takahashi, M., Tsukiura, T., and Kawashima, R. (2010). Aging and decision making under uncertainty: behavioral and neural evidence for the preservation of decision making in the absence of learning in old age. *Neuroimage* 52, 1514–1520.
- Kaasinen, V., Vilkman, H., Hietala, J., Nagren, K., Helenius, H., Olsson, H., Farde, L., and Rinne, J. O. (2000). Age-related dopamine D2/D3 receptor loss in extrastriatal regions of the human brain. *Neurobiol. Aging* 21, 683–688.
- Kahneman, D., and Tversky, A. (1979). Prospect theory – analysis of decision under risk. *Econometrica* 47, 263–291.
- Kang, M. J., Hsu, M., Krajbich, I. M., Loewenstein, G., McClure, S. M., Wang, J. T. Y., and Camerer, C. F. (2009). The wick in the candle of learning: epistemic curiosity activates reward circuitry and enhances memory. *Psychol. Sci.* 20, 963–973.
- Knutson, B., Fong, G. W., Adams, C. M., Varner, J. L., and Hommer, D. (2001). Dissociation of reward anticipation and outcome with event-related fMRI. *Neuroreport* 12, 3683–3687.
- Kovalchik, S., Camerer, C. F., Grether, D. M., Plott, C. R., and Allman, J. M. (2005). Aging and decision making: a comparison between neurologically healthy elderly and young individuals. *J. Econ. Behav. Organ.* 58, 79–94.
- Lee, T. M. C., Leung, A. W. S., Fox, P. T., Gao, J. H., and Chan, C. C. H. (2008). Age-related differences in neural activities during risk taking as revealed by functional MRI. Soc. Cogn. Affect. Neurosci. 3, 7–15.
- Li, S. C., Lindenberger, U., and Sikström, S. (2001). Aging cognition:

from neuromodulation to representation. *Trends Cogn. Sci. (Regul. Ed.)* 5, 479–486.

- Lockenhoff, C. E., and Carstensen, L. L. (2007). Aging, emotion, and healthrelated decision strategies: motivational manipulations can reduce age differences. *Psychol. Aging* 22, 134–146.
- Mata, R., Josef, A. K., Samanez-Larkin, G. R., and Hertwig, R. (2011). Age differences in risky choice: a metaanalysis. Ann. N. Y. Acad. Sci. 1235, 18–29.
- Mata, R., and Nunes, L. (2010). When less is enough: cognitive aging, information search, and decision quality in consumer choice. *Psychol. Aging* 25, 289–298.
- Mather, M. (2006). "A review of decision making processes: weighing the risks and benefits of aging," in *When I'm 64*, eds L. L. Carstensen and C. R. Hartel (Washington, DC: National Academies Press), 145–173.
- Mather, M., Knight, M., and McCaffrey, M. (2005). The allure of the alignable: younger and older adults' false memories of choice features. *J. Exp. Psychol. Gen.* 134, 38–51.
- Mell, T., Heekeren, H. R., Marschner, A., Wartenburger, I., Villringer, A., and Reischies, F. M. (2005). Effect of aging on stimulus-reward association learning. *Neuropsychologia* 43, 554–563.
- Mell, T., Wartenburger, I., Marschner, A., Villringer, A., Reischies, F. M., and Heekeren, H. R. (2009). Altered function of ventral striatum during reward-based decision making in old age. *Front. Hum. Neurosci.* 3:34. doi:10.3389/neuro.09.034.2009
- Mohr, P. N., Li, S. C., and Heekeren, H. R. (2010). Neuroeconomics and aging: neuromodulation of economic decision making in old age. *Neurosci. Biobehav. Rev.* 34, 678–688.
- Novak, D. L., and Mather, M. (2007). Aging and variety seeking. *Psychol. Aging* 22, 728–737.
- Okun, M. A. (1976). Adult age and cautiousness in decision – review of literature. *Hum. Dev.* 19, 220–233.
- Rakow, T., and Newell, B. R. (2010). Degrees of uncertainty: an overview and framework for future research

on experience-based choice. J. Behav. Decis. Mak. 23, 1–14.

- Rakow, T., Newell, B. R., and Zougkou, K. (2010). The role of working memory in information acquisition and decision making: lessons from the binary prediction task. *Q. J. Exp. Psychol.* 63, 1335–1360.
- Raven, J. C. (1982). Revised Manual for Raven's Progressive Matrices and Vocabulary Scale. Windsor: NFER Nelson.
- Raz, N., Lindenberger, U., Rodrigue,
 K. M., Kennedy, K. M., Head, D.,
 Williamson, A., Dahle, C., Gerstorf, D., and Acker, J. D. (2005).
 Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. *Cereb. Cortex* 15, 1676–1689.
- Reed, A. E., Mikels, J. A., and Simon, K. I. (2008). Older adults prefer less choice than young adults. *Psychol. Aging* 23, 671–675.
- Reyna, V. F., and Brainerd, C. J. (2008). Numeracy, ratio bias, and denominator neglect in judgments of risk and probability. *Learn. Individ. Differ.* 18, 89–107.
- Samanez-Larkin, G. R., Gibbs, S. E., Khanna, K., Nielsen, L., Carstensen, L. L., and Knutson, B. (2007). Anticipation of monetary gain but not loss in healthy older adults. *Nat. Neurosci.* 10, 787–791.
- Samanez-Larkin, G. R., Kuhnen, C. M., Yoo, D. J., and Knutson, B. (2010). Variability in nucleus accumbens activity mediates age-related suboptimal financial risk taking. *J. Neurosci.* 30, 1426–1434.
- Samanez-Larkin, G. R., Wagner, A. D., and Knutson, B. (2011). Expected value information improves financial risk taking across the adult life span. Soc. Cogn. Affect. Neurosci. 6, 207–217.
- Schott, B. H., Niehaus, L., Wittmann, B. C., Schutze, H., Seidenbecher, C. I., Heinze, H. J., and Düzel, E. (2007). Ageing and early-stage Parkinson's disease affect separable neural mechanisms of mesolimbic reward processing. *Brain* 130, 2412–2424.
- Schultz, W. (2000). Multiple reward signals in the brain. *Nat. Rev. Neurosci.* 1, 199–207.

- Simon, J. R., Howard, J. H., and Howard, D. V. (2010). Adult age differences in learning from positive and negative probabilistic feedback. *Neuropsychology* 24, 534–541.
- Wang, Y., Chan, G. L. Y., Holden, J. E., Dobko, T., Mak, E., Schulzer, M., Huser, J. M., Snow, B. J., Ruth, T. J., Calne, D. B., and Stoessl, A. J. (1998).
 Age-dependent decline of dopamine D1 receptors in human brain: a PET study. *Synapse* 30, 56–61.
- Weber, E. U., Shafir, S., and Blais, A. R. (2004). Predicting risk sensitivity in humans and lower animals: risk as variance or coefficient of variation. *Psychol. Rev.* 111, 430–445.
- Wood, S., Busemeyer, J., Koling, A., Cox, C. R., and Davis, H. (2005). Older adults as adaptive decision makers: evidence from the Iowa gambling task. *Psychol. Aging* 20, 220–225.
- Zamarian, L., Sinz, H., Bonatti, E., Gamboz, N., and Delazer, M. (2008). Normal aging affects decisions under ambiguity, but not decisions under risk. *Neuropsychology* 22, 645–657.

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Age-based differences in strategy use in choice tasks

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Darrell A. Worthy, Department of Psychology, Texas A&M University, 4235 TAMU, College Station, TX 77843-4235, USA. e-mail: worthyda@tamu.edu We incorporated behavioral and computational modeling techniques to examine age-based differences in strategy use in two four-choice decision-making tasks. Healthy older (aged 60-82 years) and younger adults (aged 18-23 years) performed one of two decision-making tasks that differed in the degree to which rewards for each option depended on the choices made on previous trials. In the choice-independent task rewards for each choice were not affected by the sequence of previous choices that had been made. In contrast, in the choicedependent task rewards for each option were based on how often each option had been chosen in the past. We compared the fits of a model that assumes the use of a win-staylose-shift (WSLS) heuristic to make decisions, to the fits of a reinforcement-learning (RL) model that compared expected reward values for each option to make decisions. Younger adults were best fit by the RL model, while older adults showed significantly more evidence of being best fit by the WSLS heuristic model. This led older adults to perform worse than younger adults in the choice-independent task, but better in the choice-dependent task. These results coincide with previous work in our labs that also found better performance for older adults in choice-dependent tasks (Worthy et al., 2011), and the present results suggest that gualitative age-based differences in the strategies used in choice tasks may underlie older adults' advantage in choice-dependent tasks. We discuss possible factors behind these differences such as neurobiological changes associated with aging, and increased use of heuristics by older adults.

Keywords: aging, decision-making, reinforcement learning, heuristics, computational modeling

INTRODUCTION

The US population is aging at a very high rate. By 2050 developed nations are projected to have substantially higher populations of older adults (26% of the population) than children under age 15 (16%; Cohen, 2003). It is thus very important to develop a deep understanding of how aging affects cognition and behavior. One task that both younger and older adults must undertake on a daily basis is decision-making. Older adults often continue to work in important jobs, and even those who retire must make important choices that will affect their well-being and the well-being of their posterity. There has recently been a surge in excellent research aimed at understanding decision-making across the lifespan (Kovalchik et al., 2004; Wood et al., 2005; Mata et al., 2007; Peters et al., 2007; Samanez-Larkin et al., 2007, 2011; Schott et al., 2007; Brown and Ridderinkhof, 2009).

One important aspect of decision-making is that decisions can rarely be considered as isolated events. Rather, our decisions often affect what possibilities are available in the future. For example, the choices of whether to attend college, what college to attend, and what to major in will affect what job prospects are available to choose from in the future. Likewise, the choices regarding how to invest and save for retirement will eventually affect the class of retirement homes that are available to choose from. It is thus important to examine how people make decisions based not only on their immediate effects, but also based on how the present decisions will affect future possibilities.

A recent study from our lab suggests that older adults may actually be better than younger adults in situations where rewards are choice-dependent (Worthy et al., 2011). Choice-dependent decision-making situations are similar to the examples presented above where the rewards available from the various options in the environment *depend* on the sequence of choices made in the past. In contrast, in choice-independent situations the rewards available from the options in the environment are not affected by the choices made in the recent past. In choice-independent laboratory paradigms the rewards available for each option on each trial are usually set by the experimenter and often vary arbitrarily based on the trial number. Many of the decision-making tasks that have been used to examine how aging affects decision-making incorporate choice-independent reward structures. This is true for tasks like the Iowa Gambling task (Denburg et al., 2005), the Behavioral Investment Allocation Strategy task (Kuhnen and Knutson, 2005; Samanez-Larkin et al., 2010), the Monetary Incentive Delay task (Samanez-Larkin et al., 2007), and the Probabilistic Object Reversal Task (Mell et al., 2005, 2009). A common finding in these tasks is poorer or, at a minimum, equivalent performance for older adults compared to younger adults. Thus, older adults have been shown to outperform younger adults on choice-dependent tasks, whereas younger adults may outperform older adults on choice-independent tasks (Worthy et al., 2011).

One reason for this interaction between age and the reward structure of the task on decision-making performance may be an

age related shift in the neural areas recruited during decisionmaking. A number of studies have shown that normal aging leads to structural and functional declines in a number of brain regions including the striatum, cerebellum, hippocampus, and prefrontal cortices (Raz, 2000; Resnick et al., 2003; Raz et al., 2005). Normal aging also leads to a loss of dopamine receptor density (Li et al., 2001). The striatum and prefrontal cortices, along with the mesencephalic dopamine system, are neural regions that have been consistently implicated in reward-based decision-making (Montague et al., 1996; McClure et al., 2003; Daw et al., 2006; Daw and Doya, 2006). Thus, the neurobiological changes associated with aging affect areas implicated in decision-making, and it is important to consider how these changes might affect behavior.

An additional distinction that has emerged in the decisionmaking literature concerns brain regions implicated in the evaluation of immediate versus future consequences of each action. The ventral striatum has often been linked to the evaluation of immediate rewards (Hariri et al., 2006; McClure et al., 2007; Samanez-Larkin et al., 2011), while areas of the prefrontal cortices, particularly the orbitofrontal cortex (OFC) and dorsolateral prefrontal cortex (DLPFC) have been associated with the evaluation of delayed rewards (Winstanely et al., 2006; McClure et al., 2007; Samanez-Larkin et al., 2011). Several behavioral studies that have examined how age affects intertemporal choice have found reduced delayed discounting in older adults (Green et al., 1994; Lockenhoff, 2011; Lockenhoff et al., 2011). Thus, older adults may focus more on the long-term benefits of their actions, whereas younger adults may focus more on immediate outcomes.

A recently proposed theory of cognitive aging, the scaffolding theory of aging and cognition (STAC; Park and Reuter-Lorenz, 2009), suggests that older adults engage a broader network of frontal areas to compensate for declines in a number of regions (Cabeza et al., 2002; Reuter-Lorenz and Cappell, 2008; Cappell et al., 2010). We propose that this frontal compensation leads older adults to focus more on the delayed effects of each action, rather than the immediate effects. This should lead older adults to outperform younger adults in choice-dependent situations, but underperform, relative to younger adults, in choice-independent situations. This is exactly what we found in a recent study (Worthy et al., 2011), however, the age-based differences in the precise computational mechanisms by which older and younger adults make repeated decisions remains underexplored, and little work has applied computational models to older and younger adults' data to better understand these mechanisms.

In the current work we seek to fill this gap by examining older and younger adults' behavior in choice-dependent and choiceindependent decision-making tasks, and by fitting a series of computational models to each participant's data that differ in their assumptions about how participants make decisions in the task. Increased frontal compensation in older adults may lead them to employ explicit, heuristic-based strategies to a greater extent than younger adults, who may show more use of less explicit, reinforcement-learning (RL) strategies. Indeed, some recent work suggests that older adults are more likely to make their decisions based on simple heuristics than younger adults (e.g., Mata et al., 2007; Castel et al., in press). To test these hypotheses we compare the fits of a heuristic-based, win-stay–lose-shift (WSLS) model with fits of two popular RL models that do not assume the use of a heuristic strategy. We provide more details on the mechanisms and assumptions of the models the next section. We first explain the mechanisms of each model and then discuss their different assumptions.

COMPUTATIONAL MODELS OF DECISION-MAKING WSLS model

Win-stay–lose-shift models have been extensively used to model decision-making behavior (Frank and Kong, 2008; Steyvers et al., 2009; Lee et al., 2011; Otto et al., 2011). These models were originally developed for simple prediction tasks where the participant chooses an option and receives a reward with a certain probability, P, or does not receive a reward with a probability (1 - P). It assumes that participants will "stay" by picking the same option on the next trial if they are rewarded (a "win" trial), or "shift" by selecting another option on the next trial if they are not rewarded (a "lose" trial).

In the tasks used in the present experiments participants select from among four options on each trial and receive between 1 and 10 points. We develop a WSLS model for these tasks by having the model assume that participants compare the reward received on the present trial to the reward received on the previous trial. The trial is a "win" trial if the reward on the present trial is equal to or greater than the reward received on the previous trial, and the trial is a "loss" trial if the reward on the present trial is less than the reward received on the present trial is less than the reward received on the previous trial.

The WSLS model has two free parameters. The first parameter represents the probability of staying with the same option on the next trial if the reward received on the current trial is equal to or greater than the reward received on the previous trial:

$$P(a_i, t | \text{choice}_{t-1} = a_i \& r(t-1) \ge r(t-2)) = P(\text{stay}|\text{win}).$$
(1)

In Eq. 1 *r* represents the reward received on a given trial. The probability of switching to another option following a win trial is 1 - P(stay|win). To determine a probability of selecting each of the other three options we divide this probability by three, so that the probabilities for selecting each option sum to one.

The second parameter represents the probability of shifting to the other option on the next trial if the reward received on the current trial is less than the reward received on the previous trial:

$$P\left(a_{j}, t | \text{choice}_{t-1} = a_{i} \& r(t-1) < r(t-2)\right) = P(\text{shift} | \text{loss}).$$
(2)

This probability is divided by three and assigned to each of the other three options. The probability of staying with an option following a "loss" is 1 - P(shiftlloss). Thus, this model assumes a simple, heuristic-based strategy that requires the reward received on the previous trial to be maintained in working memory (e.g., Otto et al., 2011).

RL models

Many common RL models used to account for decision-making behavior in choice tasks operate by developing and updating expected reward values for each option, a_j , on each trial, t_j . These EVs are denoted here and elsewhere as $EV(a_j, t)$. The EVs for each option are used to determine the model's probability for selecting each option. Action selection probabilities for each option are computed via a Softmax decision rule:

$$P(a_i, t) = \frac{e^{[\theta \cdot EV(a_i, t)]}}{\sum_{j=1}^{2} e^{[\theta \cdot EV(a_j, t)]}}$$
(3)

Here θ is an exploitation parameter that determines the degree to which the option with the highest EV is chosen. As θ approaches infinity the highest valued option is chosen more often, and as θ approaches 0 all options are chosen equally often.

Learning rules for the delta-rule and eligibility trace RL models

We fit two models that have slight differences in the assumptions regarding how EVs are updated on each trial. Both models use the Softmax rule in Eq. 1 to determine the probability of selecting each option. The Delta-Rule model assumes that the EV for the option chosen on each trial, denoted as option *i*, is updated on each trial using the following equation:

$$EV(a_i, t+1) = EV(a_i, t) + \alpha \cdot [r(t) - EV(a_i, t)]$$
(4)

This model assumes that the expected values for each option are updated only when that option is selected, and are based only on the reward received immediately after making a choice. Learning is primarily mediated by a prediction error between the reward received and the EV for the chosen option (the bracketed portion of Eq. 2). The prediction is positive if the reward received is larger than expected and negative if the reward received is less than expected. Learning is modulated by a learning rate, or recency parameter (α), $0 \le \alpha \le 1$, that weighs the degree to which participants update the EVs for each option based on the most recently received rewards. As α approaches 1 greater weight is given to the most recent rewards in updating EVs, indicative of more active updating of EVs on each trial, and as α approaches 0 rewards are given less weight in updating EVs. When $\alpha = 0$ no learning takes place, and EVs are not updated throughout the experiment from their initial starting points, $Q(a_i, t_0)$. The Delta-Rule model has been used in a number of studies, primarily when the rewards in the environment are choice-independent (e.g., Sutton and Barto, 1998; Yechiam and Busemeyer, 2005; Daw et al., 2006; Worthy et al., 2007; Otto et al., 2010).

The learning rule for the Delta-Rule model can be modified to include eligibility traces (ET) which simply assert that participants remember which options they have chosen in the recent past, and that some of the credit from the reward received on each trial goes to options chosen on previous trials, rather than all of the credit going to only the option that was just chosen. The addition of ETs in the ET model has often resulted in an improved fit (Sutton and Barto, 1998; Pan et al., 2005; Bogacz et al., 2007; Gureckis and Love, 2009). The updating equation for the ET model is:

$$EV(a_j, t+1) = EV(a_j, t) + \alpha \cdot \lambda_j [r(t) - EV(a_j, t)]$$
(5)

The model assumes that participants keep a memory for recent actions, known as an ET. The ET for each option is denoted above as, λ_i , and reflects how *eligible* each option is for learning.

On each trial, the ET, λ_j , for every option decays based on a decay parameter, ζ , $0 \le \zeta \le 1$:

$$\lambda_j = \lambda_j \cdot \zeta \tag{6}$$

Additionally, each time an option is chosen the ET for that option is incremented according to:

$$\lambda_j = \lambda_j + 1 \tag{7}$$

Eligibility traces are meant to assert that participants remember which actions they have recently selected, and in this way recent actions can be credited if they lead to increases in reward. Thus, in the ET model traces for options that are not chosen continue to decay and EVs are updated more based on recent rewards the more often they are chosen (Eq. 7). To summarize, there are two main differences between the Delta-Rule and ET models presented above. First, the ET model incorporates ETs for recent actions, and second, the ET model updates the EVs of all options on each trial based on each option's ET value, whereas the Delta-Rule model only updates the EV for the chosen option. It should also be noted that the Delta-Rule model is nested within the ET model, as the ET model is identical to the Delta-Rule model when $\zeta = 0$.

Age-based predictions for RL versus WSLS strategy use

We propose that utilizing a heuristic-based WSLS strategy will engage frontal brain regions, while utilizing an RL strategy will engage striatal brain regions. Older adults who engage in compensatory scaffolding should be more likely to utilize a WSLS strategy than an RL strategy than younger adults. Evidence for this distinction in the neural areas that mediate these two different types of strategies comes from many different sources. Reward prediction errors from RL models similar to the one presented above have been correlated with striatal activity in a number of studies (Pagnoni et al., 2002; Pessiglione et al., 2006; Hare et al., 2008). This suggests that EVs for each option may be updated in a more implicit, proceduralized manner that is not dependent on explicit processing (e.g., Frank and Claus, 2006; Frank et al., 2006).

In contrast, there is a large body of evidence that suggests that the use of heuristics, or rules, is explicit and more frontally mediated (e.g., Ashby et al., 1998; Maddox and Ashby, 2004; Ashby and Maddox, 2005). Recently, Otto et al. directly compared the fits of a WSLS strategy with fits of an Expectation-Matching strategy, with assumptions similar to the RL models presented above, to data from participants who performed a simple prediction task under either single-task or dual-task conditions. Participants who performed under single-task conditions showed more evidence of being best fit by the WSLS model, while participants who performed the task along with a concurrent, WM demanding task showed more evidence of being best fit by the Expectation-Matching model (Otto et al., 2011).

Based on the scaffolding theory outlined above, we predict that, relative to younger adults, older adults will employ more explicit strategies like WSLS due to frontal compensation. Thus, older adults' data should show more evidence of being best fit by the WSLS model, while younger adults' data should show more evidence of being best fit by one of the RL models. In the following sections we present an experiment in which older and younger adults performed either a choice-dependent or choice-independent decision-making task. We then present behavioral results, followed by results of a modeling analysis where we compare the fits of the WSLS, Delta-Rule, and ET models, as well as the fits of a Baseline model that assumes random responding. This Baseline model has three free parameters representing the probability of selecting three of the four options on any given trial. The probabilities of the three other options. This model assumes random, stochastic responding. To foreshadow, we find that the ET and WSLS models provide the best fit to the data. We directly compare the fits of these two models and find that younger adults show more evidence of being best fit by the ET model than older adults.

MATERIALS AND METHODS PARTICIPANTS

Fifty-six younger adults (18–23 years of age, M = 20.29; 9 male and 19 female; Mean education = 15.34 years) were recruited from the University of Texas community and 58 older adults (60–82 years of age M = 69.71; 31 male and 18 female; Mean education = 17.28 years) were recruited from the greater Austin community. Participants were paid \$10 per hour for participating. Older adults were administered an extensive neuropsychological testing battery to determine any mental declines not due to normal aging (detailed below).

PROCEDURE

Neuropsychological testing session

Older adults were given a series of standardized neuropsychological tests before being included in the study. The neuropsychological testing session was held separately and before the experimental session. The battery of tests was designed to assess general intellectual ability across three functional realms: memory (Wechsler Memory Scale Third Edition (WMS-III) subtests: Wechsler, 1997; California Verbal Learning Test (CVLT): Delis et al., 1987), mood (Geriatric Depression Scale, GDS: Brink et al., 1982), and executive functioning and mental flexibility [Stroop Color-Word Test: Stroop, 1935; Trail Making Test A&B (TMT): Lezak, 1995; Controlled Oral Word Association (COWA): Lezak, 1995; Wisconsin Card Sorting Task (WCST): Heaton, 1981]. The tests were administered in a single 2 h session, in the same basic order to all subjects. The delay period of these tests was kept constant, and was comprised of other tests not requiring any long-term memory storage. The testing order was: CVLT, GDS, WAIS-III Information subtest, WAIS-III Arithmetic subtest, WAIS-III Vocabulary subtest, CVLT delayed-recall, WMS-III Logical Memory subtest, Stroop, TMT A&B, WAIS-III Similarities subtest, COWA, WAIS-III Digit Span subtest, WMS-III Logical Memory delayed-recall, WMS-III Visual Reproduction subtest, WAIS-III Letter/Numbering Sequencing subtest, WCST computerized version, WMS-III Visual Reproduction delayed-recall.

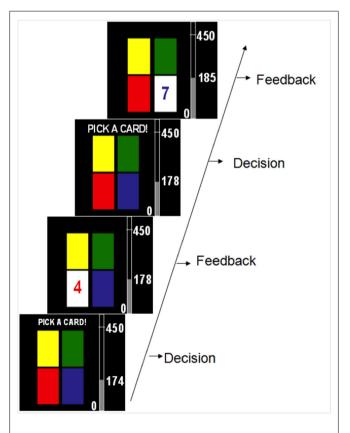
The standard, age appropriate, published norms were used to calculate normative scores for each subject. For all of the WAIS subtests, the percentile was calculated according to testing instructions, and this score was then converted to a standardized *z*-score.

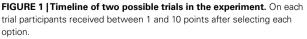
For the Stroop, CVLT, and WCST standardized *t*-scores were calculated according to testing directions, and this score was then converted to a standardized *z*-score. Finally, for the TMT and COWA standard *z*-scores were calculated according to the testing instructions. Older adults who had *z*-scores on two or more tests in the same functional realm that were 2 SD below the mean were not asked to participate in the study.

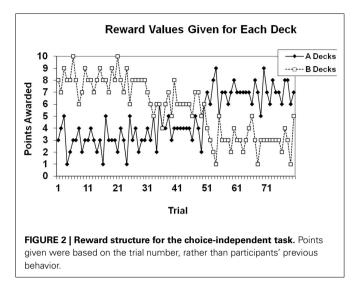
Experimental session

Each participant completed one of two decision-making tasks where all options led to gains in points and the goal was to maximize points gained. The two tasks had the same basic surface features and differed only on how the rewards for each option were structured. **Figure 1** shows a series of sample screen shots from the tasks. Each task was 80 trials long, and participants made a choice and received between 1 and 10 points on each trial. Participants performed either a choice-independent or choice-dependent tasks. The tasks used in the Experiment were four-deck versions of tasks used in a previous paper from our lab (Worthy et al., 2007). The reward structures were modified from two-deck four-deck versions by simply adding one of each type of deck.

The rewards given for each deck in the choice-independent task are shown in **Figure 2**. There were two "A" decks that gave the same reward for a given trial, and two "B" decks that gave the same reward for a given trial. The A decks gave lower rewards over



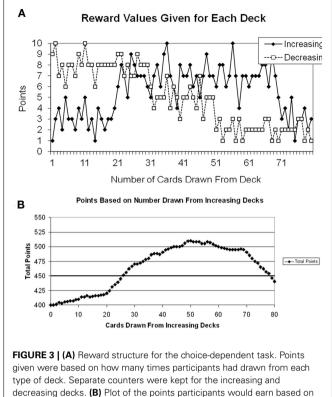




the first 50 trials of the task, but higher rewards over the final 30 trials of the task. The B decks gave higher rewards over the first 50 trials of the task, and lower rewards over the final 30 trials of the task. Optimal performance on the task required identifying and exploiting the decks that the largest gain or the smallest loss over the course of the task. The best strategy was to exploit one of the B Decks for the first 50 trials and to then switch to exploiting one of the A Decks for the final 30 trials. Participants were given a goal of earning at least 550 points by the end of the experiment. To accomplish this goal the best deck had to be exploited on approximately 90% of the trials in order for the goal criterion to be met. At the end of the session participants were told whether or not they met the goal.

The reward structure for the choice-dependent task is shown in Figure 3A. In the choice-independent task the rewards were a function of the trial number (as seen on the x-axis of Figure 2), but in the choice-dependent the rewards were based on how many cards have already been drawn from either the increasing or decreasing decks (cf. x-axis for Figure 3A). In this task there were two different types of decks: increasing decks and decreasing decks, and there were two of each type. The increasing decks gave poorer reward values at the beginning of the task, but better values as more cards were drawn from them. In contrast, the decreasing decks gave good values at the beginning of the tasks, but poorer values as more cards were drawn from them. The two increasing decks and the two decreasing decks were yoked, and separate counters were kept for each type of deck. Each time a card was drawn from one of the two increasing (or decreasing) decks the counter would increase by one and this number would be equivalent to the value on the x-axis of Figure 3A¹.

Participants were given a goal of earning at least 450 points by the end of the experiment. The goal criterion was determined



so that participants had to draw a minimum of 25 cards from the increasing decks to meet the criterion in each task. The total points earned for the gains task can be plotted as a function of the number of cards drawn from the increasing decks. This is shown in **Figure 3B**.

the number of draws from the increasing decks.

The specific instructions participants received before performing the choice-independent task are shown below. The instructions were the same for participants who performed the choicedependent task except participants were told that their goal was to earn 450, not 550, points.

Specific instructions. You will perform a gambling task where you will be asked to make selections from one of four options. After each selection you will gain a certain number of points. Your objective is to gain as many points as possible. You will have a specific goal to earn a certain number of points by the end of the task. When you begin the task your goal will be listed on the screen. Try your best to earn as many points as possible.

Four decks will appear on the screen. You will use the "W," "Z," "P," and "?/" keys to pick from these decks.

Press the "W" key to pick from the deck on the top left. Press the "Z" key to pick from the deck on the bottom left. Press the "P" key to pick from the deck on the top right. Press the "?/" key to pick from the deck on the bottom right. You will receive between 1 and 10 points each time you draw a card. Your goal is to earn at least 550 points by the end of the task.

¹It should be noted that the choice-dependent task is formally a partially observable Markov decision process (POMDP). Some research in machine learning suggests that the inclusion of ETs can help RL models cope with partial observability (e.g., Loch and Singh, 1998).

RESULTS

PERFORMANCE

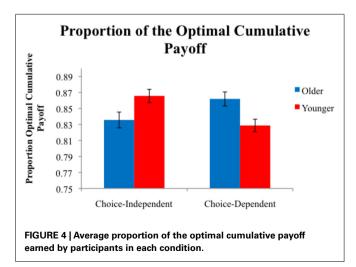
We first examined performance in each task by computing each participant's payoff relative to the payoff obtained by an optimal performer. This proportion of the optimal cumulative payoff was computed by dividing the points earned by each participant by the maximum number of points that could be earned by an omniscient observer (600 in the choice-independent task and 515 in the choice-dependent task). The proportions of the optimal cumulative payoff are shown in **Figure 4**. A 2 (Age) \times 2 (Task) ANOVA showed no main effect of age or for task, however there was a significant age \times task interaction, F(1,110) = 12.96, P < 0.001, $\eta^2 = 0.11$. We conducted pair-wise comparisons within each task to investigate the locus of the interaction. Within the choice-independent task there was a significant effect of age, $F(1,57) = 5.42, P < 0.05, \eta^2 = 0.09$. Younger adults (M = 0.87) earned a significantly higher proportion of the optimal cumulative payoff than older adults (M = 0.84). There was also a main effect of age in the choice-dependent task, F(1,53) = 7.92, P < 0.01, $\eta^2 = 0.13$. Older adults (M = 0.86) outperformed younger adults in this task (M = 0.83). Thus younger adults performed better on the choice-independent task, and older adults performed better on the choice-dependent task.

MODEL-BASED RESULTS

We fit each participant's data individually with the WSLS, Delta-Rule, ET, and the Baseline models detailed above. The models were fit to the choice data from each trial by maximizing negative log-likelihood. We used Akaike weights to compare the relative fit of each model (Akaike, 1974; Wagenmakers and Farrell, 2004). Akaike weights are derived from Akaike's information criterion (AIC) which is used to compare models with different numbers of free parameters. AIC penalizes models with more free parameters. For each model, *i*, AIC is defined as:

$$AIC_i = -2LogL_i + 2V_i \tag{8}$$

where L_i is the maximum likelihood for model *i*, and V_i is the number of free parameters in the model. Smaller AIC values indicate a better fit to the data. We first computed AIC values for each



model and for each participant's data. Akaike weights were then calculated to obtain a continuous measure of goodness-of-fit. A difference score is computed by subtracting the AIC of the best fitting model for each data set from the AIC of each model for the same data set:

$$\Delta_i(AIC) = AIC_i - \min AIC \tag{9}$$

From the differences in AIC we then computed the relative likelihood, *L*, of each model, *i*, with the transform:

$$L(M_i|\text{data}) \propto exp\left\{-\frac{1}{2}\Delta_i(\text{AIC})\right\}$$
 (10)

Finally, the relative model likelihoods are normalized by dividing the likelihood for each model by the sum of the likelihoods for all models. This yields Akaike weights:

$$w_i(AIC) = \frac{exp\left\{-\frac{1}{2}\Delta_i(AIC)\right\}}{exp\left\{-\frac{1}{2}\Delta_k(AIC)\right\}}$$
(11)

These weights can be interpreted as the probability that the model is the best model given the data set and the set of candidate models (Wagenmakers and Farrell, 2004).

We computed the Akaike weights for each model for each participant. **Table 1** shows the average Akaike weights for participants in each condition. Akaike weights were highest for the ET model for younger adults across both tasks. Older adults' had higher Akaike weights for the WSLS model in the choiceindependent task, although the ET model also provided a good fit to the data. Akaike weights were highest for the ET model for older adults in the choice-dependent task, although the WSLS model also provided a good fit to the data. The Akaike weights for the Delta-Rule model were lower than the weights for the ET model across all four conditions, indicating that adding ETs provided a better fit to the data. The baseline model did not provide a good fit to the data compared to the fit of the two TD models.

We can conclude from **Table 1** that the ET and WSLS models provided the best fit to the data. We next compared the fits of the ET model and WSLS models directly for each participant to determine if participants were using a heuristic-based WSLS strategy, or a more associative RL strategy. To obtain a relative measure of the degree to which the ET model provided a better fit to the data

Table 1 | Akaike weights for each model.

	WSLS	Delta-rule	ET	Baseline				
CHOICE-INDEP	ENDENT TAS	K						
Older adults	0.44 (0.08)	0.19 (0.03)	0.37 (0.06)	0 (0)				
Younger adults	0.34 (0.08)	0.23 (0.04)	0.43 (0.06)	0 (0)				
CHOICE-DEPENDENT TASK								
Older adults	0.36 (0.08)	0.21 (0.04)	0.40 (0.06)	0.02 (0.01)				
Younger adults	0.19 (0.07)	0.31 (0.04)	0.48 (0.05)	0.02 (0.02)				

SEM are listed in parentheses.

than the WSLS model we subtracted the AIC of the ET model from the AIC of the WSLS (Relative fit_{ET} = $\ln L_{WSLS} - \ln L_{ET}$), for each participant's data. Because lower log-likelihood values indicate a better fit, positive Relative fit_{ET} values indicate a better fit for the ET model, while negative Relative fit_{ET} values indicate a better fit for the WSLS model.

These Relative fit_{ET} values are plotted in **Figure 5**. A 2 (Age) × 2 (Task) ANOVA showed a main effect of age, F(1,53) = 4.19, P < 0.05, $\eta^2 = 0.04$. Younger adults (11.63) had higher Relative fit_{ET} values than older adults (M = 1.10), indicating more use a of an RL strategy than a heuristic-based WSLS strategy for younger adults. Relative fit_{ET} values were near 0 for older adults, indicating equal evidence for both models.

We next examined whether there was a relationship between the Relative fit_{ET} values and proportions of the optimal cumulative payoff obtained in the choice-independent and choicedependent tasks. For the choice-independent task there was a significant positive correlation between Relative fit_{ET} values and the proportions of optimal cumulative payoff (r = 0.37, P < 0.01). We examined these correlations within the younger and older adults groups. There was a significant positive correlation between Relative fit_{ET} values and proportions of the optimal cumulative payoff within the older adults group (r = 0.41, P < 0.05). The correlation between Relative fit_{ET} values and proportions of the optimal cumulative payoff was also positive, but only marginally significant within the younger adult group (r = 0.26, P < 0.10).

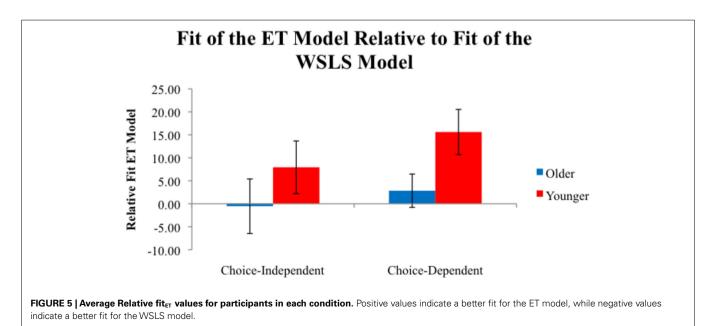
Across all participants in the choice-dependent task there was a significant negative correlation between Relative fit_{ET} values and the proportions of optimal cumulative payoff (r = -0.43, P < 0.001). This correlation was negative, but did not reach significance for the older adults (r = -0.14, P > 0.10). The correlation between Relative fit_{ET} values and the proportions of optimal cumulative payoff was negative and highly significant for younger adults (r = -0.58, P < 0.001).

NEUROPSYCHOLOGICAL TEST RESULTS AND STRATEGY USE

We examined the older adult data from the neuropsychological testing session to determine if there were any relationships between scores on those tests and strategy use in the decision-making tasks. We first examined correlations between the scores on each neuropsychological test for older adults, and the proportions of the optimal cumulative payoff they earned as well as their Relative fit_{ET} values. However, none of these correlations reached significance (all P > 0.10).

We next split up the data based on whether older adult participants' data were best fit by the ET or WSLS model. Thirty-two older adults were fit better by the WSLS model and 26 were fit better by the ET model. We examined the average *z*-scores from the neuropsychological tests for participants who were best fit by each of these models. There were two test variables for which scores significantly differed between these two groups: the CVLT's recognition for true positives score, t(55) = -2.05, P < 0.05, and the WCST's number of categories score, t(55) = -2.06, P < 0.05. Scores on both of these measures were higher for older adults who were best fit by the WSLS model compared to older adults who were best fit by the ET model (CVLT: WSLS M = 0.40, ET M = -0.02; WCST: WSLS M = 0.62, ET M = -0.05). Interestingly, *z*-scores for these two neuropsychological measures were not correlated (r = -0.07, P > 0.10).

The CVLT recognition for true positives test requires yes/no recognition of items presented earlier and has been linked to frontal lobe functioning. For example, patients with frontal lobe dysfunction have been found to underperform on this test relative to normal controls (Baldo et al., 2002). The WCST has been shown to activate the DLPFC to store earlier events in working memory and the mid-ventrolateral prefrontal cortex to signal the need for a mental shift in response to a new set (Monchi et al., 2001). Thus, while this analysis is only exploratory, the findings of superior performance on two neuropsychological tests related to frontal lobe functioning for older adults whose data were best fit



by the WSLS model is consistent with the hypothesis that a WSLS strategy is more frontally mediated.

DISCUSSION

We observed an interaction between age and the nature of the optimal task strategy on performance. Older adults performed better when rewards were choice-dependent, while younger adults performed better when rewards were choice-independent. This replicates our previous finding in the same choice-independent task, and mirrors our previous findings for two different choice-dependent tasks (Worthy et al., 2011). We fit the data with four different mathematical models to better characterize the behavior of younger and older adults when performing these tasks. Overall an RL model that included ETs provided the best fit to the data, although a WSLS model provided a good fit as well, particularly for older adults who performed the choice-independent task.

A direct comparison of the ET and WSLS model fits showed more evidence of WSLS strategy use for older adults than younger adults. Participants who were better fit by the ET model, relative to the fit of the WSLS model, tended to perform better on the choice-independent task, but worse on the choice-dependent task. A WSLS strategy may lead to sub-optimal switches from the most-rewarding options in the choice-independent task due to variation around the mean value given by each deck. A participant may switch to a different deck after receiving less on the current trial than what they received on the previous trial, even though they may be switching to a deck with a lower overall mean reward value. The ET model assumes that participants update and maintain EVs for each option. The EVs are essentially recency-weighted averages of the rewards received on previous trials, and the model predicts which option should be chosen by comparing the EV of each option with the EVs of the other options. This model should not predict as much switching from decks that give high average rewards because the decks are valued based on the average rewards received over many trials, rather than a relative comparison between the current reward and the reward received on the preceding trial.

A WSLS strategy likely helps on the choice-dependent task because participants are less likely to stay with the Decreasing options, and will select the Increasing options more due to the variation in rewards around each deck's mean reward value. A WSLS strategy should also lead participants to switch away from the Decreasing options quicker once the rewards given by the Decreasing options begin to decline. An RL strategy will consistently value the Decreasing option early in the task because selecting it leads to larger average rewards. Because the EVs are recency-weighted averages of the rewards received for each option, participants using this type of strategy will pick the Increasing option less often early in the task, leading to poorer overall performance.

Thus, the age-based differences in performance on the choiceindependent and choice-dependent tasks were due to differences

REFERENCES

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* 19, 716–723. Ashby, F. G., Alfonso-Reese, L. A., Turken, A. U., and Waldron, E. M. (1998). A neuropsychological theory of multiple systems in category learning. *Psychol. Rev.* 105, 442–481. in the types of strategies older and younger adults used to make their decisions on each trial, with older adults using a heuristicbased WSLS more often than younger adults. Other work also suggests that older adults may be more likely to use simple heuristics during decision-making than younger adults (Thornton and Dumke, 2005; Mata et al., 2007; Peters et al., 2007; Castel et al., in press). For example, Castel et al. (in press) recently found that older adults showed higher endorsement of the "hot-hand" heuristic in basketball than younger adults (i.e., the rule that the player who has made his/her last few shots should shoot the ball). Older participants in our experiment showed a similar preference for a heuristic-based WSLS strategy based on a comparison of the current and previous rewards, over an RL strategy that favored options with large expected reward values.

The differences in strategy preferences that we observed could be due to a shift in the neural areas recruited during decisionmaking, as predicted by STAC (Park and Reuter-Lorenz, 2009). A WSLS strategy may be more demanding of WM and executive attention resources than an RL strategy, which is more striatally mediated and less demanding of working memory and executive attention resources (Frank and Claus, 2006; Frank et al., 2006; Otto et al., 2011). Participants performing a concurrent working memory demanding task have been shown to be better fit by an expectation-matching model, similar to the RL models used here, relative to a WSLS model (Otto et al., 2011). While frontal compensation could be a cause for the age-based difference in strategy use, older adults may have also learned from life experience that the use of heuristics can often be an adaptive and useful way of making decisions (e.g., Gigerenzer and Todd, 1999; Broder, 2003; Scheibehenne et al., 2011). Indeed the use of a WSLS strategy was adaptive in the choice-dependent task as it led participants away from repeatedly selecting the Decreasing options. Older adults' greater experience in advantageously using heuristics in decision-making situations may have led them to prefer such strategies more than younger adults in our decision-making tasks.

CONCLUSION

This study applied a series of mathematical models to data from younger and older adults who performed either a choicedependent or choice-independent decision-making task. Older adults showed more evidence of utilizing a WSLS heuristic to make decisions than younger adults, who were best fit by an RL model that tracked recency-weighted averages of each option based on prediction errors. These results suggest that older and younger adults use qualitatively different strategies to make decisions, and that the shift in strategies may results from older adults engaging more frontal brain regions to compensate for age-based neural declines (Park and Reuter-Lorenz, 2009), and the greater experience of older adults in successfully using heuristics to make decisions.

Ashby, F. G., and Maddox, W. T. (2005). Human category learning. *Annu. Rev. Psychol.* 56, 149–178.

Baldo, J. V., Delis, D., Kramer, J., and Shimamura, A. P. (2002). Memory performance on the California Verbal Learning Test-II: findings from patients with focal lesions. *J. Int. Neuropsychol. Soc.* 8, 539–546.

- Bogacz, R., McClure, S. M., Li, J., Cohen, J. D., and Montague, P. R. (2007). Short-term memory traces for action bias in human reinforcement learning. *Brain Res.* 1153, 111–121.
- Brink, T. L., Yesavage, J. A., Lum, O., Heersema, P. H., Adey, M., and Rose, T. L. (1982). Screening tests for geriatric depression. *Clin. Gerontol.* 1, 37–43.
- Broder, A. (2003). Decision making with the "adaptive toolbox". Influence of environmental structure, intelligence, and working memory load. J. Exp. Psychol. Learn. Mem. Cogn. 29, 611–625.
- Brown, S. B. R. E., and Ridderinkhof, K. R. (2009). Aging and the neuroeconomics of decision-making. *Cogn. Affect. Behav. Neurosci.* 9, 365–379.
- Cabeza, R., Anderson, N. D., Locantore, J. K., and McIntosh, A. R. (2002). Aging gracefully: compensatory brain activity in highperforming older adults. *Neuroim*age 17, 1394–1402.
- Cappell, K. A., Gmeindl, L., and Reuter-Lorenz, P. A. (2010). Age differences in prefrontal recruitment during verbal working memory maintenance depend on memory load. *Cortex* 46, 462–473.
- Castel, A. D., Rossi, A. D., and McGillivray, S. (in press). Beliefs about the "hot hand" in Basketball across the adult lifespan. *Psychol. Aging.*
- Cohen, J. E. (2003). Human population: the next half century. *Science* 302, 1172–1175.
- Daw, N. D., and Doya, K. (2006). The computational neurobiology of learning and reward. *Curr. Opin. Neurobiol.* 16, 199–204.
- Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B., and Dolan, R. J. (2006). Cortical substrates for exploratory decisions in humans. *Nature* 441, 876–879.
- Delis, D. C., Kramer, J. H., Kaplan, E., and Ober, B. A. (1987). California Verbal Learning Test: Adult Version Manual. San Antonio, TX: The Psychological Corporation.
- Denburg, N. L., Tranel, D., and Bechara, A. (2005). The ability to decide advantageously declines prematurely in some normal older persons. *Neuropsychologia* 43, 1099–1106.
- Frank, M. J., and Claus, E. D. (2006). Anatomy of a decision: striato-orbitofrontal interactions in reinforcement learning, decisionmaking, and reversal. *Psychol. Rev.* 113, 300–326.

- Frank, M. J., and Kong, L. (2008). Learning to avoid in older age. *Psychol. Aging* 23, 392–398.
- Frank, M. J., O'Reilly, R. C., and Curran, T. (2006). When memory fails, intuition reigns: midazolam enhances implicit inference in humans. *Psychol. Sci.* 17, 700–707.
- Gigerenzer, G., and Todd, P. M. (1999). "Fast and frugal heuristics: the adaptive tool box," in *Simple Heuristics that Make us Smart*, eds G. Gigerenzer, P. Todd, and the ABC Research Group (New York: Oxford University Press), 3–34.
- Green, L., Fry, A. F., and Myerson, J. (1994). Discounting of delayed rewards: a life span comparison. *Psychol. Sci.* 5, 33–36.
- Gureckis, T. M., and Love, B. C. (2009). Learning in noise: dynamic decision-making in a variable environment. J. Math. Psychol. 53, 180–193.
- Hare, T. A., O'Doherty, J., Camerer, C. F., Schultz, W., and Rangel, A. (2008). Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. *J. Neurosci.* 28, 5623–5630.
- Hariri, A. R., Brown, S. M., Williamson, D. E., Flory, J. D., de Wit, H., and Manuck, S. B. (2006). Preference for immediate over delayed reward is associated with magnitude of ventral striatal activity. *J. Neurosci.* 20, 13213–13217.
- Heaton, R. K. (1981). A Manual for the Wisconsin Card Sorting Test. Odessa, FL: Psychological Assessment Resources.
- Kovalchik, S., Camerer, C. F., Grether, D. M., Plott, C. R., and Allman, J. M. (2004). Aging and decision making: a comparison between neurologically healthy elderly and young individuals. *J. Econ. Behav. Organ.* 58, 79–94.
- Kuhnen, C. M., and Knutson, B. (2005). The neural basis of financial risktaking. *Neuron* 47, 763–770.
- Lee, M. D., Zhang, S., Munro, M., and Steyvers, M. (2011). Psychological models of human and optimal performance in bandit problems. *Cogn. Syst. Res.* 12, 164–174.
- Lezak, M. D. (1995). *Neuropsychological Assessment*, 3rd Edn. New York: Oxford University Press.
- Li, S. C., Biele, G., Lindenberger, U., and Sikstrom, S. (2001). Aging cognition: from neuromodulation to representation. *Trends Cogn. Sci. (Regul. Ed.)* 5, 97–111.
- Loch, J., and Singh, S. P. (1998). "Using eligibility traces to find

the best memoryless policy in partially observable Markov decision processes," in *Proceedings of the Fifteenth International Conference on Machine Learning*, Madison, 323–331.

- Lockenhoff, C. E. (2011). Age, time, and decision making: from processing speed to global time horizons. *Ann. N. Y. Acad. Sci.* 1235, 44–56.
- Lockenhoff, C. E., O'Donoghue, T., and Dunning, D. (2011). Age differences in temporal discounting: the role of dispositional affect and anticipated emotions. *Psychol. Aging* 26, 274–284.
- Maddox, W. T., and Ashby, F. G. (2004). Dissociating explicit and procedural-learning systems of perceptual category learning. *Behav. Processes* 66, 309–332.
- Mata, R., Schooler, L. J., and Rieskamp, J. (2007). The aging decision maker: cognitive aging and the adaptive selection of decision strategies. *Psychol. Aging* 22, 796–810.
- McClure, S. M., Berns, G. S., and Montague, P. R. (2003). Temporal prediction errors in a passive learning task activate human striatum. *Neuron* 38, 329–337.
- McClure, S. M., Ericson, K. M., Laibson, D. I., Loewenstein, G., and Cohen, J. D. (2007). Time discounting for primary rewards. J. Neurosci. 27, 5796–5804.
- Mell, T., Heekeren, H. R., Marschner, A., Wartenburger, I., Villringer, A., and Reischies, F. M. (2005). Effects of aging on stimulus-reward association learning. *Neuropsychologia* 43, 554–563.
- Mell, T., Wartenburger, I., Marschner, A., Villringer, A., Reischies, F. M., and Heekeren, H. R. (2009). Altered function of ventral striatum during reward-based decision-making in old age. *Front. Hum. Neurosci.* 3:34. doi:10.3389/neuro.09.034.2009.
- Monchi, O., Petrides, M., Petre, V., Worsley, K., and Dagher, A. (2001). Wisconsin Card Sorting revisited: distinct neural circuits participating in different stages of the task identified by event-related functional magnetic resonance imaging. *J. Neurosci.* 21, 7733.
- Montague, P. R., Dayan, P., and Sejnowski, T. J. (1996). A framework for mesencephalic dopamine systems based on predictive Hebbian learning. *J. Neurosci.* 16, 1936–1947.
- Otto, A. R., Markman, A. B., Gureckis, T. M., and Love, B. C. (2010). Regulatory fit and systematic exploration in a dynamic decision-making environment. J. Exp. Psychol. Learn. Mem. Cogn. 36, 797–804.

- Otto, A. R., Taylor, E. G., and Markman, A. B. (2011). There are at least two kinds of probability matching: evidence from a secondary task. *Cognition* 118, 274–279.
- Pagnoni G., Zink C. F., Montague P. R., and Berns G. S. (2002). Acitivity in the human ventral striatum locked to errors of reward prediction. *Nat. Neurosci.* 5, 97–98.
- Pan, W. X., Schmidt, R., Wickens, J. R., and Hyland, B. I. (2005). Dopamine cells respond to predicted events during classical conditioning: evidence for eligibility traces in the reward-learning network. J. Neurosci. 25, 6235–6242.
- Park, D. C., and Reuter-Lorenz, P. (2009). The adaptive brain: aging and neurocognitive scaffolding. *Annu. Rev. Psychol.* 60, 173–196.
- Pessiglione, M., Seymour, B., Flandin, G., Dolan, R. J., and Frith, C. D. (2006). Dopamine-dependent prediction errors underpin rewardseeking behavior in humans. *Nature* 442, 1042–1045.
- Peters, E., Hess, T. M., Vastfjall, D., and Auman, C. (2007). Adult age differences in dual information processes: implications for the role of affective and deliberative processes in older adults' decision making. *Perspect. Psychol. Sci.* 2, 1–23.
- Raz, N. (2000). "Aging of the brain and its impact on cognitive performance: integration of structural and functional findings," in *The Handbook of Aging and Cognition*, eds F. Craik and T. A. Satlhouse (Hillsdale, NJ: Erlbaum), 1–90.
- Raz, N., Linberger, U., Rodrique, K. M., Kennedy, K. M., Head, D., Williamson, A., Dahle, C., Gerstorf, D., and Acker, J. D. (2005). Regional brain differences in aging healthy adults: general trends, individual differences and modifiers. *Cereb. Cortex* 15, 1676–1689.
- Resnick, S. M., Pham, D. L., Kraut, M. A., Zonderman, A. B., and Davatzikos, C. (2003). Longitudinal magnetic resonance imaging studies of older adults: a shrinking brain. J. Neurosci. 23, 3295–3301.
- Reuter-Lorenz, P. A., and Cappell, K. A. (2008). Neurocognitive aging and the compensation hypothesis. *Curr. Dir. Psychol. Sci.* 17, 177–182.
- Samanez-Larkin, G. R., Gibbs, S. E. B., Khanna, K., Nielsen, L., Carstensen, L. L., and Knutson, B. (2007). Anticipation of monetary gain bus not loss in healthy older adults. *Nat. Neurosci.* 10, 787–791.
- Samanez-Larkin, G. R., Kuhnen, C. K., Yoo, D. J., and Knutson, B. (2010).

Variability in nucleus accumbens activity mediates age-related suboptimal financial risk-taking. *J. Neurosci.* 30, 1426–1434.

- Samanez-Larkin, G. R., Wagner, A. D., and Knutson, B. (2011). Expected value information improves financial risk taking across the adult life span. Soc. Cogn. Affect. Neurosci. 6, 207–217.
- Scheibehenne, B., Wilke, A., and Todd, P. M. (2011). Expectations of clumpy resources influence predictions of sequential events. *Evol. Hum. Behav.* 32, 326–333.
- Schott, B. H., Niehaus, L., Wittman, B. C., Schutze, H., Seidenbecher, C. I., Heinze, H. J., and Duzel, E. (2007). Ageing and early-stage Parkinson's disease affect separable neural mechanisms of mesolimbic reward processing. *Brain* 130, 2412–2424.
- Steyvers, M., Lee, M. D., and Wagenmakers, E. J. (2009). A Bayesian analysis of human decision-making

on bandit problems. J. Math. Psychol. 53, 168–179.

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. J. Exp. Psychol. 18, 643–662.

Sutton, R. S., and Barto, A. G. (1998). Reinforcement Learning: An Introduction. Cambridge: MIT Press.

- Thornton, W. J. L., and Dumke, H. A. (2005). Age differences in everyday problem-solving and decision-making effectiveness: a meta-analytic review. *Psychol. Aging* 20, 85–99.
- Wagenmakers, E. J., and Farrell, S. (2004). AIC model selection using Akaike weights. *Psychon. Bull. Rev.* 11, 192–196.
- Wechsler, D. (1997). Wechsler Adult Intelligence Scale, 3rd Edn. San Antonio: Harcourt Brace & Company.
- Winstanely, C. A., Dalley, J. W., Theobald, D. E., and Robbins, T. W. (2006). Double dissociation between serotonergic and

dopaminergic modulation of prefrontal and orbitofrontal cortex during a test of impulsive choice. *Cereb. Cortex* 16, 106–114.

- Wood, S., Busemeyer, J., Koling, A., Davis, H., and Cox, C. R. (2005). Older adults as adaptive decisionmakers: evidence from the Iowa Gambling Task. *Psychol. Aging* 20, 220–225.
- Worthy, D. A., Gorlick, M. A., Pacheco, J. L., Schnyer, D. M., and Maddox, W. T. (2011). With age comes wisdom: decision-making in older and younger adults. *Psychol. Sci.* 22, 1375–1380.
- Worthy, D. A., Maddox, W. T., and Markman, A. B. (2007). Regulatory fit effects in a choice task. *Psychon. Bull. Rev.* 14, 1125–1132.
- Yechiam, E., and Busemeyer, J. R. (2005). Comparison of basic assumptions embedded in learning models for experience based decisionmaking. *Psychon. Bull. Rev.* 12, 387–402.

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Strategic insight and age-related goal-neglect influence risky decision-making

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Maximizing long-run gains often requires taking on some degree of risk, yet decisionmakers often exhibit risk aversion (RA), rejecting risky prospects even when these have higher expected value (EV) than safer alternatives. We investigated whether explicit strategy instruction and practice can decrease prepotent RA, and whether aging impacts the efficacy of such an intervention. Participants performed a paired lottery task with options varying in risk and magnitude, both before and after practice with a similar task that encouraged maximization of EV and instruction to use this strategy in risky decisions. In both younger and older adults (OAs), strategy training reduced RA. Although RA was age-equivalent at baseline, larger training effects were observed in younger adults (YAs). These effects were not explained by risk-related (i.e., affective) interference effects or computation ability, but were consistent with a progressive, age-related neglect of the strategy across trials. Our findings suggest that strategy training can diminish RA, but that training efficacy is reduced among OAs, potentially due to goal neglect. We discuss implications for neural mechanisms that may distinguish older and YAs' risky decision-making.

Keywords: risk aversion, goal neglect, strategy training, aging, decision-making

INTRODUCTION

Risk taking plays an essential role in the transactions, investments, and decisions that comprise daily life. Assuming a decision-maker wishes to maximize long-run gains, they should select according to expected value (EV): the product of probability and amount, in a given lottery. However, behavioral economists have demonstrated that choices during risky decision-making are best described by a non-linear transformation of both amount and probability values (Kahneman and Tversky, 1979). In particular, decision-makers act as if they find risk aversive by undervaluing risky gains relative to their EV. One operational definition (that we adopt in this paper) of risk aversion (RA) is when decision-makers select a more likely gain with lower EV over a less likely gain with higher EV, on forced-choice, paired lotteries.

Two psychological explanations for RA have different implications for potential interventions. One explanation involves a dual-process tug-of-war between slow deliberation on one side, and automatic, effortless processing on the other (Epstein, 1994; Loewenstein et al., 2001). Automatic, predominantly affective responses to risk (fear or anticipatory regret, for example) are prepotent in that they drive decisions toward safer options even when deliberative assessments warrant risk taking (Thaler et al., 1997; Loewenstein et al., 2001; Slovic et al., 2005). Thus deliberative decision-making may depend on cognitive control processes that facilitate emotion regulation and/or the inhibition of automatic affective responses to risk.

Another explanation is that the difference between RA and a balanced assumption of risk hinges on knowledge of, and experience utilizing, optimal decision-making strategies. Decision-makers may be risk-averse primarily because they do not realize that selecting on the basis of EV will yield higher longrun returns than minimizing risk on individual decisions. Instead, they rely on a sub-optimal strategy like deciding on the basis of probabilities alone. If RA stems primarily from a lack of knowledge and application of an EV-based decision-making strategy, then training to promote insight and experience with this strategy should reduce RA.

Strategy training has improved performance in a variety of cognitive domains (Hartley and Anderson, 1986; McNamara and Scott, 2001; Saczynski et al., 2002; Touron and Hertzog, 2004; Paxton et al., 2006; Dunlosky and Kane, 2007), and spontaneous adaptive strategy shifts have been observed in risky decision-making contexts (Mata et al., 2007, 2010). However, it has not been tested whether simply providing explicit instructions and practice with optimal decision-making strategies can reduce RA.

Even if strategy training reduces RA, cognitive resources may constrain the efficacy of the intervention. Computing and selecting on the basis of EV is more complicated than heuristics like probability maximization, thus placing greater demands on working memory. Decision-makers with diminished working memory may, therefore, make more mistakes when trying to implement the EV-selection strategy. Cognitive control may also be important for several reasons. According to the dual-process account, deliberative EV-based responding will conflict with automatic, risk-averse responding, and cognitive control processes may be required to resolve this response conflict (Botvinick et al., 2001). It is important to note that the lack-of-insight and dual-process explanations of RA are not mutually exclusive. A decision-maker might be less risk averse when they have insight about, and practice selecting based on EV, but only if they can also inhibit automatic response tendencies, for example, by down-regulating their initial affective response to risk. Cognitive control may also play an important role in boosting signals of goal-relevant stimulus features (e.g., EV) in valuation centers of the brain during decision-making (Hare et al., 2009). Hence, even if optimal strategy insight and training reduce RA, training might be less effective for decision-makers with either (or both) diminished working memory or cognitive control.

Older adults (OAs) represent one such population. It is well established that OAs exhibit declines in both working memory and cognitive control (Salthouse, 1990; Park and Reuter-Lorenz, 2009). Reduced working memory, along with reduced processing speed, has been shown to explain apparent RA among OAs across decision-making tasks (Henninger et al., 2010). Another potential handicap for OAs is an age-related impairment in the cognitive control function of goal maintenance (Braver and West, 2008). If overcoming RA depends on goal-directed, top-down biasing of EV-based selection over prepotent risk avoidance, then success with this decision-making strategy will critically depend on cognitive control. Yet, OAs frequently exhibit goal neglect: a progressive tendency to make prepotent, but goal-irrelevant responses over goal-appropriate ones (Duncan et al., 1996; De Jong, 2001; West, 2002; Butler and Zacks, 2006). Thus, OAs are a good population in which to test the limitations of strategy training for reducing RA.

In the current study, younger and OAs were assessed for evidence of RA, both before and after explicit strategy training in EV-based decision-making. The paradigm involved paired lotteries varying explicitly in reward magnitude and probability (cf. Holt and Laury, 2002). We operationalized RA in terms of the proportion of trials in which the lower-risk option was selected when the other (higher-risk) option had a higher EV. In training, participants were instructed to compute and maximize EV and were given practice and feedback explicitly informative of the EV associated with each choice. In the post-training phase, participants were encouraged to use this EV-based decision-making strategy and told it would maximize payoffs.

Our primary goal was to determine whether RA results from a lack of strategy insight and practice, independent of ability to inhibit affective responses to risk. We predicted that if insight matters, our strategy training should be effective in reducing RA, even without targeting affective control. Alternatively, if RA results solely from affective responses to risk, then our strategy training should be ineffective. A secondary goal was to test whether age-related cognitive decline would limit training efficacy among OAs. We further predicted that if implementation of an EVbased decision-strategy critically depends on working memory or cognitive control, reduced training effects should be observed in OAs.

MATERIALS AND METHODS

PARTICIPANTS

Participants included 40 younger ($M_{age} = 21.0$, SD = 2.5, range = 18–33) and 46 OAs ($M_{age} = 75.4$, SD = 7.4, range = 65–95). Younger adults (YAs) were recruited from the Washington University in Saint Louis undergraduate community, while OAs were recruited from the Volunteers for Health community

database. All participants self-reported no history of neurological or psychiatric disease, and provided informed consent approved by the Human Research Protection Office human subject committee at Washington University in Saint Louis.

PROCEDURE

Participants performed a paired lottery task that was programmed and presented in E-Prime 2.0. At the beginning of the experiment, participants were instructed to make a series of choices between paired offers worth different point values. Participants were encouraged to earn as many points as possible since points would later be converted to real money (at an unspecified conversion rate). At the end of the experiment, participants were shown their total point earnings, told the conversion rate, and the amount of money they earned, based on their performance (**Figure 1**).

Participants were given 7.5 s during each trial to select between the paired offers. A sliding bar indicated the time remaining on each trial. If participants did not make a selection in time, they received feedback indicating that their response was too slow and the next trial was presented. Though trials were time-limited, responses were practically self-paced since 7.5 s apparently provided ample time for most responses for both younger (M = 3.23 s, SD = 1.49 s) and OAs (M = 4.13 s, SD = 1.55 s). Likewise, speed of responding was de-emphasized with the fixed response window, in that faster responses did not increase the rate at which trials were completed.

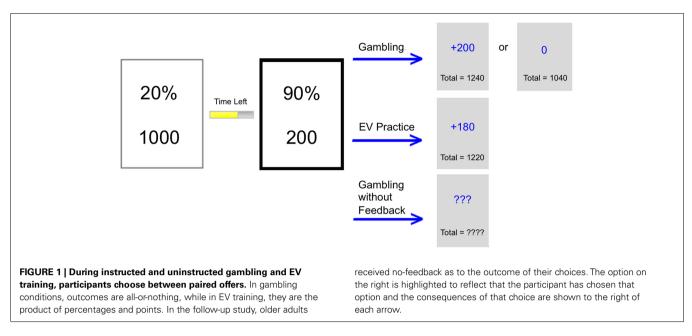
Two decision-making blocks were performed in counterbalanced order, uninstructed gambling and EV training, followed by a last decision-making block: instructed gambling. During uninstructed gambling, participants were permitted to make their selections by any strategy they wanted in an attempt to maximize earnings. After participants chose an offer, they were informed about the outcome: all-or-none points earned in that trial, and a cumulative total of earnings throughout the experiment.

In the EV-training block, participants were instructed to practice computing and maximizing EV. Trial parameters in this block included reward points, and a percentage indicating the fraction of those points that they were guaranteed to receive. The instructions were to multiply the points and the percentages (i.e., to explicitly compute EV for each offer), decide which offer was larger, and then use this as the basis for their decision. Earnings were always the precise product (equivalent to EV in an all-or-nothing gamble) of their choice. After participants decided, they were informed of the outcome as before: earnings in that trial, and those earned throughout the experiment.

The last block, instructed gambling, was identical to uninstructed gambling but was preceded by explicit instructions that the EV-based selection strategy was in fact optimal and that it should be consistently applied during decision-making in order to maximize earnings.

INSTRUCTIONS PRIOR TO INSTRUCTED GAMBLING

Before starting the instructed gambling block, participants read the following instructions. Note that these referred to the uninstructed and instructed gambling blocks "Probabilistic" and "Deterministic," respectively, reflecting the key distinction between blocks that



outcome was either probabilistic or deterministic in relationship to choice.

SCREEN 1:

Before we begin the next round, we would like to tell you one more thing. In previous versions of this study, we have found that people tend to use very different strategies in the Probabilistic and Deterministic conditions. You might have noticed yourself doing this too!

In the Probabilistic condition, we find that most people tend to choose the higher probability option because it feels "safer," whereas in the Deterministic condition people tend to multiply the probability by the amount on each side and then to choose the larger.

SCREEN 2:

In fact, people's tendency to choose the higher probability reward in the Probabilistic condition usually results in them earning many fewer points than they could. Mathematically, it is far better to use the SAME strategy in both conditions. If you do this, you will tend to earn many more points.

Specifically, you will tend to make the most points if you treat the Probabilistic condition just like the Deterministic condition. In other words, instead of thinking only about the probability of winning, you should always multiply the probability by the amount on each side and choose the larger. Although this may result in smaller gains on some individual turns, over the course of the entire experiment, you will earn many more points. SCREEN 3:

Now, you will begin doing the PROBABILISTIC version of the task. However, we would like you to use the strategy we just told you about. You should now make all your choices the same way you would make them in the DETERMINISTIC condition: by multiplying the probability times the amount for each option, and choosing the larger. If you do this, you will earn more points (and hence, more money) than if you used a different strategy.

Table 1 | Probability and amount parameters used to generate the list of 96 trials experienced by every participant.

Probabilities (%)	Magnitudes
LOW-RISK/LOW-REWARD (LL)	
50	100
70	200
90	300
100	400
HIGH-RISK/HIGH-REWARD (HH)	
10	250
20	500
40	750
60	1000

TRIAL PARAMETERS AND IMPLICATIONS FOR DETECTING RA

The same 96 different trials (orthogonal combinations of probabilities and amounts) were used in each of the three blocks described above, presented in pseudo-random order for each participant, and were generated using the following procedure. First, four levels of probability (expressed in percent likelihood) and four levels of amount (expressed as points) were selected for lowrisk, low-reward (LL) and high-risk, high-reward (HH) sets of choice parameters (**Table 1**). Next, for each set, the probabilities and amounts were combined factorially, producing 16 different probability/amount trials for each set. The 16 trials of the LL set were then crossed with the 16 trials of the HH set, producing 256 possible trials.

Because practical constraints precluded presentation of all 256 trials in each experimental condition, a subset of 96 trials were selected according to the following criteria. First, the 256 trials were sorted based on the absolute difference in EVs between the two decks. Values ranged from 0 (identical EVs for both decks) to 550 (one deck had an EV 550 points greater than the other). A majority of the 100 trials with the lowest absolute difference

(range = 0-110 points) were selected for inclusion in the final set of 96 trials. These trials represented relatively "difficult" choices, i.e., trials on which the EV of one option was not substantially larger than the other (though there was still substantial variability across trials). The rest of the 96 trials were deliberately selected to (a) have a relatively large difference in EVs between the two sets and (b) roughly equate the number of trials in which each parameter level was presented (e.g., roughly the same number of offers involving probabilities of 10, 20, 40%, etc.). By this method, all 96 trials involved a pairing from a distribution of LL (high probability, Hi Prob) values (*point range* = 100–400, M = 237.5; probability range = 50-100%, M = 78.5%), while the other involved a pairing from a set of HH (lower-probability) values (point range = 250-1000, M = 622.4; probability range = 10-60%, M = 31.4%). Care was also taken to ensure that the two sets (LL and HH) were closely matched in mean EV ($M_{LL} = 187, M_{HH} = 183$).

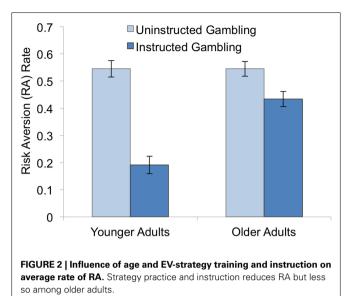
In a critical subset of trials (38 of 96), which we refer to as conflict (CF) trials, EV was higher in one option while probability was higher in the other option (e.g., 90% chance of winning 200 points vs. 20% chance of winning 1000). Thus, choosing the Hi Prob option on these trials represents a clear case of RA. In the remainder of the trials, the low-risk option had either equal (EQ) or higher EV than the high-risk option (thus termed nonconflict; NC). Consequently, these trials are non-diagnostic of the particular decision-strategy employed by participants. However, they were included as buffer trials, to make the conflict present in conflict trials less obvious to participants, and to increase the variation of probabilities, rewards, and EVs present across trials. The analyses reported below focused on performance within the conflict trials, except where otherwise noted.

RESULTS

All 96 trials, the average rate of RA on each trial in uninstructed gambling, and the average RA rate in instructed gambling (after the training) are given in the **Table A1** in Appendix.

BASIC TRAINING EFFECTS

To determine whether strategy training was effective at reducing RA, we performed a $2 \times 2 \times 2$ Block (instructed vs. uninstructed gambling) × Order (uninstructed gambling before EV training or vice versa) × Age (OAs vs. YAs) ANOVA. The dependent measure was the RA rate (i.e., proportion of conflict trials in which the low-risk option was chosen instead of the high-EV option). Results revealed a main effect of instruction block [F(2, 86) = 90.34]p < 0.01] (Figure 2). RA rate was lower in instructed gambling (0.31) than uninstructed gambling (0.55). Thus, training was successful in reducing RA by promoting EV-based decision-making. Moreover, the effect was significant in each group separately [YA: F(1, 38) = 100.39, p < 0.01, OA: F(1, 44) = 10.95, p < 0.01, indicating its robustness. Block order did not interact with the block effect [F(1, 82) = 2.37, p = 0.13], nor was the three-way interaction (Age × Order × Block) significant [F(1, 82) = 0.11, p = 0.74]. Importantly, strategic insight generated a significant reduction in RA from uninstructed to instructed gambling (the main effect of Block) even for the subset of participants who practiced EV-based selection before baseline uninstructed gambling [i.e., for those participants who first gambled after practicing EV-based selection, but



before being told EV-based selection could be used to maximize outcomes in gambling; F(1, 42) = 28.96, p < 0.01]. Comparing means in each Order group, uninstructed gambling RA was not significantly lower after EV training rather than before it [uninstructed gambling before EV training: RA = 0.58; uninstructed gambling after EV training: RA = 0.51; t(84) = 1.62, p = 0.11]. These results suggest that practice computing EV has little effect on RA, and that the critical factor in optimizing decision-making is the qualitative insight provided by the explicit instructional manipulation.

Although the training effect was significant in both age groups, there was also a significant main effect of Age [F(1, 82) = 13.28, p < 0.01], and an Age × Block interaction [F(1, 82) = 24.33, p < 0.01] revealing that strategy training was less effective in OAs compared to YAs. Average RA in the instructed gambling block was higher for OAs (0.44) than YAs [0.19; t(85) = -6.11, p < 0.01], despite the fact that RA was identical in the two groups during uninstructed gambling (OA: RA = 0.55, YA:RA = 0.55; t < 1). Based on these results, we conducted a series of analyses to better understand both why training reduced RA in both groups, and also why EV training was less effective for OAs.

POTENTIAL EXPLANATIONS OF TRAINING EFFECTS

Training was successful in reducing RA, but this could have resulted from some combination of increased reliance on EV, as the training was designed to promote, or increased ability to inhibit the automatic affective response to risk. In the former case, EV-related trial parameters should become more important predictors of choice after training. In the latter case, choice probabilities should become less important predictors of choice after training since choice probabilities presumably drive the automatic affective response.

A multiple regression was conducted to test the influence of trial-by-trial parameters on choice. Specifically, we tested the extent to which EV-related or RA-related predictor variables could predict the pattern of choice on each trial out of the full set of 96 decision trials (indexed by t) performed by participants (Eq. 1).

For this analysis, the dependent measure was the proportion of participants (indexed by *i*) choosing the Hi Prob option. Because each participant received the exact same 96 trials but in permuted order, it is possible to treat the choice pattern across the 96 trials, averaged across participants, as an independent random effect. Two trial-level predictors were selected as independent variables: the probability value of the Hi Prob option, and the difference in EV between the Hi Prob and low probability options (i.e., $\Delta EV = EV$ Hi Prob option – EV low probability option; –/+ for conflict/non-conflict trials). These two predictor variables were chosen out of a set of three potential RA-related variables and three potential EV-related variables on the basis of relative reliability. Prior to inclusion the two trial-level predictors were z-scored, while the dependent variable was logit-transformed and then zscored. Note that for the purpose of transforming proportions of 1 (e.g., where all participants selected the Hi Prob option on a non-conflict trial), a small constant, equal to the smallest, non-zero proportion value across all trials (0.025) was added to the numerator and denominator of the logit function. This ad hoc solution is recommended for logit transformations while introducing minimal bias (Warton and Hui, 2011).

$$logit\left(\frac{\sum_{i=1}^{k_{j,m,t}} RA \operatorname{responses}_{i,j,m,t}}{k_{j,m,t}}\right)$$

= $\beta_0 + \beta_1 Hi \operatorname{Prob}_{j,m,t} + \beta_2 \Delta EV_{j,m,t} + \beta_3 Block_{j,m,t}$
+ $\beta_4 \Delta EV_{j,m,t} \times Block_{j,m,t} + \beta_4 Hi \operatorname{Prob}_{j,m,t}$
 $\times Block_{j,m,t} + \varepsilon_{j,m,t}$ (1)

The first analysis focused on YAs (age-group indexed by m; here $m = younger \ adults$), since this was the group showing the largest effects of strategy training in the instructed relative to uninstructed gambling block. To determine the source of this effect, we compared performance on both blocks of the task (indexed by j), examining block-related effects by including a dummycoded block predictor variable in the analysis (Block_{*i*,*m*,*t*} = -1/1for uninstructed/instructed gambling, respectively), with additional predictor variables coding for the interaction of block with the Hi Prob and ΔEV trial-level variables. The results of this multiple regression analysis are presented in Table 2. Both the RA and EV-related parameters were found to be significant predictors of choice. Critically, however, training increased the influence of the EV-related predictor (as evidenced by the significant $\Delta EV \times Block$ interaction), but had no effect on the influence of the RA-related variable (the Hi Prob × Block interaction). This finding is consistent with the hypothesis that strategy training was effective because it promoted a goal of EV-based selection rather than promoting general affective control.

POTENTIAL EXPLANATIONS OF AGING EFFECTS

A second multiple regression analysis (Eq. 2) was conducted to examine the source of age differences (age indexed by m) that were observed in the instructed gambling block (block indexed by j; here j = instructed gambling), which indicated increased RA among OAs (participant indexed by i) on all 96 trials (trial indexed by t). We tested whether this apparent increased RA in OAs might be due relative inability to control the affective response to risk, which should be reflected in a relatively greater influence of Hi Prob, the RA-related predictor variable. Specifically, a plausible hypothesis is that relatively greater sensitivity to the affective consequences of risk among OAs interfered with their attempts to select based on EV in instructed gambling. To examine this hypothesis we compared performance of the OAs and YAs in the instructed gambling condition, examining age effects by including a dummy-coded age-group predictor variable in the analysis (Age_{*j*,*m*,*t* = -1/1 for YA/OAs, respectively), with additional predictor variables coding for the interaction of age group with the Hi Prob and Δ EV trial-level variables. The results of this regression analysis are presented in **Table 3**.}

$$logit\left(\frac{\sum_{i=1}^{k_{j,m,t}} RA responses_{i,j,m,t}}{k_{j,m,t}}\right)$$

= $\beta_0 + \beta_1 Hi \operatorname{Prob}_{j,m,t} + \beta_2 \Delta EV_{j,m,t} + \beta_3 Age_{j,m,t}$
+ $\beta_4 \Delta EV_{j,m,t} \times Age_{j,m,t} + \beta_4 Hi \operatorname{Prob}_{j,m,t}$
 $\times Age_{i,m,t} + \varepsilon_{i,m,t}$ (2)

This analysis provided no support for the affective response to risk hypothesis of aging effects. Although Hi Prob, the RA-related predictor, remained significant in the instructed gambling block,

Table 2 | Multiple regression of standardized, logit-transformed proportion of high probability choices among $k_{j,young,t} \leq 40$ younger adults on 96 independent trials with one RA-related predictor (the probability of the high probability option, Hi Prob), one EV-related predictor (the difference in EVs: \triangle EV), and a dummy variable for block.

Term	β	SE	t	p	
Hi Prob	0.20	0.04	4.68	<0.01	
ΔΕν	0.69	0.04	15.96	< 0.01	
Block	-0.26	0.04	-6.22	< 0.01	
$\Delta \text{EV} \times \text{block}$	0.21	0.04	4.97	< 0.01	
$Hi\:Prob\timesblock$	-0.01	0.04	-0.20	0.84	

Trial-level predictors were z-scored. $N = 2 \times 96 = 192$ (blocks × trials per block).

Table 3 | Multiple regression of the standardized, logit-transformed proportion of high probability choices on 96 independent trials in the instructed gambling block by *k* younger or older adults, with one RA-related predictor (Hi Prob), one EV-related predictor (\triangle EV), and a dummy-coded age variable.

Term	β	SE	t	p	
Hi Prob	0.17	0.05	3.69	<0.01	
$\Delta {\sf EV}$	0.70	0.05	14.46	< 0.01	
Age	0.15	0.05	3.31	< 0.01	
$\Delta \text{EV} imes \text{age}$	-0.30	0.05	-6.47	< 0.01	
Hi Prob × age	-0.04	0.05	-0.80	0.43	

Trial-level parameters were z-scored. $k_{j,m,t} \le 40/46$ for younger/older adults. N = 2 × 96 = 192 (age groups × trials per group). there was no interaction of this variable with age group. This suggests that the Hi Prob had no greater influence over choice in OAs. In contrast, a significant interaction of ΔEV and age was observed, the sign of which reflected reduced EV influence on choice among OAs. Thus, the results suggest that the apparent age-related increase in RA during the instructed gambling block was not due to a greater influence of probability on choice, but instead to the reduced influence of EV-related information in this age group, after explicit strategy training and instruction.

Another key prediction of the affective interference account is that more frequent (negative) feedback promotes risk-averse behavior (cf. Thaler et al., 1997). Thus, OAs might have shown reduced training effects because these were counteracted by experiences with negative feedback when selecting high-risk options. We tested for feedback effects by conducting a followup study with a second group of OAs (N = 40; $M_{age} = 74.0$, SD = 6.1, range = 66-88) who experienced the exact same paradigm and procedure but without trial-by-trial feedback regarding decision outcome eliminated in the last, post-training block (i.e., instructed gambling). Comparing the effect of training on RA in the two older adult groups in a 2×2 Training (uninstructed gambling vs. instructed gambling) × Feedback Group (present vs. absent) ANOVA, demonstrated that the main effect of training was still present [F(1, 84) = 29.25, p < 0.01, RA: $M_{\text{uninstructed}} = 0.54$, $M_{\text{instructed}} = 0.39$], but there was neither a significant main effect of Feedback [F(1, 84) = 2.18, p = 0.14, RA: $M_{\rm no-feedback} = 0.43, M_{\rm feedback} = 0.49$ nor Block × Feedback interaction [F(1, 84) = 2.14, p = 0.15]. Likewise, when comparing the no-feedback older adult group with the YAs, we replicated the Block \times Age interaction observed in the original analysis [F(1,(78) = 8.02, p < 0.01].

Alternative explanations for OAs' relatively higher RA after training include: an age-related impairment in the ability to compute and compare EVs, and an age-related bias toward a probability (as opposed to amount) maximization heuristic, independent of EV. Because the training block explicitly required participants to compute and select on the basis of EV, we used participants' average performance in this block as a measure of their EV-computation ability in a hierarchical regression analysis of individual RA in instructed gambling (Table 4). We also included their frequency of selecting the Hi Prob option on EQ trials as yet another predictor, reasoning that it represents a measure of how much participants' decisions are biased by probability (as opposed to amount) when their preference regarding EV is neutralized. This predictor was added after the EV-selection ability measure since a decisionmaker would have to compute EV correctly to know that that choice dimension was irrelevant on a given equivalence trial.

As expected, EV-computation ability explained a significant component of between-participants variance in average (averaged across an individual's choices) instructed gambling RA when controlling for baseline RA (in uninstructed gambling). Also, the bias to select based on probability (as measured by the tendency to select the Hi Prob option on EQ trials) in instructed gambling explained a significant amount of variance when controlling for baseline RA and EV-computation ability. Importantly, however, age was still a significant predictor of RA during instructed gambling even after controlling for uninstructed Table 4 | Hierarchical regression analysis of alternative explanations of relatively higher RA among older adults in instructed gambling including EV-selection ability and probability-based selection bias.

	β	SE	t	adj R ²	ΔR^2
STEP 1					
Baseline (uninstructed) RA	0.26	0.11	2.46*	0.07	-
STEP 2					
EV-computation ability	0.53	0.09	5.82**	0.32	0.25**
(EV-training block accuracy)					
STEP 3					
Probability-based selection	0.35	0.08	4.11**	0.43	0.11**
bias (EQ high-probability					
choice)					
STEP 4					
Age	0.86	0.15	5.73**	0.59	0.16**

*p < 0.05; **p < 0.01.

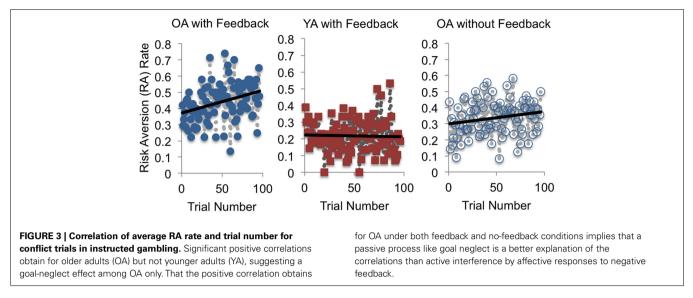
The dependent variable is the proportion of RA choices on conflict trials in instructed gambling across both age groups. All proportion data is logit-transformed then standardized. Age is dummy coded (-1/1 for younger/older adults).

gambling RA, EV-selection ability, and probability-based selection bias. This implies that even though EV-selection ability and probability-based selection bias constrained training efficacy, they do not fully explain the age differences in training effects.

AGING AND GOAL NEGLECT

Our preferred interpretation of OAs' increased propensity to revert to RA after training is that it reflects goal neglect, rather than affective interference, impaired EV-selection abilities, or some other bias to select on the single dimension of probability. The goal-neglect account suggests that even in the absence of active interference, OAs are more likely to commit goal-inconsistent behavior because their goal representations are particularly prone to progressive, but passive decay, when not supported by their environment (Duncan et al., 1996). A key prediction of this account is a decreasing tendency to select on the basis of EV, and a corresponding increase in RA, throughout the instructed gambling block. We tested this by computing the correlation between trial number and RA (Figure 3). Among OAs, a significant positive correlation was observed (r = 0.33, p < 0.01), while in YAs no such correlation was present (r = -0.03, p = 0.77). That is, selectively for OAs, there was a greater tendency to exhibit RA on conflict trials encountered later rather than earlier in the block (i.e., farther removed from training and instructions). The positive correlation was also obtained in the second, independent, sample of OAs who received no-feedback (r = 0.20, p = 0.049), providing further evidence that OAs' relative failure to maintain the goal of EV-based selection results from passive decay, rather than active feedback-related interference.

An alternative explanation for the steady rise in RA rates among OAs in the instructed gambling block, and one that we believe is incorrect, is that OAs were selectively fatigued by 96 consecutive decisions and thus were simply making more errors



as each block progressed. We do not believe this to be the correct explanation for multiple reasons. First, if OAs are prone to fatigue across 96 consecutive trials, we would expect to observe an increasing error rate across the 96 trials of the EV-training block, since in this participants are also explicitly instructed to engage in effortful EV computation. Instead of increasing errors, however, the error rate gradually decreased among OAs during EV training (r = -0.35, p < 0.01). Thus, rather than fatigue effects, OAs showed evidence of improvement, reflective of practice effects across the block.

An analysis of response times (RTs) also provides evidence against a fatigue account. Instead, it supports the goal-neglect consistent explanation that OAs attempted to implement the EV-selection strategy throughout the block, even though their resulting decisions were progressively less biased by their goal to select on the basis of EV. RT analyses are complicated by the fact that participants were not encouraged to respond rapidly, but instead given ample time to respond. However, it is still possible to make predictions regarding the RTs trends expected if participants were becoming fatigued. The average RT to conflict trials among OAs was slower in instructed (4489 ms) compared to uninstructed gambling [4101 ms; t(189) = -8.21, p < 0.01], implying that, as expected, the more complicated EV-selection strategy took longer to implement. If OAs suffered fatigue, their RTs should have either progressively increased, as they took still longer to implement the strategy, or progressively decreased, if they instead relinquished the more taxing strategy and utilized the simpler probability maximization heuristic. However, we observed neither of these trends. Instead, RTs on conflict trials were uncorrelated with trial number among OAs (r = -0.05, p = 0.701). Importantly, this stands in contrast to RT trends on the other two trial types, NC (r = -0.19, p = 0.06) and EQ (r = -0.28, p < 0.01), both of which showed a progressive drop in RTs, reflective of practice effects. Taken together, these two findings are inconsistent with a fatigue account: (a) OAs slowed down after EV instruction and then maintained this slowing on conflict trials, while (b) showing a progressive speeding on non-conflict and equivalence trials, demonstrating that RTs are sensitive to practice effects

occurring on some trials. The RT results are most consistent with the interpretation that OAs continued to treat conflict trials as a special case, despite the fact that they were increasingly likely to make the RA choice as the trials progressed. In other words, we suggest that OAs attempted utilize the EV-computation strategy throughout the instructed gambling block; however, as predicted by goal neglect, their behavior became progressively less biased by the goal to actually make selections on the basis of EV.

DISCUSSION

Our results have two important implications for understanding RA. First, we show that RA can be explained in terms of a lackof-insight regarding which decision-making strategy to employ to maximize returns. Simply orienting participants to the optimal EV-based strategy substantially reduced RA, without any effort to down-regulate automatic, affective biases. Conversely, mere practice at mental computation and selection of EV was not sufficient to reduce RA, demonstrating that the root problem was not an inability or unwillingness to mentally compute EV, but a failure to apply this as an optimal strategy. If practice was sufficient, then a significant reduction in RA should have occurred after the EV-training block, even before receiving explicit instructions. However, we found that the block order of EV training did not significantly affect the amount of benefit obtained by explicit instruction. Conscious insight obtained by explicit instruction was necessary to enable robust implementation of the newly practiced strategy. By suggesting that practice is insufficient to ameliorate RA, we leave open the possibility that spontaneous insight into the nature of the task acquired in the course of practice might indeed exert such a shift in strategy. In an independent set of data (Yarkoni, T., and Braver, T. S., in preparation), we have in fact observed an effect of block order that appears to be attributable to some participants spontaneously realizing that they can apply a maximizing strategy across multiple conditions. The critical point is that it is the strategic insight and not the practice at computing EV that is the essential element.

Second, the gradual return to risk-averse decision-making among OAs appeared to reflect passive decay of goal representations rather than the biasing effects of feedback toward affective responding. The complete removal of feedback did not have a significant effect on the amount of RA (though there was a slight numerical reduction) observed among a second group of OAs in a follow-up study. On the other hand, OAs displayed increasing RA for decisions farther removed from training, suggesting passive decay of representations of the goal to select on the basis of EV. The progressive rise occurred independent of feedback, demonstrating that cumulative feedback effects did not cause it. The progressive rise in RA was also specific to OAs; YAs showed no gradual decay in performance, consistent with the idea that OAs are particularly susceptible to goal neglect and the broader context of age-related decline in cognitive control (Duncan et al., 1996; De Jong, 2001; West, 2002; Nieuwenhuis et al., 2004; Braver and West, 2008).

Our study also adds to the growing literature examining the role of cognitive factors in older adult decision-making. Prior work has suggested that OAs tend to adopt simpler, less-demanding decision-making strategies (Kim et al., 2005; Rafaely et al., 2006; Peters et al., 2007), and that this might be explained in terms of age-related declines in fluid intelligence (Mata et al., 2007). Concomitantly, the mixed findings regarding whether aging is associated with increased RA per se (Dror et al., 1998; Bellante and Green, 2004; Deakin et al., 2004; Denburg et al., 2005; see Mather, 2006) have led some to argue that RA depends more on decisionmakers' cognitive capacities and the nature of the decision-making task, than on inherent effects of age. For example, a recent metaanalysis (Mata et al., 2011), found that age-related differences in risk preference tend to disappear when decision-makers are provided with explicit probability information as opposed to when they must learn about probabilities through experience. Our finding of equivalent baseline RA across age groups is consistent with this literature, since our task involves explicit probability information. Another recent study emphasized the role of the decision-makers' cognitive capacities rather than age by demonstrating that OAs can evince both relatively elevated risk seeking and elevated RA across tasks with different demands, and that outcomes are mediated by processing speed and working memory (Henninger et al., 2010). Our results agree in that under naïve conditions that are likely promote low-demand, heuristic decision strategies, OAs exhibit equivalent levels of RA to YAs. It was only when the task emphasized the cognitively demanding EV-selection strategy that age-related differences in RA emerged. Nevertheless, even though reduced cognitive capacities, such as working memory, may have limited the effectiveness of EV-strategy training in OAs, the data suggest it is not a full account of age differences, since these were present even after controlling for EV-selection ability.

These findings have important implications for both the theoretical understanding and practical remediation of decisionmaking deficits in OAs. If, as we have argued, such deficits result in part from passive decay of goal representations, efforts to improve older adult decision-making should focus on developing interventions that emphasize environmental support and contextual information, and not affect regulation. Evidence for

the potentially important role of environmental support can be found in a recent study of risky decision-making (Samanez-Larkin et al., 2011). In this study, one condition provided a visual representation of the running EV of options, thereby furnishing continuous, if implicit, environmental support for an EVselection strategy. Under this condition, performance improved for both older and YAs, with the older group matching YAs' baseline performance. Unlike our study, however, they did not instruct participants which strategy to use. Instead, participants came to utilize EV signals through reinforcement learning, an approach taken throughout much of the risky decision-making literature. The advantage of explicit insight is that decisionmakers in the real world are more commonly presented with single, one-off decisions for which the application of decontextualized, abstract decision strategies may be crucial. If individuals can be given insight, and supported by their environment to apply EV-selection strategies whenever they encounter a risky decision, they might make better choices even in entirely novel decisions.

Our account of the strategy training effects and putative goal neglect among OAs during instructed gambling implies specific predictions regarding neural mechanisms that could be tested in future imaging studies. One prediction that follows from our interpretation is that cognitive control processes related to task-set (goal) maintenance will be engaged preferentially in the instructed gambling block in order to implement the EV-selection strategy. Thus, we would expect to see a neural signature of this strategy in frontoparietal cognitive control networks. Indeed, in preliminary data from YAs, increased frontoparietal activity was observed when comparing the EV-training condition to uninstructed gambling (Yarkoni, 2010). We would further expect this pattern when comparing instructed to uninstructed gambling. A particular region of interest might be the anterior prefrontal cortex (aPFC). Sustained activity in this region has been thought to reflect abstract (or higher-order) task-set maintenance (Braver and Bongiolatti, 2002; Braver et al., 2003; Sakai, 2008). In the context of decision-making, increased sustained activity in aPFC has been observed when decision strategies needed to be maintained across a temporally extended interval (Yarkoni et al., 2005). Thus, we predict increased sustained activity in aPFC in instructed compared to uninstructed gambling, but similar activity in EV practice and instructed gambling. Further, the degree of similarity between EV practice and instructed gambling should predict behavioral findings of greater EV maximization during instructed gambling.

Brain activity dynamics can also provide a convergent test of our account of the age-related findings observed here. As the behavioral signature of goal neglect was a progressive rise in RA, the neural signature of goal neglect would be a progressive decay in sustained aPFC activity, reflecting the loss of task-set. Such a finding would be consistent with prior work, which demonstrated a reduction in sustained aPFC activity among OAs during task-switching, a pattern that was also interpreted as impaired task-set maintenance (Jimura and Braver, 2010). Finally, it would be useful to examine activity dynamics in brain regions responsive to risk and negative feedback (e.g., insula, amygdala, anterior cingulate cortex; Kahn et al., 2002; Kuhnen and Knutson, 2005; Brown and Braver, 2007). Our interpretation of the results is that training and age effects are not due to an altered response to risk and/or negative feedback; thus, we predict that these regions would be active during the gambling conditions (but not EV training, which eliminates the risk component of decision-making), and would show equivalent activity in younger and OAs, along with no decrease in activity among these regions when comparing in instructed to uninstructed gambling. Together, this pattern of imaging results would provide strong support that an interaction of insight and age-related cognitive control processes, such as task-set maintenance, are what differentiate age groups, but not necessarily the affective response to risk.

Our preferred interpretation of the steady return to RA among OAs is age-related goal neglect. Other interpretations are possible, however. OAs may have evinced increasing RA because they progressively abandoned the EV-selection strategy for other unknown reasons. For example, it may have been an intentional decision (instead of an implicit one, based on goal maintenance difficulties), made because of progressive discomfort with utilizing the novel instructed strategy, relative to their greater familiarity and experience in using more heuristic, risk-based decisionmaking strategies. OAs may have experienced this familiarity asymmetry between experienced-based and the instructed strategy more acutely than YAs, given their longer life-time of experience. However, we did assess compliance with the instructions in a post-experiment debriefing questionnaire, and there was no indication of any participant intentionally switching strategies during the instructed gambling block. Indeed, most participants explicitly reported utilizing the instructed strategy throughout the whole block (in a few cases the question was either not answered, the answer was ambiguous, or, in the case of one participant, the instructions were misunderstood). Nevertheless, in future studies, it may be useful to examine this issue more systematically.

A related account, and one that was not considered in our original design, relates to the age-dependent experience of arousal and emotion regulation. OAs tend to experience arousing stimuli as more aversive than YAs (Keil and Freund, 2009). Despite their relatively enhanced emotion regulation strategies, sustained durations of emotional distress may be more difficult for OAs to overcome (for a review, see Charles, 2010). If selecting the riskier (low probability) option on conflict trials causes arousal in a way that OAs find increasingly aversive and difficult to cope with, they may have found the instructed strategy more discomforting to implement, and instead would develop an accumulating bias against the high-EV option, as it acquires a punishing character. This would be true even for the group of OAs who received no-feedback (and therefore no error signals), because the arousal associated with greater risk taking itself is aversive. However, if OAs are sensitive to the negative valence of arousal associated with risk taking in this paradigm, it is unclear why they would not also be sensitive to the valence consequences of feedback. The fact that feedback did not influence OAs' RA therefore implies that affective consequences of arousal were not the primary driver of RA among OAs. Nevertheless, more rigorously determining whether the age-related experience of arousal influenced decision-making for OAs would require independent measures of arousal, which were not collected. Hence we cannot rule out that arousal-related aversion to risk taking contributed to what we believe to be age-related goal neglect. The mechanisms that contribute to goal neglect are themselves not fully understood. It is thus possible that goal neglect could be influenced by reinforcement learning (as from punishing arousal) about co-existing, competing goals. Future study is required to understand how aversive arousal may contribute to goal neglect among OAs.

Finally, while we have explained the efficacy of our insight manipulation in terms of task-sets and the proper weighting of choice dimensions (probability and amount in EV), we note that our results could also be accounted for by the behavioral economic theory of "narrow framing" (Barberis et al., 2006; Barberis and Huang, 2009). Narrow framing means that the consequences of a gamble are considered in isolation rather than in the context of the decision-maker's overall risk profile (including, for example, their income and housing risks). According to the theory, a decision-maker may avoid an independent, actuarially favorable gamble because they do not weigh the benefit of diversifying their risk portfolio, focusing instead on the potential regret associated with losing the gamble. While our results are consistent with helping participants overcome narrow framing, our manipulation was directed at changing participants' task construal such that they select on the basis of EV. We did not explicitly manipulate whether participants were instructed to select choices in the context of their overall risk profile. Other studies that have done so have found significant changes in individuals' risk preference parameters. For example, van der Heijden et al. (2011) incited decision-makers to consider multiple gambles at once and found a reduction in RA relative to when they considered single gambles in isolation, consistent with the narrow framing theory. Similarly, Guiso (2009) saw a reduction in RA when participants were asked to consider their future income probability distribution prior to considering a gamble. Future work may consider whether our manipulation promoting a strategy of EV-based selection is convergent with the economic concept of narrow framing.

The primary conclusion of our study is that insight and strategy training can yield better decision-making, but the benefits may be constrained by age-related factors that impact the decisionmaker's ability or willingness to implement the trained strategy. We hypothesize that one important factor to consider is cognitive control and goal maintenance ability. If correct, this hypothesis suggests that apparent RA might manifest under situations in which cognitive control demands drive decision-making. In contrast, under naïve situations, RA may reflect most prominently a lack of knowledge about which strategies are optimal and a lack of practice in implementing them. The benefits of insight were not trivial in our paradigm. Knowing about EV-selection prompted many more decision-makers to take calculated risks. To illustrate, consider a decision between a 90% chance of 200 points and a 20% chance of 1000 points. Prior to training, 56 out of 86 (65%) decision-makers chose the 200-point "safe-bet." After training, that number reduced to 23, with 73% of participants (63 out

of 86) instead preferring the riskier (but higher EV) 1000-point option. Our findings suggest that the role of strategy and insight in decision-making under risk have been underappreciated, and

REFERENCES

- Barberis, N., and Huang, M. (2009). Preferences with frames: a new utility specification that allows for the framing of risks. J. Econ. Dyn. Control 33, 1555–1576.
- Barberis, N., Huang, M., and Thaler, R. H. (2006). Individual preferences, monetary gambles, and stock market participation: a case for narrow framing. *Am. Econ. Rev.* 1069–1090.
- Bellante, D., and Green, C. A. (2004). Relative risk aversion among the elderly. *Rev. Financ. Econ.* 13, 269–281.
- Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., and Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychol. Rev.* 108, 624–652.
- Braver, T. S., and Bongiolatti, S. R. (2002). The role of frontopolar cortex in subgoal processing during working memory. *Neuroimage* 15, 523–536.
- Braver, T. S., Reynolds, J. R., and Donaldson, D. I. (2003). Neural mechanisms of transient and sustained cognitive control during task switching. *Neuron* 39, 713–726.
- Braver, T. S., and West, R. (2008). "Working memory, executive control, and aging," in *The Handbook of Aging and Cognition*, 3rd Edn, eds F. I. M. Craik and T. A. Salthouse (New York, NY: Psychology Press), 311–372.
- Brown, J. W., and Braver, T. S. (2007). Risk prediction and aversion by anterior cingulate cortex. *Cogn. Affect. Behav. Neurosci.* 7, 266–277.
- Butler, K. M., and Zacks, R. T. (2006). Age deficits in the control of prepotent responses: evidence for an inhibitory decline. *Psychol. Aging* 21, 638–643.
- Charles, S. T. (2010). Strength and vulnerability integration: a model of emotional well-being across adulthood. *Psychol. Bull.* 136, 1068–1091.
- De Jong, R. (2001). Adult age differences in goal activation and goal maintenance. *Eur. J. Cogn. Psychol.* 13, 71–89.
- Deakin, J., Aitken, M., Robbins, T., and Sahakian, B. J. (2004). Risk taking during decision-making in

normal volunteers changes with age. J. Int. Neuropsychol. Soc. 10, 590–598.

- Denburg, N. L., Tranel, D., and Bechara, A. (2005). The ability to decide advantageously declines prematurely in some normal older persons. *Neuropsychologia* 43, 1099–1106.
- Dror, I. E., Katona, M., and Mungur, K. (1998). Age differences in decision making: to take a risk or not?. *Gerontology* 44, 67–71.
- Duncan, J., Emslie, H., Williams, P., Johnson, R., and Freer, C. (1996). Intelligence and the frontal lobe: the organization of goaldirected behavior. *Cogn. Psychol.* 30, 257–303.
- Dunlosky, J., and Kane, M. J. (2007). The contributions of strategy use to working memory span: a comparison of strategy assessment methods. Q. J. Exp. Psychol. 60, 1227–1245.
- Epstein, S. (1994). Integration of the cognitive and the psychodynamic unconscious. *Am. Psychol.* 49, 709–724.
- Guiso, L. (2009). A Test of Narrow Framing and Its Origin (Working paper No. ECO 2009/02). European University Institute. Available at: http:// cadmus.eui.eu/bitstream/handle/ 1814/10169/ECO_2009_02.pdf
- Hare, T. A., Camerer, C. F., and Rangel, A. (2009). Self-control in decisionmaking involves modulation of the vmPFC valuation system. *Science* 324, 646–648.
- Hartley, A. A., and Anderson, J. W. (1986). Instruction, induction, generation, and evaluation of strategies for solving search problems. *J. Gerontol.* 41, 650–658.
- Henninger, D. E., Madden, D. J., and Huettel, S. A. (2010). Processing speed and memory mediate age-related differences in decision making. *Psychol. Aging* 25, 262–270.
- Holt, C. A., and Laury, S. K. (2002). Risk aversion and incentive effects. *Am. Econ. Rev.* 92, 1644–1655.
- Jimura, K., and Braver, T. S. (2010). Age-related shifts in brain activity dynamics during task switching. *Cereb. Cortex* 20, 1420–1431.
- Kahn, I., Yeshurun, Y., Rotshtein, P., Fried, I., Ben Bashat, D., and Hendler, T. (2002). The role of

could lead to the development of new intervention programs designed to remediate decision-making deficits in both younger and older adults.

the amygdala in signaling prospective outcome of choice. *Neuron* 33, 983–994.

- Kahneman, D., and Tversky, A. (1979). Prospect theory: an analysis of decision under risk. *Econometrica* 47, 263–291.
- Keil, A., and Freund, A. M. (2009). Changes in the sensitivity to appetitive and aversive arousal across adulthood. *Psychol. Aging* 24, 668.
- Kim, S., Goldstein, D., Hasher, L., and Zacks, R. T. (2005). Framing effects in younger and older adults. J. Gerontol. B Psychol. Sci. Soc. Sci. 60, P215–P218.
- Kuhnen, C. M., and Knutson, B. (2005). The neural basis of financial risk taking. *Neuron* 47, 763–770.
- Loewenstein, G. F., Weber, E. U., Hsee, C. K., and Welch, N. (2001). Risk as feelings. *Psychol. Bull.* 127, 267–286.
- Mata, R., Josef, A. K., Samanez-Larkin, G. R., and Hertwig, R. (2011). Age differences in risky choice: a metaanalysis. *Ann. N. Y. Acad. Sci.* 1235, 18–29.
- Mata, R., Schooler, L. J., and Rieskamp, J. (2007). The aging decision-maker: cognitive aging and the adaptive selection of decision strategies. *Psychol. Aging* 22, 796–810.
- Mata, R., von Helversen, B., and Rieskamp, J. (2010). Learning to choose: cognitive aging and strategy selection learning in decision making. *Psychol. Aging* 25, 299–309.
- Mather, M. (2006). "A review of decision-making processes: weighing the risks and benefits of aging," in When I'm 64. Committee on Aging Frontiers in Social Psychology, Personality Developmental Psychology, ed. C. R. Hartel (Washington, DC: The National Academies Press), 145–173.
- McNamara, D. S., and Scott, J. L. (2001). Working memory capacity and strategy use. *Mem. Cognit.* 29, 10–17.
- Nieuwenhuis, S., Broerse, A., Nielen, M. M. A., and DeJong, R. (2004). A goal activation approach to the study of executive function: an application to antisaccade tasks. *Brain Cogn.* 56, 198–214.
- Park, D. C., and Reuter-Lorenz, P. (2009). The adaptive brain: aging and neurocognitive scaffolding. *Annu. Rev. Psychol.* 60, 173–196.

- Paxton, J. L., Barch, D. M., Storandt, M., and Braver, T. S. (2006). Effects of environmental support and strategy training on older adults' use of context. *Psychol. Aging* 21, 499–509.
- Peters, E., Hess, T. M., Västfjäll, D., and Auman, C. (2007). Adult age differences in dual information processes: implications for the role of affective and deliberative processes in older adults' decision making. *Perspect. Psychol. Sci.* 2, 1–23.
- Rafaely, V., Dror, I. E., and Remington, B. (2006). Information selectivity in decision making by younger and older adults. *Int. J. Psychol.* 41, 117–131.
- Saczynski, J. S., Willis, S. L., and Schaie, K. W. (2002). Strategy use in reasoning training with older adults. *Neuropsychol. Dev. Cogn. B Aging Neuropsychol. Cogn.* 9, 48–60.
- Sakai, K. (2008). Task set and prefrontal cortex. Annu. Rev. Neurosci. 31, 219–245.
- Salthouse, T. A. (1990). Working memory as a processing resource in cognitive aging. *Dev. Rev.* 10, 101–124.
- Samanez-Larkin, G. R., Wagner, A. D., and Knutson, B. (2011). Expected value information improves financial risk taking across the adult life span. Soc. Cogn. Affect. Neurosci. 6, 1–11.
- Slovic, P., Peters, E., Finucane, M. L., and MacGregor, D. G. (2005). Affect, risk, and decision making. *Health Psychol.* 24(Suppl. 4), S35–S40.
- Thaler, R. H., Tversky, A., Kahneman, D., and Schwartz, A. (1997). The effect of myopia and loss aversion on risk taking: an experimental test. *Q. J. Econ.* 112, 647–661.
- Touron, D. R., and Hertzog, C. (2004). Distinguishing age differences in knowledge, strategy use, and confidence during strategic skill acquisition. *Psychol. Aging* 19, 452–466.
- van der Heijden, E., Klein, T., Müller, W., and Potters, J. J. (2011). Nudges and Impatience: Evidence from a Large Scale Experiment (Working Paper No. 1110). University of Vienna. Available at: http:// homepage.univie.ac.at/Papers.Econ/ RePEc/vie/viennp/vie1110.pdf
- Warton, D. I., and Hui, F. K. C. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92, 3–10.

- West, R. (2002). Lapses of intention and performance variability reveal agerelated increases in fluctuations of executive control. *Brain Cogn.* 49, 402–419.
- Yarkoni, T. (2010). The Role of Strategy in Decision-Making Under Risk: An fMRI Investigation. Doctoral Dissertation, ProQuest Dissertations and Theses database, (Pub. No. AAT 3368691), Saint Louis.
- Yarkoni, T., Gray, J. R., Chrastil, D. M., Barch, D., Green, L., and Braver, T. S. (2005). Sustained neural activity associated with cognitive control during temporally extended decision making. *Brain Res. Cogn. Brain Res.* 23, 71–84.
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APPENDIX

Table A1 | Parameters for each of the 96 trials as well as average rate of risk aversion on each trial both in uninstructed gambling (UG) and instructed gambling (IG), after the training; Trial types include conflict (CF), Non-conflict (NC), for which the high expected value option also has the higher probability, and Equivalence (EQ) trials for which the expected value of the two options is equivalent.

Trial type	Low	-risk	High	n-risk		Older adults			Younger	adults
	Prob.	Amt.	Prob.	Amt.	UG	IG	Change in RA*	UG	IG	Change in RA*
CF	1	100	0.2	750	0.54	0.49	-0.05	0.85	0.23	-0.63
CF	0.7	100	0.2	500	0.65	0.41	-0.24	0.73	0.15	-0.58
CF	0.7	300	0.4	750	0.68	0.47	-0.21	0.73	0.18	-0.55
CF	0.7	100	0.4	250	0.57	0.50	-0.07	0.75	0.20	-0.55
CF	1	100	0.6	250	0.57	0.55	-0.03	0.75	0.21	-0.54
CF	0.7	100	0.1	750	0.51	0.49	-0.02	0.78	0.23	-0.54
CF	0.7	100	0.2	750	0.57	0.36	-0.20	0.65	0.13	-0.53
CF	0.9	200	0.4	500	0.57	0.41	-0.17	0.68	0.15	-0.53
CF	0.9	200	0.2	1000	0.60	0.34	-0.26	0.70	0.18	-0.53
CF	0.9	100	0.4	250	0.53	0.51	-0.02	0.85	0.35	-0.50
CF	0.9	100	0.2	500	0.64	0.53	-0.11	0.70	0.20	-0.50
CF	0.7	400	0.4	750	0.68	0.70	0.01	0.78	0.31	-0.47
CF	0.7	100	0.1	1000	0.46	0.28	-0.18	0.55	0.10	-0.45
CF	0.9	400	0.4	1000	0.53	0.38	-0.15	0.50	0.08	-0.43
CF	0.9	100	0.2	1000	0.40	0.41	0.01	0.48	0.05	-0.43
CF	0.7	200	0.2	750	0.72	0.47	-0.26	0.78	0.38	-0.40
CF	1	300	0.4	1000	0.50	0.67	0.17	0.55	0.15	-0.40
CF	0.9	300	0.4	1000	0.49	0.30	-0.19	0.45	0.08	-0.38
CF	0.9	100	0.1	1000	0.59	0.48	-0.11	0.50	0.13	-0.38
CF	0.7	200	0.2	1000	0.55	0.37	-0.18	0.43	0.08	-0.35
CF	0.5	100	0.2	750	0.44	0.65	0.21	0.45	0.10	-0.35
CF	0.9	300	0.6	500	0.68	0.49	-0.19	0.68	0.40	-0.28
CF	0.5	200	0.2	1000	0.50	0.33	-0.17	0.38	0.10	-0.28
CF	0.5	100	0.2	500	0.45	0.36	-0.09	0.38	0.10	-0.28
CF	0.5	300	0.2	1000	0.50	0.46	-0.04	0.35	0.08	-0.28
CF	0.9	300	0.4	750	0.72	0.64	-0.09	0.83	0.55	-0.28
CF	0.9	400	0.6	750	0.61	0.62	0.01	0.73	0.46	-0.26
CF	0.7	200	0.6	250	0.72	0.68	-0.04	0.68	0.43	-0.25
CF	0.7	200	0.4	1000	0.43	0.24	-0.19	0.28	0.03	-0.25
CF	0.7	400	0.4	1000	0.49	0.43	-0.06	0.30	0.05	-0.25
CF	0.5	300	0.4	500	0.40	0.28	-0.12	0.28	0.08	-0.20
EQ	1	200	0.4	500	0.76	0.72	-0.03	0.88	0.68	-0.20
CF	0.7	400	0.6	500	0.45	0.30	-0.14	0.58	0.38	-0.19
EQ	1	300	0.6	500	0.43	0.81	-0.02	0.93	0.75	-0.18
EQ	1	100	0.2	500	0.76	0.77	0.01	0.88	0.70	-0.18
CF	0.6	250	0.5	400	0.49	0.16	-0.33	0.23	0.05	-0.18
EQ	0.5	200	0.0	1000	0.43	0.60	-0.14	0.63	0.45	-0.18
EQ	0.5	200	0.2	500	0.68	0.81	0.13	0.85	0.43	-0.17
EQ	0.6	200 250	0.2	300	0.08	0.81	-0.03	0.60	0.08	-0.17
CF	0.0	100	0.5	1000	0.47	0.43	-0.10	0.00	0.44	-0.15
EQ	0.9	300	0.4	750	0.48 0.68	0.38	0.08	0.18	0.03	-0.13 -0.13
EQ	0.5 1	300	0.2	750 750	0.88	0.76	0.08	0.75	0.82	-0.13 -0.13
CF	0.7	300	0.4 0.6	750 500	0.78	0.85	-0.12	0.90	0.77	-0.13 -0.13
NC	0.7	300 100	0.8	250	0.34 0.87	0.22	-0.09	0.23	0.10	-0.13 -0.13
EQ	0.9 1	100	0.2 0.4	250 250	0.87	0.79	-0.09 -0.02	0.98 0.95	0.85	-0.13 -0.13
CF	0.5	100	0.4 0.4	250 250	0.79	0.77	-0.02 -0.13	0.95	0.83	-0.13 -0.10
EQ	0.5	100	0.2	250	0.83	0.77	-0.06	0.78	0.68	-0.10

(Continued)

Table A1 | Continued

Trial type	rpe Low-risk		High	ı-risk		Older adults			Younger adults			
	Prob.	Amt.	Prob.	Amt.	UG	IG	Change in RA*	UG	IG	Change in RA*		
CF	1	400	0.6	750	0.79	0.83	0.04	0.78	0.68	-0.10		
EQ	1	400	0.4	1000	0.66	0.79	0.13	0.73	0.63	-0.10		
EQ	0.5	400	0.2	1000	0.70	0.64	-0.06	0.65	0.58	-0.08		
EQ	1	200	0.2	1000	0.66	0.61	-0.05	0.75	0.68	-0.08		
NC	1	300	0.4	500	0.91	0.89	-0.03	0.98	0.90	-0.08		
EQ	0.5	200	0.4	250	0.74	0.73	-0.01	0.75	0.68	-0.08		
NC	0.9	300	0.2	1000	0.85	0.81	-0.04	0.85	0.79	-0.06		
NC	1	400	0.4	500	0.87	0.83	-0.04	1.00	0.95	-0.05		
NC	1	200	0.2	250	0.89	0.89	0.00	1.00	0.95	-0.05		
NC	1	200	0.6	250	0.89	0.89	0.00	1.00	0.95	-0.05		
NC	0.6	500	0.5	100	0.87	0.91	0.04	1.00	0.95	-0.05		
NC	1	100	0.1	500	0.83	0.91	0.09	0.98	0.93	-0.05		
NC	0.6	750	0.5	400	0.82	0.76	-0.07	0.98	0.95	-0.03		
NC	0.9	200	0.4	250	0.87	0.85	-0.02	0.98	0.95	-0.03		
NC	0.7	300	0.2	500	0.89	0.89	0.00	0.98	0.95	-0.03		
NC	0.7	100	0.2	250	0.74	0.76	0.02	0.98	0.95	-0.03		
NC	1	100	0.1	250	0.87	0.91	0.04	1.00	0.98	-0.03		
NC	1	300	0.2	750	0.81	0.87	0.06	1.00	0.98	-0.03		
NC	1	400	0.6	500	0.87	0.96	0.09	0.98	0.95	-0.03		
EQ	1	100	0.1	1000	0.70	0.81	0.11	0.75	0.73	-0.03		
CF	0.5	200	0.4	1000	0.37	0.11	-0.26	0.05	0.03	-0.03		
NC	1	200	0.2	750	0.79	0.76	-0.03	0.95	0.93	-0.02		
NC	0.9	400	0.4	750	0.85	0.89	0.04	0.93	0.92	0.00		
NC	0.9	200	0.2	750	0.85	0.83	-0.02	0.93	0.93	0.00		
NC	0.9	400	0.2	500	0.83	0.85	0.02	1.00	1.00	0.00		
NC	1	400	0.1	1000	0.85	0.87	0.02	0.95	0.95	0.00		
NC	0.7	400	0.1	250	0.93	0.96	0.02	1.00	1.00	0.00		
NC	1	400	0.4	750	0.85	0.89	0.04	0.93	0.93	0.00		
NC	1	300	0.2	250	0.00	0.96	0.04	0.98	0.98	0.00		
NC	1	300	0.2	250 750	0.31	0.30	0.12	1.00	1.00	0.00		
NC	0.7	300	0.1	500	0.78	0.83	0.01	0.80	0.83	0.02		
NC	0.9	300	0.4	500	0.82	0.83	-0.13	0.80	0.83	0.02		
NC	0.9	400	0.4	500	0.89	0.77	-0.09	0.95	0.93	0.03		
NC	0.5	400	0.0	250	0.89	0.81	-0.09	0.95	1.00	0.03		
NC	0.5	400 200	0.1	1000	0.87	0.79	-0.09	0.98	0.85	0.03		
NC	0.7	200 300	0.6	250	0.87	0.83	0.02	0.83	1.00	0.03		
NC	0.9	300					0.02	0.98	0.98	0.03		
			0.6	250	0.79	0.81						
NC	0.7	400	0.1	500	0.77	0.79	0.02	0.98	1.00	0.03		
NC	0.9	200	0.6	250	0.77	0.83	0.06	0.95	0.98	0.03		
NC	0.6	1000	0.5	100	0.85	0.96	0.11	0.98	1.00	0.03		
NC	0.9	200	0.1	500	0.81	0.74	-0.07	0.95	1.00	0.05		
NC	0.9	200	0.1	750 750	0.85	0.83	-0.02	0.95	1.00	0.05		
NC	0.5	400	0.2	750	0.83	0.82	-0.01	0.88	0.93	0.05		
NC	0.5	300	0.1	250	0.89	0.93	0.04	0.95	1.00	0.05		
NC	1	100	0.1	750	0.87	0.96	0.09	0.85	0.95	0.10		
NC	0.9	100	0.1	750	0.78	0.89	0.11	0.88	0.98	0.10		
EQ	0.5	100	0.1	500	0.64	0.71	0.07	0.55	0.68	0.13		
NC	0.5	200	0.1	750	0.79	0.89	0.11	0.75	0.95	0.20		
NC	0.7	100	0.1	500	0.87	0.85	-0.02	0.78	1.00	0.23		

*Change in RA refers to the change in the frequency of selecting the high probability option, which, during conflict trials, was the operational measure of RA in our study.



Effects of Age, Sex, and Neuropsychological Performance on Financial Decision-Making

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Natalie L. Denburg, Department of Neurology, University of Iowa Hospitals and Clinics, #2007 RCP, 200 Hawkins Drive, Iowa City, IA 52242-1053, USA. e-mail: natalie-denburg@uiowa.edu The capacity to make sound financial decisions across the lifespan is critical for interpersonal, occupational, and psychological health and success. In the present study, we explored how healthy younger and older adults make a series of increasingly complex financial decisions. One-hundred sixteen healthy older adults, aged 56-90 years, and 102 college undergraduates, completed the Financial Decision-Making Questionnaire, which requires selecting and justifying financial choices across four hypothetical scenarios and answering questions pertaining to financial knowledge. Results indicated that Older participants significantly outperformed Younger participants on a multiple-choice test of acquired financial knowledge. However, after controlling for such pre-existing knowledge, several age effects were observed. For example, Older participants were more likely to make immediate investment decisions, whereas Younger participants exhibited a preference for delaying decision-making pending additional information. Older participants also rated themselves as more concerned with avoiding monetary loss (i.e., a prevention orientation), whereas Younger participants reported greater interest in financial gain (i.e., a promotion orientation). In terms of sex differences, Older Males were more likely to pay credit card bills and utilize savings accounts than were Older Females. Multiple positive correlations were observed between Older participants' financial decision-making ability and performance on neuropsychological measures of non-verbal intellect and executive functioning. Lastly, the ability to justify one's financial decisions declined with age, among the Older participants. Several of the aforementioned results parallel findings from the medical decision-making literature, suggesting that older adults make decisions in a manner that conserves diminishing cognitive resources.

Keywords: aging, decision-making, financial, cognition

INTRODUCTION

The population of the United States (US) has undergone a dramatic age shift in the last 10 years. To ignore predictions that this trend will significantly accelerate in future years may have catastrophic societal ramifications. In 2008, approximately 39 million US citizens were age 65 or older, constituting nearly 13% of Americans (Federal Interagency Forum on Aging-Related Statistics, 2010). However, as the baby boomer generation enters this age bracket, the older adult population is forecasted to exceed 70 million Americans by 2030, totaling one-fifth of the US population (He et al., 2005). In fact, with nearly every country anticipated to undergo dramatic population aging in the near future, major implications throughout the economic, social, and political world can be expected (United Nations, 2009).

In the US, the growing population of older adults will be characterized by increased racial diversity and higher educational attainment than any preceding generation, as well as a net worth that has risen 80% in the last 20 years (Federal Interagency Forum on Aging-Related Statistics, 2010). Increasing longevity, geographical dispersion, and the modern emphasis on self-reliance will require older adults to maintain complex decision-making faculties as they age (Finucane et al., 2002). Financial decision-making abilities, in particular, will be critical for this population segment, which has benefited from a higher level of prosperity than any of its elder generational predecessors, as measured by a steady rise in incomes for older Americans since 1976 and a decrease in elders living below the poverty line (Federal Interagency Forum on Aging-Related Statistics, 2010).

To increase the opportunities available to older adults and facilitate optimal decision-making, lawmakers often assume that more information and disclosures will help elders tailor choices to their specific needs and desires. It remains unclear, however, whether older adults are able to use such information to their benefit in complex domains, such as health care or financial decisionmaking. In an analysis of decision-making capacity when evaluating health care plans, Finucane et al. (2002) found that older adults displayed inferior comprehension, regardless of the information being presented and the complexity of the question. As age increased, participants revealed significantly more comprehension errors and slightly greater inconsistencies in preference when choosing a health plan, even after controlling for sex, education, income, health, self-rated skill, and attitude. Considering the simplicity of their stimuli compared to real-world health care contracts, the rate of comprehension difficulties among older adults warrants cause for serious concern (Finucane et al., 2002).

These findings are in keeping with literature regarding the effects of marketing on older consumers (John and Cole, 1986; Yoon et al., 2009), which suggest that older adults may encounter difficulties in decision-making when presented with large amounts of data. The most significant declines in decision-making performance by older consumers occurred during unfamiliar tasks that contained large quantities of information, had formats that hindered encoding, with limited guidance to aid information processing, and demanding answer formats. These authors recommended that future experimental stimuli (as well as public policy) targeting older adults focus on keeping information limited, well organized, and integrated with visual stimuli as appropriate.

The need for well-validated measures of decision-making capacity able to assess individual fitness to perform a task or make a decision autonomously will only rise as the population of older adults grows, with simultaneously increasing rates of cognitive deficits, dementia, other medical and neurological illnesses, and risk for elder abuse or exploitation within this group. This task is formidable, as no widely accepted instrumental validity standard for capacity assessment currently exists, with prior assessments having been made on the presence or absence of a medical diagnosis or global indicator of mental status (Move and Marson, 2007). Of course, an additional important goal for future measures must be their ability to be tailored to individuals so that areas in need of protection can be identified without disqualifying or restricting rights in which full capacity remains. With the shift to identification and assessment of such task-related capacity domains, it becomes equally necessary to validate new measures - and new constructs - using convergence with other indicators of capacity (i.e., clinical diagnosis), cognitive tests, and consistency over time (Moye and Marson, 2007). One critical area for future assessment will be financial decision-making competence, as this skill is crucial not only to retaining autonomy in society, but also requires the use of intact higher-order cognitive functioning (Moye and Marson, 2007).

The majority of work assessing financial skill has been carried out in neurological populations. Marson et al. (2000) created the Financial Capacity Instrument (FCI), a standardized, psychometric, technician-administered instrument based on their tripartite model which views financial decision-making as requiring: (1) basic declarative knowledge (e.g., knowledge of currency); (2) procedural knowledge (e.g., writing checks); and (3) higherorder judgment, or the ability to evaluate novel or ambiguous situations and make financial decisions in one's best interest (Moye and Marson, 2007). Not surprisingly, patients with mildly severe Alzheimer's disease demonstrated emerging global impairment across most financial tasks and most domains, whereas patients with moderately severe Alzheimer's disease demonstrated advanced global impairment across all financial tasks and domains (Marson et al., 2000). Defects in complex financial skills, such as checkbook management and bank statement management, were also observed in individuals with mild cognitive impairment as

compared to healthy older adults. Furthermore, patients with MCI who had converted to Alzheimer's disease by the 1-year follow-up exhibited significantly greater declines in procedural skills, such as bill payment and cash transactions, despite intact conceptual understanding of each item (Triebel et al., 2009).

Lusardi (2010) examined the financial capabilities of the American public across four general domains: living within one's means, planning for the future, navigating financial products (e.g., credit cards, stocks, mortgages), and financial literacy. Data from the National Financial Capability Study showed that the average American reports higher levels of knowledge than those actually displayed on tests of financial capacity, and that the costs of such disparity is being evidenced in failure to plan for retirement or emergencies and poor investment choices, particularly among those with low income and education.

In a study of financial knowledge and its relation to successful retirement planning, Lusardi and Mitchell (2011b) found that only 50% of adults aged 50 years and older could correctly respond to questions regarding interest compounding and inflation. Moreover, less than 20% of the older adult sample felt that their retirement planning had been successful, with those displaying the highest levels of financial knowledge being most likely to have placed money in savings accounts or more complex investments (e.g., stocks, mutual funds) (Boersch-Supan and Essig, 2005).

International research shows high rates of financial illiteracy in both well-developed markets, such as Germany, Japan, and Sweden, as well as those that are quickly changing (e.g., Russia). Individuals with the highest level of financial knowledge are the most likely to successfully plan for their own retirement, however, older adults have been shown across numerous countries to routinely overestimate their level of financial knowledge when asked to complete basic financial measures (Lusardi and Mitchell, 2011a). A longitudinal study of the investment strategies of German nationals found that over 70% of the German population had their assets in a conventional savings account, whereas only 20% of older adults reported holding any stocks or mutual funds compared with 40% of younger adults (aged 35 years and below). Though younger adults placed a larger portion of their income into savings accounts relative to older adults, the latter were considerably more likely to report that they "always have a lot" or "often have some" money left at the end of each month.

The anterior portion of the frontal lobe, responsible for reasoning, judgment, decision-making, and emotional processing, is a brain area that may be critical for sound financial decision-making ability. A series of studies by Denburg et al. (2005, 2006, 2007) and Denburg and Harshman (2010) showed that a sizeable portion of neurologically and psychiatrically healthy older adults might nevertheless suffer from impaired decision-making skills due to subclinical dysfunction within a neural system that includes the ventromedial prefrontal cortex (VMPC). Age-related declines were evidenced by a large subset of healthy, older adults (35-40%) using the Iowa Gambling Task (IGT; Bechara, 2007), a well-validated laboratory test of decision-making. Compared to unimpaired older adults, those with decision-making deficits ("impaired") failed to shift their choices from Bad to Good decks as the task progressed, instead making disadvantageous choices throughout, in a manner consistent with VMPC lesion patients (Denburg et al., 2005). Too,

these impaired older adults evidenced abnormal somatic states (Denburg et al., 2006) as well as higher rates of falling prey to misleading and deceptive advertising (Denburg et al., 2007).

The present study involved an exploratory analysis examining how healthy younger and older adults make a series of increasingly complex financial decisions. Additionally, among the older adults, we examined how males and females may differ in their financial decision-making. Finally, the association between neuropsychological (i.e., intelligence, attention, working memory, numerical skill, visual spatial, language, memory, and executive function) variables to financial decision-making ability was investigated.

MATERIALS AND METHODS

PARTICIPANTS

Participants were 116 community-dwelling older adults, aged 56– 90 years (63% female), and 102 college undergraduates¹ attending The University of Iowa Tippie College of Business. The health of the Older participants was confirmed via a semi-structured screening interview that assessed neurological status, current medications, alcohol/drug consumption, and mood (after Tranel et al., 1997).

MEASURES

Financial Decision-Making Questionnaire (FDMQ)

This questionnaire assessed financial knowledge and decisionmaking ability (Cole and Denburg, 2008). Participants proceed through four hypothetical scenarios, in which they receive increasingly complex financial information and are asked to select between the options provided and to justify each decision. In Scenario 1 (hereafter referred to as *Personal Finance*), the measure lists a monthly income, interest rates (for both a credit card and savings account), and bills due (i.e., rent, credit card statement) for a fictional individual; respondents are then asked to allocate the available assets for the month using the information provided among three options: (1) rent, (2) credit card bill, and (3) savings account. Following this choice is a short answer portion in which participants are asked to provide justification for each monetary decision.

In Scenario 2 (hereafter referred to as *Impulse Purchase*), participants are asked to recall the same hypothetical individual from Scenario 1, and to imagine that this individual chose not to pay his/her credit card debt from the previous bill. They are then told that this person has just passed a storefront where the TV that he/she wishes to buy has been placed on sale for a discount of 50% off the original price. Keeping in mind that the individual is currently carrying an unpaid credit card balance from the preceding month, participants are asked in Scenario 2 to indicate whether or not they would purchase the discounted TV using the credit card if they were in this situation and to provide justification for their decision.

Next, participants are supplied with a small table detailing various financial investment options (e.g., Savings Account, Certificate of Deposit, Mutual Fund). This begins Scenario 3 (hereafter referred to as *Low Precision Investment*), in which participants are asked to imagine that they have just inherited \$20,000 unexpectedly. Below the table, participants are asked to indicate whether or not they would make an immediate decision regarding how to allocate the inheritance between the options listed. Those who indicate "Yes" are asked to proceed to Scenario 4 on the following page; participants who answer "No" in Scenario 3 are asked to please indicate what additional information they would seek before being able to make a decision regarding the allocation of these funds.

Scenario 4 (hereafter referred to as *Financial Management*) builds upon Scenario 3 in that participants receive an expanded investment table and are asked to complete it as though they have actually inherited \$20,000 and must now allocate the money accordingly. Participants may distribute the funds as they see fit across any of the options provided, including a Savings Account, Certificate of Deposit, Business Venture, Payment of Credit Card Debt, Managed Mutual Fund, and Unmanaged Mutual Fund. Each option is presented with a brief description, including the interest rate, rate of return, and expected rate of loss for those to which it is applicable. Following the table, participants are asked to provide a justification for each allocation. Scenario 4 ends with two 7-point Likert scales, in which participants indicate how important making money and avoiding financial loss were to their decision-making process (hereafter referred to as *Financial Behavior*).

At the conclusion of the packet is a five-question quiz pertaining to financial knowledge. All of the questions are True/False in nature, and are written to be challenging to the average participant (hereafter referred to *Acquired Financial Knowledge*). (The Financial Decision-Making Questionnaire (FDMQ) is available by request to the corresponding author.)

Neuropsychological battery

Current and premorbid intelligence. Current intelligence was measured using the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999), which consists of four subtests (two verbal and two non-verbal): vocabulary, Similarities, Block Design, and Matrix Reasoning. The Vocabulary subtest asks participants to provide definitions for single words. In the Similarities subtest, a task of abstract verbal reasoning, participants are asked to state how two words are similar or alike. During the Block Design subtest, participants replicate two-dimensional patterns with redand white-colored blocks. In the Matrix Reasoning subtest, participants need to complete an unfinished visuospatial pattern by choosing from a five-alternative forced choice array. Premorbid intellect was measured using the Wide Range Achievement Test – 3 (WRAT-3) Reading subtest (Wilkinson, 1993), a single-world reading task.

Attention and working memory. Simple and divided attention (also referred to as working memory) was measured with the Digit Span and Letter-Number Sequencing subtests from the Wechsler Adult Intelligence Scale – Third Edition (WAIS-III; Wechsler, 1997). In the Digit Span subtest, participants are asked to repeat strings of numbers in both a forward and backward order. During the Letter-Number Sequencing subtest, participants must recite back a string of jumbled numbers and letters by first sequencing the numbers followed by the letters.

¹For the undergraduate sample, limited demographic information was available, and neuropsychological evaluation was not performed.

Numerical skill. Participants mentally solve increasingly difficult arithmetic problems in the Arithmetic subtest of the WAIS-III (Wechsler, 1997). We also measured participants' numeracy skill, defined as the ability to understand and use basic probability and mathematical concepts, via Lipkus' Numeracy Scale (Lipkus et al., 2001).

Visual spatial. The Rey–Osterrieth Complex Figure Test-Copy Condition (Rey-O Copy; Rey, 1941) consists of presenting a multipart figure, which the participant is instructed to copy. The copy performance measures both visual perception and visual construction. The Benton Facial Recognition Test (Benton Faces; Benton et al., 1994) is a measure of visual perceptual discrimination that requires the matching of identical or near-identical faces.

Language. The Controlled Oral Word Association Test (COWAT; Benton and Hamsher, 1989) is a verbal fluency measure, in which participants are given 1 min to say as many words as they can that begin with a designated letter. In the Boston Naming Test (BNT; Kaplan et al., 1983), a measure of confrontation naming, participants are presented with a series of line drawings, and have 20 s to correctly name each object. Here, we utilized a validated, short form of the BNT (Barrash et al., 1999).

Memory. The Rey Auditory-Verbal Learning Test (RAVLT; Rey, 1964) is a verbal learning and memory task. Participants are provided five trials to learn a list of 15 unrelated words. They are then asked to recite these words again following a 30-min incidental delay period. Visual memory was assessed with the Rey–Osterrieth Complex Figure Test-Delay Condition (Rey-O Delay; Rey, 1941), in which participants are asked to reproduce from memory the figure they copied 30 min previously. The Benton Visual Retention Test-Revised (BVRT-R; Benton, 1945) assessed short-term retention. Participants are asked to reproduce from immediate memory each of 10 designs containing one or more figures, following a 10-s study period.

Executive function. In the Wisconsin Card Sorting Test (WCST; Heaton et al., 1993), a measure of problem solving and mental flexibility, participants must correctly categorize cards based on immediate feedback. The Trail Making Test, Part B (Trail Making B; Spreen and Strauss, 1998), is a set-shifting task involving the alternation between numbers and letters. The IGT (Bechara, 2007) is a well-validated, computer-administered laboratory task of decision-making under ambiguity.

PROCEDURES

Older participants completed the aforementioned measures as part of a larger neuropsychological battery. Each testing session lasted approximately 3 h, with a single experimenter working oneon-one with the older participant. There was no time limit on completion of the FDMQ, although Older participants generally completed the instrument in 30 min to 1 h. As stated previously, the Younger participants completed only the FDMQ in a supervised classroom setting over a 50-min period; none of the undergraduate sample had difficulty finishing the questionnaire in the time allotted. Finally, calculators were not provided for completion of any portion of the FDMQ, however, participants could perform pencil and paper calculations as needed.

DATA ANALYSIS

Preliminary analyses were conducted to examine the data for the presence of outliers and the appropriateness of assumptions of linearity, independence of errors, and multicollinearity. Logistic regression analyses were then conducted to examine the contributions of Age Group (i.e., Younger vs. Older), Sex (i.e., Older Male vs. Older Female), and neuropsychological performance to financial decision-making, as measured by responses to the FDMQ Scenarios. The first set of regression analyses examined the contribution of Age to the FDMQ Scenarios. For each scenario, the variables of Age and FDMQ were entered into a predictive model to identify whether an individual was a Younger or Older participant. In the second set of regression analyses, which were limited to the Older participants, the contribution of Sex to the FDMQ Scenarios was examined and subsequently entered into a predictive model to identify whether an individual was a Male or Female participant. For each logistic model, Acquired Financial Knowledge was included in the analysis to control for pre-existing financial knowledge. Finally, among the Older participants, correlational analyses were conducted to examine the associations between responses to the FDMQ Scenarios and neuropsychological performance. As the study was exploratory, no adjustment was made for multiple testing.

RESULTS

AGE ANALYSES

Table 1 displays the results from the logistic regression analyses of responses to the FDMQ Scenarios between the Younger and Older participants.

Personal finance

The first regression model examined the contributions of *Acquired Financial Knowledge* and allocations of monthly income (i.e., Rent, Credit Card, Savings Account) in predicting Age Group (i.e., Younger vs. Older). Collectively, these variables made a significant contribution in predicting whether an individual was a Younger or Older participant. Inspection of the partial test for individual variables revealed that *Acquired Financial Knowledge* significantly predicted a participant's Age Group. Specifically, the odds that an individual was an Older participant were 1.68 greater for every unit increase in *Acquired Financial Knowledge*. Said another way, for every one-point increase in *Acquired Financial Knowledge*, the odds that an individual was an Older participant increased by $68\%^2$.

After controlling for *Acquired Financial Knowledge*, Credit Card Allocation (p = 0.038) and Savings Account Allocation (p < 0.0001) were significantly predictive of Age Group. That is, for each one-point increase in allocation toward the credit card payment, the odds of an individual being an Older participant increased by 10%. By contrast, a one-point increase in allocation

²In fact, *Acquired Financial Knowledge* was predictive of Age Group for each of the Scenarios except Scenario 4 (*Financial Management*), with odds ranging from 32 to 68%.

Table 1 Logistic Regression Models of FDMQ Scenarios to Age (i.e	÷.,
Younger vs. Older).	

Variable	Exp(b)*	95% C exp(b		<i>Partial</i> p-value	<i>Overall</i> p-value
		Lower	Upper		
PERSONAL FINANCE					
Acquired knowledge	1.684	1.234	2.298	0.001	0.000
Rent allocation	1.004	0.931	1.082	0.923	
Credit card allocation	1.095	1.005	1.194	0.038	
Saving account allocation	0.923	0.900	0.947	0.000	
IMPULSE PURCHASE					
Acquired knowledge	1.327	1.017	1.732	0.037	0.054
Buy television	0.617	0.300	1.268	0.189	
LOW PRECISION INVEST	IMENT				
Acquired knowledge	1.407	1.085	1.823	0.010	0.008
Decision	1.788	0.952	3.360	0.071	
FINANCIAL MANAGEME	INT				
Acquired knowledge	1.333	0.966	1.840	0.080	0.000
Savings account	0.977	0.956	0.998	0.030	
Certificate of deposit	1.011	0.993	1.028	0.235	
Business venture	0.981	0.959	1.003	0.095	
Credit card payment	0.954	0.777	1.170	0.649	
Spending	0.968	0.917	1.022	0.240	
Managed mutual fund	1.008	0.990	1.027	0.364	
Unmanaged mutual fund	1.008	0.988	1.029	0.441	
FINANCIAL BEHAVIOR					
Acquired knowledge	1.515	1.150	1.996	0.003	0.000
Promotion-oriented	0.727	0.576	0.916	0.007	
Prevention-oriented	1.179	0.988	1.408	0.068	

*Exp(b) values are the exponentiated regression coefficient estimates.

toward the savings account decreased the odds of an individual being an Older participant by 8% (thus, Younger participants were more likely to allocate to savings).

Impulse purchase

The second regression model examined the contribution of *Acquired Financial Knowledge* and a participant's decision to purchase a Television in predicting Age Group (i.e., Younger vs. Older). Together, the two variables were marginally significant (p = 0.054) in predicting whether an individual was a Younger or Older participant, and non-significant after controlling for *Acquired Financial Knowledge*.

Low precision investment

The third regression model examined the contribution of *Acquired Financial Knowledge* and a participant's decision whether to invest money based on minimal information in predicting Age Group (i.e., Younger vs. Older). Collectively, both variables predicted whether an individual was a Younger or Older participant. After controlling for *Acquired Financial Knowledge*, there was a trend toward Older participants being more likely to make a decision with minimal information as compared to Younger participants (p = 0.07).

Financial management

In the fourth regression model, we examined the contribution of Acquired Financial Knowledge and inheritance allocations (i.e., Savings Account, Certificate of Deposit, Business Venture, Credit Card Payment, Spending, Managed Mutual Fund, Unmanaged Mutual Fund) in predicting Age Group (i.e., Younger vs. Older). Taken together, these variables predicted whether an individual was a Younger or Older participant based on inheritance allocations. Inspection of the partial test indicated that after controlling for the effect of Acquired Financial Knowledge and other inheritance allocations (i.e., Certificate of Deposit, Business Venture, Credit Card Payment, Spending, Managed Mutual Fund, Unmanaged Mutual Fund), only the amount allocated into the Savings Account was significantly predictive of Age Group (p = 0.03). In particular, every percentage increase in amount placed in the Savings Account decreased the odds of an individual being an Older participant by 2%. Said differently, Younger participants were significantly more likely to place money into a savings account.

Financial behavior

In the final model, we examined the contribution of *Acquired Financial Knowledge* and an individual's behavior toward investment (i.e., gaining money or promotion-oriented vs. avoiding monetary loss or prevention-oriented) in predicting Age Group (i.e., Younger vs. Older). Overall, the model was predictive of Age Group. Partial test inspections revealed that an increase in one-point on promotion-oriented responses decreased the odds of an individual being an Older participant by 27% (p = 0.007). In other words, Younger participants were significantly more likely to make decisions toward gaining money. (There was a trend toward Older participants being more likely to make decisions toward avoiding monetary loss, p = 0.07.)

SEX ANALYSES

Table 2 displays the results from the logistic regression analyses of responses to the FDMQ Scenarios between Older Male and Female participants.

Personal finance

The first regression model examined the contribution of *Acquired Financial Knowledge* and allocations of monthly income (i.e., Rent, Credit Card, Savings Account) in predicting Sex (i.e., Male vs. Female). Together, this group of variables predicted whether an individual was a Male or Female participant. For this model, *Acquired Financial Knowledge*, after controlling for the effect of response to the scenario, was non-significant predicting Sex of a participant³. Inspection of the partial test for individual variables revealed that after controlling for *Acquired Financial Knowledge*, Credit Card Allocation (p < 0.05), and Savings Account Allocation (p = 0.017) were significant in predicting Sex of a participant. That is, for every unit increase in Credit Card payment, the odds of an individual being a Male participant increased by 14%. Similarly, for every unit increased in Savings Account allocation, the odds of an individual being a Male participant increased by 5%.

³Acquired Financial Knowledge was non-significant in predicting Sex of a participant for all subsequent models, after controlling for the effect of response to the scenario.

Table 2 Logistic Regression Models of FDMQ Scenarios to Sex (i.e.
Male vs. Female).

Variable	able Exp(b)* 95% C.I. for 		<i>Partial</i> p-value	<i>Overall</i> p-value	
		Lower	Upper		
PERSONAL FINANCE					
Acquired knowledge	0.596	0.343	1.035	0.066	0.005
Rent allocation	0.888	0.692	1.139	0.349	
Credit card allocation	0.860	0.742	0.996	0.044	
Saving account allocation	0.953	0.916	0.991	0.017	
IMPULSE PURCHASE					
Acquired knowledge	0.754	0.485	1.174	0.212	0.378
Buy television	0.855	0.307	2.377	0.855	
LOW PRECISION INVEST	IMENT				
Acquired knowledge	0.742	0.477	1.154	0.185	0.236
Decision	0.631	0.235	1.696	0.361	
FINANCIAL MANAGEME	INT				
Acquired knowledge	0.679	0.383	1.203	0.184	0.064
Savings account	0.948	0.892	1.006	0.079	
Certificate of deposit	0.953	0.899	1.010	0.105	
Business venture	0.946	0.887	1.009	0.092	
Credit card payment	0.846	0.478	1.498	0.566	
Spending	0.891	0.794	1.000	0.050	
Managed mutual fund	0.952	0.897	1.011	0.107	
Unmanaged mutual fund	0.936	0.880	0.994	0.032	
FINANCIAL BEHAVIOR					
Acquired knowledge	0.766	0.481	1.218	0.259	0.547
Promotion-oriented	1.039	0.770	1.403	0.802	
Prevention-oriented	1.084	0.841	1.395	0.534	

*Exp(b) values are the exponentiated regression coefficient estimates.

Impulse purchase

The second regression model examined the contribution of *Acquired Financial Knowledge* and a participant's decision to purchase a Television to predicting Sex (i.e., Male vs. Female). The model indicated that the decision to make an impulse purchase was non-significant in predicting Sex of a participant.

Low precision investment

The third regression model examined the contribution of *Acquired Financial Knowledge* and a participant's decision whether to invest money based on minimal information in predicting Sex (i.e., Male vs. Female). The overall model suggests that both variables were non-significant in predicting Sex of a participant.

Financial management

In the fourth regression model, we examined the contribution of *Acquired Financial Knowledge* and inheritance allocations (i.e., Savings Account, Certificate of Deposit, Business Venture, Credit Card Payment, Spending, Managed Mutual Fund, Unmanaged Mutual Fund) in predicting Sex (i.e., Male vs. Female). Collectively, these variables were marginally significant in predicting whether an individual was a Male or Female participant based on inheritance allocations. After controlling for the effect of Acquired Financial Knowledge and other inheritance allocations, only the amount allocated into Spending (p = 0.05) and Unmanaged Mutual Fund (p = 0.032) were significantly predictive of Sex of a participant. In particular, every percentage increase in amount placed in Spending increased the odds of an individual being a Male participant by 11%. Similarly, every percentage increase in amount placed in an Unmanaged Mutual Fund increased the odds of an individual being a Male participant by 6%.

Financial behavior

In the final model, we examined the contribution of *Acquired Financial Knowledge* and a participant's behavior toward investment (i.e., gaining money or promotion-oriented vs. avoiding monetary loss or prevention-oriented) in predicting Sex of a participant. Overall, the model was non-significant in predicting Sex of a participant.

CORRELATIONAL ANALYSES

Pearson's *r* correlations were conducted in order to examine the associations between responses to the FDMQ Scenarios and neuropsychological performance, among the Older participants (see **Table 3**). A single composite variable was computed for the FDMQ based upon the justifications participants provided for each of their financial decisions (hereafter referred to as *Depth of Reasoning*). To do this, scores were calculated based upon the collective responses to seven short answer questions found throughout Scenarios 1, 2, and 4, in which participants were asked to justify why they had made each preceding monetary decision. Responses were graded on a 3-point scale, with those answers showing the greatest comprehension and sophistication (i.e., one must pay the credit card bill to avoid interest accrual and future rate increases) receiving higher scores than those that simply restated the question (i.e., you must pay the bill because it is due this month).

Correlational analyses revealed several significant correlations. In terms of demographic variables, *Depth of Reasoning* correlated with Age (r = -0.24) and Education (r = 0.21). That is, as age increased, *Depth of Reasoning* among Older participants declined (was poorer). Too, Older participants with higher levels of educational attainment provided stronger *Depth of Reasoning* for the FDMQ Scenarios.

There was an absence of association between Depth of Reasoning and the neuropsychological domains of Premorbid Intellect, Attention and Working Memory, Numerical Skill, Visual Spatial, Language, and Memory (average r = |0.09|). By contrast, Current Intelligence and Executive Functioning were associated with Depth of Reasoning. Specifically, two measures of non-verbal current intelligence (WASI Block Design and Matrix Reasoning) were positively and significantly associated with Depth of Reasoning (r = 0.31 and r = 0.21, respectively). For the cognitive domain of Executive Functioning, all variables were significantly associated with Depth of Reasoning. That is, on a test of problem solving and mental flexibility (WCST Perseverative Errors), Depth of Reasoning decreased as number of Perseverative Errors increased (r = -0.24). Similarly, on a test of simple executive functions involving speeded set-shifting (Trail Making B), Depth of Reasoning decreased as time to complete the task increased (r = -0.22). Lastly, on a laboratory task of decision-making, the IGT, Depth

Table 3 Association of FDMQ Depth of Reasoning with	
Neuropsychological Performance.	

Characteristics	Mean (SD)	Pearson r	Significance	
DEMOGRAPHICS				
Age (years)	73.62 (8.60)	-0.239*	0.015	
Education (years)	15.97 (2.72)	0.211*	0.032	
PREMORBID AND CURREN	T INTELLIGENO	E		
WRAT-3 Reading	51.36 (4.00)	0.128	0.205	
WASI Vocabulary	66.65 (6.86)	0.099	0.322	
WASI Similarities	38.55 (4.26)	0.068	0.493	
WASI Block Design	36.61 (11.44)	0.307**	0.002	
WASI Matrix Reasoning	23.07 (6.12)	0.205*	0.038	
ATTENTION AND WORKING	MEMORY			
WAIS-III Digit Span	17.17 (3.90)	0.002	0.984	
WAIS-III Letter-Number	10.11 (2.50)	0.100	0.316	
NUMERICAL SKILL				
WAIS-III Arithmetic	14.51 (3.36)	0.127	0.204	
Numeracy	8.25 (2.35)	0.133	0.183	
VISUAL SPATIAL				
Benton Facial Recognition	46.77 (4.19)	0.115	0.255	
Rey-O Complex Figure Copy	32.45 (2.82) -0.060		0.552	
LANGUAGE				
COWAT	44.17 (11.66)	0.023	0.822	
Boston Naming Test	18.75 (1.47)	0.095	0.373	
MEMORY				
AVLT 30 min Delay	9.90 (2.85)	0.070	0.484	
Rey-O Complex Figure Delay	16.26 (6.50)	0.155	0.122	
BVRT-R Errors	4.36 (2.37)	0.109	0.285	
EXECUTIVE FUNCTIONING	ì			
WCST Perseverative Errors	11.58 (9.70)	-0.237*	0.020	
Trail Making B	78.94 (29.32)	-0.216*	0.030	
lowa Gambling Task	12.14 (38.01)	0.205*	0.041	

*p < 0.05; **p < 0.01.

of *Reasoning* increased with higher levels of risk aversiveness (r = 0.21).

DISCUSSION

The present exploratory study compared how healthy Younger and Older participants make a series of increasingly complex financial decisions. Additionally, among the Older participants, we examined the contribution of demographic and neuropsychological variables to financial decision-making ability. The study yielded multiple findings. Older participants outperformed Younger participants on a multiple-choice test of *Acquired Financial Knowledge*, a finding that may be due in part to the experience conferred by age. Nevertheless, even after controlling for this preexisting financial knowledge, several important, and striking differences were observed between Younger and Older participants throughout the FDMQ.

In both the *Personal Finance* and *Financial Management* scenarios, Younger participants were more likely to place money into a Savings Account than were Older participants. By contrast, Older participants were more likely to pay off their Credit Card bills in the *Personal Finance* scenario than were Younger participants. Older participants also displayed greater interest in making immediate decisions regarding the allocation of an unexpected inheritance during the *Low Precision Investment* scenario of the FDMQ, whereas the Younger participants exhibited a preference for delaying decision-making until additional resources could be accessed. Furthermore, Older participants rated themselves as having significantly less interest in using the hypothetical inheritance funds for purposes of monetary gain (i.e., a promotion orientation) than Younger participants, while also displaying a trend of favoring investment strategies which avoided potential monetary loss (i.e., a prevention orientation).

Among the Older participants, few differences were demonstrated between the two sexes. However, we did observe that Males were more likely to pay their Credit Card bill and contribute money to a Savings Account in the *Personal Finance* scenario than Females. Males were also more likely to allocate money to the Savings Account and Unmanaged Mutual Fund options than Females, during the *Financial Management* scenario. Reasons for these sex preferences are unknown, though it may be speculated that Older Males' preference for investment in an Unmanaged Mutual Fund stems from their greater experience and comfort with investing (Ozerol et al., 2011).

Among the Older participants, multiple significant correlations were found between the FDMQ *Depth of Reasoning* composite variance and performance on aspects of the neuropsychological battery. *Depth of Reasoning* was positively correlated with nonverbal intelligence and executive functioning. Level of education was also positively correlated with *Depth of Reasoning* scores. Too, age showed an inverse correlation with *Depth of Reasoning* such that the ability to justify one's financial decisions significantly declined with increasing age. Finally, we did not observe an association between numerical skill and FDMQ *Depth of Reasoning*, which came as somewhat of a surprise given that Marson et al. (2000) found that changes in basic numerical skills, such as the ability to perform simple calculations, were one of the strongest predictors of a loss of financial capacity in patients with Alzheimer's disease.

Taken together, our findings are supported by the work of Korniotis and Kumar (2010), who similarly deduced that sound cognitive abilities play a critical role in the capacity to make high quality financial decisions across the lifespan. However, the relationship between cognitive fitness and financial decisionmaking capacity is complex and difficult to characterize. Although the experience and financial knowledge accumulated by older investors would be predicted to buffer age-associated declines, the cognitive declines associated with normal aging may offset such safeguards by preventing the effective application of previously learned principles (Korniotis and Kumar, 2010).

Ultimately, it may be this underlying decline in cognition associated with normal aging that accounts for the trend observed in the *Low Precision Investment* scenario whereby Older participants preferred to make immediate investment decisions while Younger participants seek out more information. In a simulated financial decision-making task involving maximizing profit at a yard sale, Chen and Sun (2003) found that younger and older adults adopted different strategies (although age did not ultimately predict total monetary gain). While younger adults demonstrated flexibility by switching strategies as needed during the task, older adults adopted a consistent and less memory-demanding strategy. These findings imply that advancing age can lead to a preferential selection of less cognitively demanding decision-making strategies (Chen and Sun, 2003). So it may be in the present study that the Older participants preferred to make an immediate decision with regards to an unexpected inheritance in an effort to reduce cognitive load, whereas the Younger participants did not because no such cognitive burden was experienced.

Interestingly, our age-related financial decision-making findings are notably similar to the literature examining the effect of aging on medical decision-making. That is, the medical decisionmaking literature has indicated that older adults demonstrate declines in the thoroughness of the information search process and in the amount of information used (Meyer et al., 1995; Zwahr et al., 1999), as well as a shorter interval between symptom onset and the decision to seek medical care (Leventhal et al., 1993, 1995). Such findings have been interpreted as suggesting that older adults may be may be attempting to conserve diminishing cognitive and emotional resources by making medical decisions in the aforementioned manner.

With regard to sex differences, Older participants were more likely to pay the Credit Card Bill and invest in the Savings Account option each time it was presented. Interestingly, a study of sexspecific risk attitudes among undergraduates at the University of Zurich and the Swiss Federal Institute found a similar tendency for males to make less risky financial choices than females under controlled economic parameters (Schubert et al., 1999). However, given the cross-sectional nature of the present study and the absence of demographic data on the Younger participants, it cannot be empirically determined at this time whether the observed sex differences are stable throughout the lifespan or if they would have been displayed by the college-aged cohort. Not being able to examine this empirically is an obvious limitation of the current study.

Given the utility of the FDMQ as shown in the present work, directions for future research should focus on expanding the population under study, and the inclusion of neuroimaging technology in order to empirically assess the brain regions associated with real-world financial decision-making and the effects of aging and cognitive decline on performance at the biological level. Knutson and Bossaerts (2007) have previously used functional neuroimaging to systematically measure patterns of

REFERENCES

- Barrash, J., Cross, S., and Manzel, K. (1999). The validity of Boston Naming Test short forms. J. Int. Neuropsychol. Soc. 5, 118.
- Bechara, A. (2007). Iowa Gambling Task (IGT) Professional Manual. Lutz: Psychological Assessment Resources.
- Benton, A. L. (1945). A visual retention test for clinical use. Arch. Neurol. Psychiatry 54, 212–216.
- Benton, A. L., and Hamsher, K. (1989). Multilingual Aphasia

Examination. Iowa City, IA: AJA Associates.

- Benton, A. L., Sivan, A. B., Hamsher, K, Varney, N. R., and Spreen, O. (1994). Contributions to Neuropsychological Assessment: A Clinical Manual, 2nd Edn. New York, NY: Oxford University Press.
- Boersch-Supan, A. H., and Essig, L. (2005). "Household savings in Germany: results of the first SAVE study," in Analyses in the Economics of Aging, ed. D. A. Wise (Chicago: University of Chicago Press), 317–356.

neural activation during a task of basic financial decision-making. The experimenters manipulated expected value by varying the magnitude and probability of monetary reward, finding that anticipatory activation of the ventral striatum predicted risky financial investment choices, whereas anticipatory activation of the insula predicted safe investments. Interestingly, neither pattern of activation was significantly associated with either optimal or suboptimal investment decisions (Knutson and Bossaerts, 2007).

The present study also has noteworthy implications for future research and public policy. Further studies should explore the tendency observed among older adults to make immediate financial decisions, investigating whether interventions might be designed to facilitate this population in using their extensive financial knowledge to evaluate all of the available information before committing to financial investments. Additionally, if future research is able to replicate the findings that men, particularly older males, are more likely to pay credit card bills and utilize savings accounts than women, this would be a significant focus for public policy targeting older females. Because the life expectancy of women is significantly higher than that of men, there are a population segment of older women who may be thrust into the financial decision-making arena following the (often unexpected) death of a spouse. Consequently, these older adults might benefit from targeted education and intervention attempts.

In consideration of the present findings, and those of Korniotis and Kumar (2010), that financial decision-making performance drops steadily after age 70 relative to what prior performances would predict, participation in the stock market and other complex financial endeavors may not be in the best interest of some older adults irrespective of prior experience, particularly with advancing age. Furthermore, legal protections must be put in place to ensure that at-risk older adults are not extorted by those seeking to benefit from the impaired financial decision-making abilities of this population. This issue will become even more pressing as more financial and business transactions begin to take place online and older adults are faced with learning entirely new ways to perform previously well-known tasks, such as bill payment and electronic funds transfers.

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- Chen, Y., and Sun, Y. (2003). Age differences in financial decision-making: using simple heuristics. *Educ. Gerontol.* 29, 627–635.
- Cole, C. A., and Denburg, N. L. (2008). *Financial Decision Making Questionnaire (FDMQ)*. Iowa City, IA: University of Iowa Carver College of Medicine, Department of Neurology.
- Denburg, N. L., Cole, C. A., Hernandez, M., Yamada, T. H., Tranel, D., Bechara, A., and Wallace, R. B. (2007). The orbitofrontal cortex,

real-world decision-making, and normal aging. *Ann. N. Y. Acad. Sci.* 1121, 480–498.

- Denburg, N. L., and Harshman, L. (2010). "Why so many seniors get swindled: brain anomalies and poor decision-making in older adults," in *The Dana Foundation's Cerebrum: Emerging Ideas in Brain Science* (New York: Dana Press), 123–131.
- Denburg, N. L., Recknor, E. C., Bechara, A., and Tranel, D. (2006). Psychophysiological anticipation of positive outcomes promotes

advantageous decision-making in normal older persons. *Int. J. Psychophysiol.* 61, 19–25.

- Denburg, N. L., Tranel, D., and Bechara, A. (2005). The ability to decide advantageously declines prematurely in some normal older persons. *Neuropsychologia* 43, 1099–1106.
- Federal Interagency Forum on Aging-Related Statistics. (2010). Older Americans 2010: Key Indicators of Well-Being. Washington, DC: Government Printing Office.
- Finucane, M. L., Slovic, P., Hibbard, J. H., Peters, E., Mertz, C. K., and MacGregor, D. G. (2002). Aging and decision-making competence: an analysis of comprehension and consistency skills in older versus younger adults considering healthplan options. J. Behav. Decis. Mak. 15, 141–164.
- He, W., Sengupta, M., Velkoff, V. A., and DeBarros, K. A. (2005). 65+ *in the United States: 2005.* U.S. Census Bureau, Current Population Reports, P23-209. Washington, DC: U.S. Government Printing Office.
- Heaton, R. K., Chelune, G. J., Talley, J. L., Kay, G. G., and Curtiss, G. (1993). Wisconsin Card Sorting Test Manual: Revised and Expanded. Odessa, FL: Psychological Assessment Resources.
- John, D. R., and Cole, C. A. (1986). Age differences in information processing: understanding deficits in young and elderly consumers. J. Consum. Res. 13, 297–315.
- Kaplan, E. F., Goodglass, H., and Weintraub, S. (1983). *Boston Naming Test*. Philadelphia, PA: Lea & Febiger.
- Knutson, B., and Bossaerts, P. (2007). Neural antecedents of financial decisions. J. Neurosci. 27, 8174–8177.

- Korniotis, G. M., and Kumar, A. (2010).
 "Cognitive abilities and financial decisions," in *Behavioral Finance*, eds
 H. K. Baker and J. R. Nofsinger (Hoboken, NJ: John Wiley & Sons, Inc.), 559–576.
- Leventhal, E. A., Easterling, D., Leventhal, H., and Cameron, L. (1995). Conservation of energy, uncertainty reduction, and swift utilization of medical care among the elderly: study II. *Med. Care* 33, 988–1000.
- Leventhal, E. A., Leventhal, H., Schaefer, P., and Easterling, D. (1993). Conservation of energy, uncertainty reduction, and swift utilization of medicalcare among the elderly. *J. Gerontol.* 48, 78–86.
- Lipkus, I. M., Samsa, G., and Rimer, B. K. (2001). General performance on a numeracy scale among highly educated samples. *Med. Decis. Making* 21, 37–44.
- Lusardi, A. (2010). *Americans' Financial Capacity*. Report prepared for the Financial Crisis Inquiry Commission, Washington, DC.
- Lusardi, A., and Mitchell, O. S. (2011a). Financial literacy across the world: an overview. *J. Pension Econ. Financ.* 10, 497–508.
- Lusardi, A., and Mitchell, O. S. (2011b). "Financial literacy and planning: implications for retirement wellbeing," in *Financial Literacy: Implications for Retirement Security and the Financial Marketplace*, eds O. S. Mitchell and A. Lusardi (New York, NY: Oxford University Press), 17–39.
- Marson, D. C., Sawrie, S. M., Snyder, S., McInturff, B., Stalvey, T., Boothe, A., Aldridge, T., Chatterjee, A., and Harrell, L. E. (2000). Assessing financial capacity in patients with Alzheimer disease: a conceptual model and prototype instrument. *Arch. Neurol.* 57, 877–884.

- Meyer, B. J. F., Russo, C., and Talbot, A. (1995). Discourse processing and problem solving: decisions about the treatment of breast cancer by womenacross the life span. *Psychol. Aging* 10, 84–103.
- Moye, J., and Marson, D. C. (2007). Assessment of decision-making capacity in older adults: an emerging area of practice and research. *J. Gerontol.* 62, 3–11.
- Ozerol, H., Camgoz, S. M., Karan, M. B., and Ergeneli, A. (2011). Determining the performance of individual investors: the predictive roles of demographic variables and trading strategies. *Int. J. Bus. Soc. Sci.* 2, 86–92.
- Rey, A. (1941). L'examen psychologique dans les cas d'encephalopathie traumatique. Arch. Psychol. 28, 286–340.
- Rey, A. (1964). L'examen Clinique en Psychologie. Paris: Presses Universitaires de France.
- Schubert, R., Brown, M., Gysler, M., and Brachinger, H. W. (1999). Financial decision-making: are women really more risk-averse? *Am. Econ. Rev.* 89, 381–385.
- Spreen, O., and Strauss, E. (1998). A Compendium of Neuropsychological Tests, 2nd Edn. New York, NY: Oxford University Press.
- Tranel, D., Benton, A., and Olson, K. (1997). A 10-year longitudinal study of cognitive changes in elderly persons. *Dev. Neuropsychol.* 13, 87–96.
- Triebel, K. L., Martin, R., Griffith, H. R., Marceaux, J., Okonkwo, O. C., Harrell, L., Clark, D., Brockington, J., Bartolucci, A., and Marson, D. C. (2009). Declining financial capacity in mild cognitive impairment. *Neurology* 73, 928–934.
- United Nations. (2009). World Population Ageing 2009. New York, NY: United Nations.

- Wechsler, D. A. (1997). Wechsler Adult Intelligence Scale – III. New York, NY: Psychological Corporation.
- Wechsler, D. A. (1999). Wechsler Abbreviated Scale of Intelligence. New York, NY: Psychological Corporation.
- Wilkinson, G. S. (1993). Wide Range Achievement Test – 3. Wilmington, DE: Jastak Associates, Inc.
- Yoon, C., Cole, C. A., and Lee, M. (2009). Consumer decision making and aging: current knowledge and future directions. *J. Consum. Psychol.* 19, 2–16.
- Zwahr, M. D., Park, D. C., and Shifren, K. (1999). Judgments about estrogen replacement therapy: the role of age, cognitive abilities, and beliefs. *Psychol. Aging* 14, 179–191.

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Age differences in striatal delay sensitivity during intertemporal choice in healthy adults

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Gregory R. Samanez-Larkin, Psychological Sciences, Vanderbilt University, 111 21st Avenue South, Nashville, TN 37212, USA. e-mail: g.samanezlarkin@vanderbilt .edu Intertemporal choices are a ubiquitous class of decisions that involve selecting between outcomes available at different times in the future. We investigated the neural systems supporting intertemporal decisions in healthy younger and older adults. Using functional neuroimaging, we find that aging is associated with a shift in the brain areas that respond to delayed rewards. Although we replicate findings that brain regions associated with the mesolimbic dopamine system respond preferentially to immediate rewards, we find a separate region in the ventral striatum with very modest time dependence in older adults. Activation in this striatal region was relatively insensitive to delay in older but not younger adults. Since the dopamine system is believed to support associative learning about future rewards over time, our observed transfer of function may be due to greater experience with delayed rewards as people age. Identifying differences in the neural systems underlying these decisions may contribute to a more comprehensive model of age-related change in intertemporal choice.

Keywords: aging, reward, decision making, discounting, intertemporal choice, ventral striatum, experience

INTRODUCTION

Intertemporal choice describes any decision making scenario that involves selecting between outcomes available at different times in the future. A broad range of decisions made in everyday life (e.g., healthy eating, retirement savings, exercise) require trade-offs between immediate satisfaction and long-term health and wellbeing. Economic models of age-related change in intertemporal preferences begin with assumptions about how utility changes across the life span. Assertions are made about reproductive fitness or the physical wherewithal available to enjoy rewards and then conclusions are drawn on this basis about how decision making ought to depend on age (Rogers, 1994; Trostel and Taylor, 2001; Read and Read, 2004). This approach has produced theories asserting that delay discounting (i.e., the preference for sooner, smaller rewards relative to larger, later rewards) should decline with age (Rogers, 1994), increase with age (Trostel and Taylor, 2001), or be minimized in middle age (Read and Read, 2004). Empirical results from psychology and behavioral economics are similarly conflicting (Green et al., 1994, 1996, 1999; Harrison et al., 2002; Read and Read, 2004; Chao et al., 2009; Reimers et al., 2009; Whelan and McHugh, 2009; Simon et al., 2010; Jimura et al., 2011; Löckenhoff et al., 2011). One important potential contribution to models of intertemporal choice over the life span, which has been overlooked to date, may be that older and younger adults rely differently on the brain systems that underlie valuation of future outcomes.

Decision neuroscience promises to enable a systems-level understanding of the neural and cognitive changes that underlie

the age-dependence of intertemporal choice. Recent decision neuroscience research reveals a network of subcortical and cortical brain regions involved in intertemporal decision making (Peters and Büchel, 2011). Several studies have shown that regions associated with the mesolimbic dopamine system, including the ventral striatum (VS), ventromedial prefrontal cortex, and posterior cingulate cortex, play a primary role in the representation of subjective value (Kable and Glimcher, 2007; Peters and Büchel, 2009, 2010) and are more active in the presence of immediately available rewards in young adults (McClure et al., 2004, 2007; Luo et al., 2009). A different network of brain areas related to cognitive control including the dorso and ventrolateral prefrontal cortex (collectively, LPFC) and the posterior parietal cortex (PPC) has been proposed to promote the selection of relatively delayed outcomes (Peters and Büchel, 2011). Higher levels of activation in LPFC and PPC relative to mesolimbic regions is associated with selection of larger, delayed rewards (McClure et al., 2004), and disruption of left LPFC through transcranial magnetic stimulation leads to increased selection of immediate over delayed rewards (Figner et al., 2010). There is also related evidence that working memory-related anterior PFC activity is associated with increased selection of delayed outcomes (Shamosh et al., 2008). LPFC regions play a causal role in valuation and self-control during decision making (Camus et al., 2009), possibly through top-down interactions with medial prefrontal regions to bias choice toward options with better long-term over short-term value (Hare et al., 2009).

How age-related alterations in the mesolimbic dopamine system and lateral cortical regions combine to affect judgments is an active area of investigation (Mohr et al., 2009). Although some age-related impairments in risky decision making have been linked to cognitive limitations related to processing speed and memory (Henninger et al., 2010) or learning to implement cognitively demanding strategies (Mata et al., 2010), in other decision making scenarios that are not as cognitively demanding the LPFC is similarly engaged and performance is equal between younger and older adults (Hosseini et al., 2010). In contrast, age-related changes in the function of the mesolimbic dopamine system are the focus of the present work. Numerous neurophysiological changes are known to occur as people age. Age-related declines in the striatal dopamine receptors have been well documented and are linked to cognitive impairment (Bäckman et al., 2006). In fact, previous neuroimaging studies have attributed age-related deficits in decision making during novel probabilistic learning tasks to disruption of striatal signals (Mell et al., 2009; Samanez-Larkin et al., 2010).

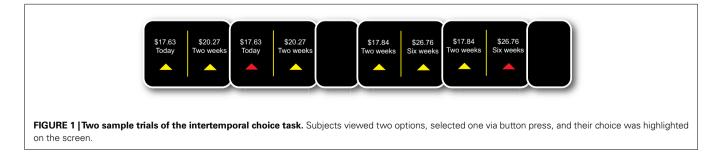
Although there is evidence for age differences in the function of the striatum in time-limited learning tasks (Aizenstein et al., 2006; Mell et al., 2009; Samanez-Larkin et al., 2010), there is also evidence for stability in striatal responses correlated with reward magnitude (Samanez-Larkin et al., 2007, 2010; Schott et al., 2007; Cox et al., 2008). Behavioral experiments with animals have also demonstrated equivalent sensitivity to both magnitude and delay in younger and older rats (Simon et al., 2010), suggesting that the basic computational resources needed to make intertemporal decisions do not change much with age. Likewise, standard models of discounting fit the behavior of younger and older adults equally well (Green et al., 1999; Whelan and McHugh, 2009), suggesting that similar choice processes are involved. Thus, although the rate of discounting may differ, a differential structure of discounting functions between age groups does not explain any observed differences (Green et al., 1999). In spite of the age-related declines observed in the dopamine system and the striatum, it may be that gradual declines in the dopamine system with age do not disrupt the slow changes in associative learning from repeated experience with delayed rewards over decades of the life course. This experience with the realization of delayed rewards is highly relevant for making intertemporal decisions, as one has to make predictions about the future value of various courses of action at the time of choice (Löckenhoff, 2011; Löckenhoff et al., 2011).

Theories about dopamine function posit that these neurons signal reward value in mesolimbic regions as a consequence of direct associative learning (Montague et al., 1996; Schultz et al., 1997). Reinforcement learning models developed to capture these

data are notoriously slow to learn about delayed outcomes (Sutton and Barto, 1998). As a consequence it may take substantial time and experience (Logue et al., 1984) for mesolimbic dopamine regions to develop robust responses to cues predicting rewards at long time delays. Although older adults may suffer from declines in fluid cognitive ability that may constrain their decision making competence, they also have decades of experience over their young adult counterparts with the realization of delayed rewards which may lead to similar decisions behaviorally (Agarwal et al., 2009). Thus, reasoning from such models, we did not make strong predictions about behavioral differences in decision making but did expect that older adults as compared to their younger counterparts may show increased mesolimbic responses to delayed rewards. In the present study, we examined age differences between healthy younger and older adults in the neural systems that support intertemporal decision making. We predicted that younger adults would show a larger difference in mesolimbic neural signal change in the presence of an immediately available reward, but that older adults would show similar levels of neural activation for immediate or delayed rewards.

MATERIALS AND METHODS BEHAVIORAL TASK DESIGN

Twelve younger adults (age range 19–26, mean 22.0; seven female) and 13 older adults (age range 63-85, mean 73.4; six female) completed an intertemporal decision making task while undergoing functional magnetic resonance imaging (fMRI). Older adults were screened with the Mini-Mental State Exam prior to participation to ensure that individuals at risk for Mild Cognitive Impairment or dementia were excluded from participation (all scores above 25). All subjects gave written informed consent, and the experiment was approved by the Institutional Review Board of Stanford University. We measured the blood-oxygen-level-dependent (BOLD) signal of subjects as they made a series of intertemporal choices between early monetary rewards (\$R available at delay d; R = reward, d = delay) and later monetary rewards (\$R' available at delay d'; d' > d; following the methods of McClure et al., 2004). On each trial, subjects viewed the two options, pressed a button to make a selection, and their choice was highlighted on the screen (Figure 1). The task was incentive-compatible. At the end of the experiment one trial was selected at random to be paid out at the chosen time (personal checks were used for both immediate and delayed rewards). All subjects responded with the right hand (index finger for choice on the left, middle finger for choice on the right). The total trial length including the inter-trial interval was 12 s. Decisions were self-paced, the highlighted choice was



displayed for 2 s, and the inter-trial interval was set to 10 s minus choice reaction time. Older adults responded more slowly than younger adults, $t_{23} = 2.79$, p < 0.05, but on average both groups responded within 4 s (older mean = 3.3 s, SD = 0.25 s; younger mean = 2.4 s, SD = 0.21 s). Adding reaction time as a covariate to any of the analyses reported does not change any of the effects. All significant effects remain significant.

The early option always had a lower (undiscounted) value than the later option (i.e., R < R'). The two options were separated by a minimum time delay of 2 weeks. In some choice pairs, the early option was available "immediately" (i.e., at the end of the scanning session; d = 0). In other choice pairs, even the early option was available only after a delay (d > 0). The early option varied from "today" to "2 weeks" to "1 month," whereas the later option varied from "2 weeks" to "1 month" to "6 weeks." Each subject completed 82 trials.

NEUROIMAGING DATA ACQUISITION AND ANALYSIS

Neuroimaging data were collected using a 1.5-T General Electric MRI scanner using a standard birdcage quadrature head coil. Twenty-four 4-mm thick slices (in-plane resolution $3.75 \text{ mm} \times 3.75 \text{ mm}$, no gap) extended axially from the mid-pons to the top of the skull. Functional scans of the whole brain were acquired at a repetition time of 2 s with a T2*-sensitive in-/outspiral pulse sequence (TE = 40 ms, flip = 90°) designed to minimize signal dropout at the base of the brain (Glover and Law, 2001). High-resolution structural scans were acquired using a T1weighted spoiled GRASS (gradient acquisition in the steady state) sequence (TR = 100 ms; TE = 7 ms, flip = 90°), facilitating localization and coregistration of functional data. Preprocessing and whole brain analyses were conducted using analysis of functional neural images (AFNI) software (Cox, 1996). For preprocessing, voxel time series were slice-time corrected within each volume, corrected for three-dimensional motion across volumes, slightly spatially smoothed (FWHM = 4 mm), converted to percentage signal change (relative to the mean activation over the entire experiment), and high-pass filtered. Visual inspection of motion correction estimates confirmed that no subject's head moved more than 4 mm in any dimension from one volume acquisition to the next.

A dual-system model with one present-oriented component and another more delay-oriented component was used to create regressors of interest for the neuroimaging analyses (McClure et al., 2004, 2007). We used a simplified utility function where we approximate these two systems with average discount rates β and δ :

$$V(R, d) = (1 - \omega) R\beta^d + \omega R\delta^d.$$

The " δ system" discounts exponentially with factor δ . The " β system" discounts exponentially with factor β to capture the extra weight given to immediate rewards. Lower values of β and δ correspond to steeper discounting. Generally, the more impatient and present-oriented β component of this function discounts reward at a much greater rate than does the more patient δ component. Thus, the δ -system can be interpreted as indexing more modest discounting (i.e., relatively reduced sensitivity to delay when

compared to the β -system). This model has been previously associated with functionally distinct neural systems (McClure et al., 2004, 2007), a result we replicate in the present study. The relative weighting of the two valuation systems in determining choice is given by ω ($0 \le \omega \le 1$). The discount function resulting from the combination of these two exponential systems has been referred to as quasi-hyperbolic (Laibson, 1997).

Based on the observed choices across all presented pairs of rewards (R) and delays (d), four parameters were estimated per subject (β , δ , ω , m) using a simulated annealing algorithm to maximize the likelihood of the observed choices (fits restricted such that $0 < \beta < \delta < 1$). Choices were assumed to follow a softmax decision function with temperature parameter m (the slope of the decision function). Higher values of m correspond to a stronger bias for selection of the higher subjective value option, whereas lower values of m correspond to a weaker bias for the selection of the higher subjective value option. Low values of m may indicate more random responding. We did not observe age differences in *m*. Additionally, although both age groups showed some level of present bias (β), the age groups did not differ in β or any other model parameter. The two groups did not differ significantly in β , Z = 0.136, p = 0.89 (young mean = 0.51, old mean = 0.47), $\delta, Z = 0.109, p = 0.91$ (young mean = 0.99, old mean = 0.99), ω , Z = -0.446, p = 0.66 (young mean = 0.94, old mean = 0.92), m, Z = 0.272, p = 0.79 (young mean = 2.07, old mean = 1.82), or the fit of the model, Z = -0.49, p = 0.62 (log-likelihood: young mean = -27.01, old mean = -26.88). The best fitting β and δ for each subject were used in the regression models described below. Additionally, we fit behavior using a generalized hyperbolic discount function of the form $V(R,d) = R(1 + \alpha d)^{-\beta/\alpha}$ (Loewenstein and Prelec, 1992). We find no significant differences in either α , $Z = 0.326, p = 0.74, \text{ or } \beta, Z = 0.218, p = 0.83.$

Preprocessed time series data for each individual were analyzed with multiple regression in AFNI. The regression model contained two regressors of interest corresponding to the β-system and δ -system. For the β -system regressor, we modeled the sum of the β -weighted values for the two options available on that trial (i.e., $R\beta^{d} + R'\beta^{d'}$). Similarly, for the δ -system regressor, we modeled the sum of the δ -weighted values for the two options available on that trial (i.e., $R\delta^d + R'\delta^{d'}$). Additional covariates included residual motion (in six dimensions) and polynomial trends across the experiment. Regressors of interest were convolved with a gamma-variate function that modeled a prototypical hemodynamic response before inclusion in the regression model. Maps of *t*-statistics representing each of the regressors of interest were transformed into Z-scores, resampled at 2 mm^3 and spatially normalized by warping to Talairach space. Statistical maps were then generated using one-sample t-tests to examine effects across all subjects and independent-samples t-tests to examine differences between groups (older adults > younger adults). Voxel-wise thresholds for statistical significance at the whole brain level were set at p < 0.005, uncorrected. All regression analyses were conducted with resampled 2 mm³ voxels with a minimum cluster size of 56 voxels for a p < 0.05 whole brain corrected threshold estimated using AFNI's AlphaSim (Cox, 1996) using a mask generated from an average brain image across subjects in the study. Small volume correction was applied to the VS by using 16-mm diameter

spherical masks bilaterally and at p < 0.005 a cluster size of 9 voxels was estimated using AlphaSim for a p < 0.05 corrected threshold. For follow-up inspection of regression coefficients and timecourse analyses, regions of interest were specified at the peak voxel of significant clusters that emerged in group analyses. These 8-mm diameter spheres were shifted within individuals to ensure that only data from gray matter were extracted. Timecourse analyses examined whether activation during decision making (i.e., signal averaged from time points 4 and 5 in each trial to account for HRF peak shift) differed from baseline in these volumes of interest in the presence of an immediate option (d = ``today,'')d' = 2 weeks," or "1 month") or absence of an immediate option (d = "2 weeks," d' = "1 month," or "6 weeks"). We did not include the d = "1 month" trials in these timecourse analyses, because this delay can only be combined with d' = 6 weeks" resulting in far fewer trials for this condition.

In all fMRI analyses, care was taken to minimize potential confounds associated with age differences in subject characteristics, brain morphology, and hemodynamics (Samanez-Larkin and D'Esposito, 2008). Each individual's brain was warped into Talairach space with reference to 11 hand-placed anatomical landmarks (superior edge of anterior commissure, posterior margin of anterior commissure, inferior edge of posterior commissure, two mid-sagittal points, most anterior point, most posterior point, most superior point, most inferior point, most left point, most right point). Structural and functional brain imaging data were inspected for abnormalities in each individual. None were excluded due to abnormalities. Four additional individuals (not included in the 25 subjects described above) were excluded due to a data acquisition error (68 year old female), excessive motion (75 year old male), not completing the task (19 year old female), or difficulty with data fitting given the selection of the sooner option on every trial (32 year old female).

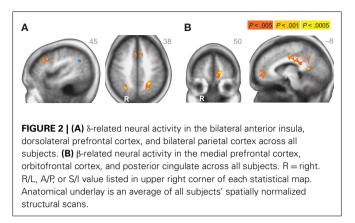
RESULTS

BEHAVIORAL RESULTS

There were no behavioral differences in intertemporal preferences between the younger and older groups on the experimental task we used in the present experiment. The two groups did not differ in the proportion of smaller, sooner choices selected, $t_{24} = 0.20$, p = 0.84 (young mean = 0.46, old mean = 0.44). Nor were there age differences in the parameters derived from either of two discount functions fit to the data. For comparison of fMRI results, comparable behavioral responding is advantageous since it reduces the influence of numerous potential confounds and facilitates interpretation of differences in brain responses.

NEUROIMAGING RESULTS

Across age groups, functional neuroimaging analyses identified brain regions that correlated with the β and δ components of the subjective value function described by Eq. 1. Across all subjects, δ -related neural activity was observed in the right dorsolateral prefrontal cortex, bilateral anterior insula, and a large cluster in the occipital cortex with peaks extending into bilateral PPC (Figure 2A; Table 1). In contrast, β -related neural activity was observed in the mesolimbic dopamine system including the ventromedial prefrontal cortex



and posterior cingulate (**Figure 2B**; **Table 1**). A subthreshold-sized cluster also emerged in the left nucleus accumbens (Z = 3.066; -9, 9, -8; 6 voxels) at p < 0.005 uncorrected (see **Figure A1** in Appendix). Similar results to the β effects were observed using a hyperbolic model with a single discount factor (see **Table A1** and **Figure A2** in Appendix).

When directly comparing older to younger adults, we observed an age-related shift in the brain areas that respond to immediate and delayed rewards. Comparing brain areas that show low discount rates (& component) across age groups revealed significant differences in a lateral region of the VS (ventral putamen; VPut) with relatively greater loading on this regressor in older subjects (Figure 3A; Table 2). Further inspection of the coefficients extracted from VPut within age groups revealed a significant relationship with the δ regressor in older subjects, $t_{12} = 2.705$, p = 0.02, but not younger subjects, $t_{11} = -1.55$, p = 0.15 (Figure 3B). Additional analyses of time courses extracted from the VPut in the younger adults revealed significant activation (greater than baseline) when the earliest reward was available today, $t_{11} = 2.392$, p = 0.02, but not when the earliest reward was delayed 2 weeks, $t_{11} = -0.124$, p = 0.90. However, for older adults activation of the VPut was greater than baseline when the earliest reward was available either today, $t_{12} = 2.187$, p = 0.02, or delayed 2 weeks, $t_{12} = 2.168$, p = 0.03 (**Figure 3C**). This pattern was specific to VPut; age differences did not emerge in the nucleus accumbens (see Figure A3 in Appendix). Overall, the results suggest that the VPut shows modest sensitivity to delay in older subjects.

Age differences were also observed in the LPFC (**Table 2**). However, the age differences in the LPFC are suspect for two reasons that together lead us to believe it is not of functional importance. First, the regions are located near the edge of the brain where spatial variability across subjects is highest. Second, inspection of the coefficients indicated that the age differences arose from nonsignificant activation in older subjects and a decrease in activation in younger subjects. No age differences were observed with respect to the β component of the valuation model (**Table 2**) or when generating regressors based on subjective value using a hyperbolic model (**Table A2** in Appendix).

To examine whether activation in the VPut was related to choice behavior, we computed differences in signal change between trials when the later option was chosen versus when the sooner option

Table 1 | Brain regions with low (δ) and high (β) discount rates across all subjects.

Region	R	Α	S	Z	Voxels
8 COMPONENT					
R middle frontal gyrus	45	25	28	3.601	60
L anterior insula	-29	23	8	4.560	160
R anterior insula	31	21	6	4.621	165
R middle frontal gyrus	35	11	22	4.488	134
R medial frontal gyrus	7	7	48	5.312	353
L precentral gyrus	-43	-1	28	4.376	93
L middle frontal gyrus	-27	-5	46	4.495	124
L parahippocampal gyrus	-15	-13	-16	-4.100	56
R supramarginal gyrus	61	-53	28	-4.182	136
L middle temporal gyrus	-45	-59	22	-4.089	235
R middle occipital gyrus (extends to bilateral IPL)	29	-85	14	5.715	6518
β COMPONENT					
L medial frontal gyrus	-9	53	-2	3.995	203
R medial frontal gyrus	13	41	36	3.920	58
L superior frontal gyrus	-17	35	38	4.170	145
R anterior cingulate	1	35	16	3.501	81
R middle frontal gyrus	27	27	34	3.640	106
L superior frontal gyrus	-17	21	44	4.644	325
R cingulate gyrus	13	3	38	4.006	235
L middle temporal gyrus	-55	-9	-18	3.602	62
R paracentral lobule	17	-33	54	3.599	95
R inferior parietal lobule	35	-41	50	3.907	130
L posterior cingulate	-9	-51	12	4.090	964
L superior temporal gyrus	-45	-57	26	3.925	142
L middle temporal gyrus	-49	-61	10	3.715	66

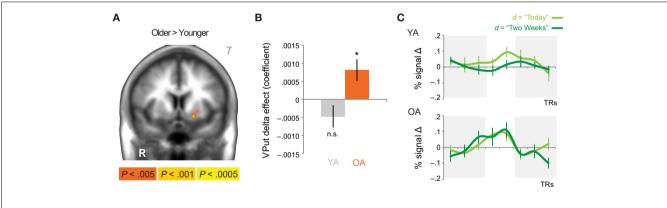


FIGURE 3 | (A) The δ component (low discount rate) was more strongly associated with neural activity in the VPut (ventral putamen) in older compared to younger adults. R = right. A = 7. Anatomical underlay is an average of all subjects' spatially normalized structural scans. **(B)** Significant δ -related neural activity in the VPut in older but not younger adults. *p < 0.05,

n.s., not significant; error bars are SEM; YA, younger adults; OA, older adults. (C) For younger adults the VPut is active only when the earliest option is available immediately, but not when it is delayed. However, for older adults activation in the VPut increases for both immediate and delayed options. Error bars are SEM.

was chosen and correlated this signal difference with the overall proportion of later choices made (controlling for age). Individuals with larger differences in brain activity in the VPut on trials when they chose the later option relative to the sooner option also made more later choices overall, r = 0.58, p < 0.005, (see **Figure 4**). A similar relationship was observed in the nucleus accumbens (see **Figure A4** in Appendix).

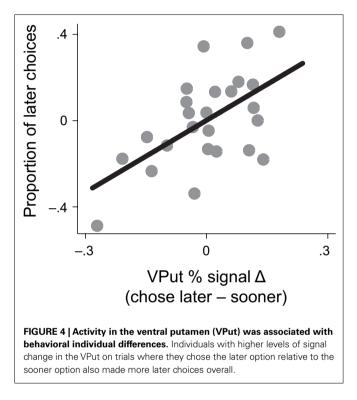
DISCUSSION

In the present study, we did not observe behavioral age differences in decision making with monetary intertemporal choices. The preference for sooner, smaller over larger, later rewards was not significantly stronger in younger compared to older adults. Given the small sample size, statistical power for this behavioral comparison is limited and we are hesitant to conclude anything

Region	R	Α	S	Ζ	Voxels
δ COMPONENT					
L middle frontal gyrus	-27	57	20	4.197	120
L middle frontal gyrus	-31	31	42	4.110	109
L ventral striatum	-19	7	-8	3.503	19
β COMPONENT					
None					

Table 2 | Age differences in regions with low (δ) and high (β) discount rates (older > younger).

Positive Z-scores indicate larger effects in older adults than younger adults.



from this behavioral result. Many prior studies find either stability (Green et al., 1996; Chao et al., 2009) or reductions in discounting across adult age (Green et al., 1994, 1999; Harrison et al., 2002; Reimers et al., 2009; Simon et al., 2010; Jimura et al., 2011; Löckenhoff et al., 2011), but others have reported increases in discounting from young adulthood to older age (Read and Read, 2004). Overall, the existing behavioral literature is conflicting. These discrepancies in existing studies may be partially related to interactions between individual difference variables (e.g., age) and state variables such as context or framing of the decisions (e.g., choices presented as delay lengths or the actual date of receipt; Peters and Büchel, 2011). These potential framing issues will not be fully resolved until they are directly examined in future studies. However, even while these issues remain unresolved, progress toward a more complete understanding of age-related change in intertemporal choice may be aided by examining age differences in the neural systems supporting these decisions.

Although we replicate findings that brain regions associated with the mesolimbic dopamine system respond preferentially to immediate rewards, we find a separate region of the putamen, within the VS, that responds to both immediate and delayed rewards in older but not younger adults. We also showed that relatively greater activation in the VS for delayed over sooner rewards was associated with an overall preference for delayed rewards. This effect may, at first, seem to contradict prior studies linking VS activity with a preference for immediate over delayed rewards in younger adults. However, the results are quite compatible with these prior findings. Specifically, individuals in the upper right quadrant of Figure 4 and Figure A4 in Appendix show greater VS sensitivity to delayed rewards and choose delayed rewards more often. Individuals in the lower left quadrant of Figure 4 and Figure A4 in Appendix show less VS sensitivity to delayed rewards (greater sensitivity to immediate rewards) and choose delayed rewards less often (and immediate rewards more often). Overall, this result clearly confirms a relationship between activation of this region and decision making on the task.

Previous studies, exclusively focused on younger adults, have shown that VS activity leads to more impulsive choice (McClure et al., 2004, 2007; Hariri et al., 2006). Prior work has emphasized that top-down input from the LPFC functions to overcome a VS-mediated present bias and enable more far-sighted choices (McClure et al., 2004, 2007; Figner et al., 2010). The results of the present study suggest that a different mechanism may apply to older adults. It is possible that the contributions of LPFC control are reduced with age as signals in the VS are tuned with experience. We hypothesize that experience may underlie the fact that subregions of the VS show modest sensitivity to time in older subjects.

The age differences were observed when examining regions that corresponded to δ -related representations of delayed reward value, but not for β -related representations of reward value. This pattern is consistent with the results of a recent study that included a much larger behavioral sample of young, middle-aged, and older adults and found age differences in 8-related discount rates but not β -related discount rates (Löckenhoff et al., 2011). That same study is the only experiment that has systematically attempted to explain the mediating variables between adult age differences and intertemporal choice (Löckenhoff et al., 2011). The study shows that emotional and motivational variables account for age differences in intertemporal choice. Basic neuropsychological measures that are presumed to rely on prefrontal resources do not explain the age differences. Consistent with prior research that older adults are better at forecasting future emotional states (Lachman et al., 2008; Nielsen et al., 2008; Scheibe et al., 2011), more positive emotional predictions of delayed rewards are associated with both older age and reduced discounting (Löckenhoff et al., 2011). Although we did not assess emotional forecasts of delayed rewards here, the results of the present study may provide a neural mechanism through which these previously observed age differences operate.

Since the dopamine system is believed to respond in anticipation of future rewards through associative learning (Montague et al., 1996; Schultz et al., 1997), our observed transfer of function may be due to greater experience with delayed rewards as people age. This increase in experience with delayed rewards through associative learning (Enomoto et al., 2011) over the course of decades may contribute to the improvement in forecasting the emotional impact of future events as discussed above. A number of studies have shown that anticipatory activation in the VS is modulated by the magnitude of an upcoming but not yet received reward and this activation is also correlated with anticipatory subjective emotional experience (Knutson and Greer, 2008).

Importantly, we are not suggesting that the appropriate valuation of rewards delayed by several weeks requires decades of experience to accurately estimate. Young adults in their twenties show neural activation in mesolimbic regions that correlates with delayed reward values (discounted subjective value; Kable and Glimcher, 2007; Peters and Büchel, 2009), and midbrain dopamine neurons in monkeys encode both immediate and delayed reward values through associative learning from experience over the course of weeks (Enomoto et al., 2011). Rather, we are suggesting that the additional experience with the realization of delayed rewards that older adults have accumulated over the lifetime may shape the sensitivity of this ventral striatal region. Although adults in their twenties will have some experience with shorter-term delayed rewards, the age differences may be even more pronounced for financial investments, for example, where there is a small but relatively reliable long-term rate of return (e.g., mutual funds). A 22-year old simply has not had the opportunity to appreciate the value of an 8% return over several decades.

Although age-related changes observed in the dopamine system and striatum have been associated with age-related declines in learning and decision making (Aizenstein et al., 2006; Mohr et al., 2009; Samanez-Larkin et al., 2010), it may be that gradual declines in the dopamine system with age do not disrupt the slow changes in associative learning from repeated experience with delayed rewards over decades of the life course. Furthermore, the dopaminergic changes that occur during healthy aging are not likely to be sufficiently dramatic to overwhelm the effects of accumulated experience. In contrast, the much more dramatic dopaminergic changes in Parkinson's disease have been shown to influence discounting (Housden et al., 2010; Voon et al., 2010). In general, adult age differences are more apparent in decision making tasks that require rapid learning in a novel environment than when decisions can be made based solely on the information

REFERENCES

Agarwal, S., Driscoll, J. C., Gabaix, X., and Laibson, D. I. (2009). "The age of reason: financial decisions over the life-cycle with implications for regulation," in *Brookings Papers on* *Economic Activity*, 51–117. Available at: http://muse.jhu.edu/journals/ eca/summary/v2009/2009.2.agarwal. html

Aizenstein, H. J., Butters, M. A., Clark, K. A., Figurski, J. L., Stenger, V. A., Nebes, R. D., Reynolds, C. F., presented (Mata et al., 2011) as is the case with these intertemporal choice tasks.

Although experience may play a role in human age differences, other factors likely contribute. Demographic factors like education and income also influence discounting and can interact with age (Green et al., 1996; Reimers et al., 2009). In fact, changes in income over the life span (e.g., related to investment experience) may be partially correlated with the age-related changes that we are attributing to experience. It is important to note that subjects in the present study were recruited by a market research company and matched across age groups on socioeconomic status (education, current or previous profession, income). One limitation of this approach is that the resulting San Francisco Bay area/Silicon Valley sample is healthier, wealthier, and more highly educated than the general population which may limit generalizability. However, a great strength of this targeted sampling strategy is that the contributions of differences in demographic factors to between-group differences in either behavior or neural activity have been minimized here. Aside from demographic factors, there is also recent evidence for behavioral differences in discounting between young and aged rats where experience with delayed rewards over the lifetime is relatively controlled (Simon et al., 2010). Thus, there may be neurobiological changes that are not experience-related that contribute to age differences in intertemporal choice.

Far-sighted behavior is an important target for behavioral interventions to counter challenges like the anemic retirement savings in America and the inability to withstand small inconveniences (e.g., taking medicine daily, exercise) that are critical for longterm health. The majority of evidence for shaping intertemporal decision making in younger adults has focused on prefrontal mechanisms (Peters and Büchel, 2011). However, the same strategies may not apply to older adults. In other domains, it is known that younger adults are best affected by informational messages that presumably alter behavior via the LPFC, whereas older adults respond better to emotional messages that may target regions like the VS and amygdala (Carstensen, 2006; Mikels et al., 2010; Samanez-Larkin et al., 2011). For far-sighted behaviors, a similar difference may exist for younger and older adults. Whereas adults may benefit by targeting cognitive control, individuals may also benefit from nudges to emotional systems.

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and Carter, C. S. (2006). Prefrontal and striatal activation in elderly subjects during concurrent implicit and explicit sequence learning. *Neurobiol. Aging* 27, 741–751.

Bäckman, L., Nyberg, L., Lindenberger, U., Li, S.-C., and Farde, L. (2006). The correlative triad among aging, dopamine, and cognition: current status and future prospects. *Neurosci. Biobehav. Rev.* 30, 791–807.

Camus, M., Halelamien, N., Plassmann, H., Shimojo, S., O'Doherty, J., Camerer, C., and Rangel, A. (2009). Repetitive transcranial magnetic stimulation over the right dorsolateral prefrontal cortex decreases valuations during food choices. *Eur. J. Neurosci.* 30, 1980–1988.

- Carstensen, L. L. (2006). The influence of a sense of time on human development. *Science* 312, 1913–1915.
- Chao, L.-W., Szrek, H., Pereira, N. S., and Pauly, M. V. (2009). Time preference and its relationship with age, health, and survival probability. *Judgm. Decis. Mak.* 4, 1–19.
- Cox, K. M., Aizenstein, H. J., and Fiez, J. A. (2008). Striatal outcome processing in healthy aging. *Cogn. Affect. Behav. Neurosci.* 8, 304–317.
- Cox, R. W. (1996). AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Comput. Biomed. Res.* 29, 162–173.
- Enomoto, K., Matsumoto, N., Nakai, S., Satoh, T., Sato, T. K., Ueda, Y., Inokawa, H., Haruno, M., and Kimura, M. (2011). Dopamine neurons learn to encode the long-term value of multiple future rewards. *Proc. Natl. Acad. Sci. U.S.A.* 108, 15462–15467.
- Figner, B., Knoch, D., Johnson, E. J., Krosch, A. R., Lisanby, S. H., Fehr, E., and Weber, E. U. (2010). Lateral prefrontal cortex and self-control in intertemporal choice. *Nat. Neurosci.* 13, 538–539.
- Glover, G. H., and Law, C. S. (2001). Spiral-in/out BOLD fMRI for increased SNR and reduced susceptibility artifacts. *Magn. Reson. Med.* 46, 515–522.
- Green, L., Fry, A. F., and Myerson, J. (1994). Discounting of delayed rewards: a life-span comparison. *Psychol. Sci.* 5, 33–36.
- Green, L., Myerson, J., Lichtman, D., Rosen, S., and Fry, A. (1996). Temporal discounting in choice between delayed rewards: the role of age and income. *Psychol. Aging* 11, 79–84.
- Green, L., Myerson, J., and Ostaszewski, P. (1999). Discounting of delayed rewards across the life span: age differences in individual discounting functions. *Behav. Processes* 46, 89–96.
- Hare, T. A., Camerer, C. F., and Rangel, A. (2009). Self-control in decisionmaking involves modulation of the vmPFC valuation system. *Science* 324, 646–648.
- Hariri, A. R., Brown, S. M., Williamson, D. E., Flory, J. D., de Wit, H., and Manuck, S. B. (2006). Preference for immediate over delayed rewards is associated with magnitude of ventral striatal activity. *J. Neurosci.* 26, 13213–13217.

- Harrison, G. W., Lau, M. I., and Williams, M. B. (2002). Estimating individual discount rates in Denmark. Am. Econ. Rev. 92, 1606–1617.
- Henninger, D. E., Madden, D. J., and Huettel, S. A. (2010). Processing speed and memory mediate agerelated differences in decision making. *Psychol. Aging* 25, 262–270.
- Hosseini, S. M. H., Rostami, M., Yomogida, Y., Takahashi, M., Tsukiura, T., and Kawashima, R. (2010). Aging and decision making under uncertainty: behavioral and neural evidence for the preservation of decision making in the absence of learning in old age. *Neuroimage* 52, 1514–1520.
- Housden, C. R., O'Sullivan, S. S., Joyce, E. M., Lees, A. J., and Roiser, J. P. (2010). Intact reward learning but elevated delay discounting in Parkinson's disease patients with impulsive-compulsive spectrum behaviors. *Neuropsychopharmacology* 35, 2155–2164.
- Jimura, K., Myerson, J., Hilgard, J., Keighley, J., Braver, T. S., and Green, L. (2011). Domain independence and stability in young and older adults' discounting of delayed rewards. *Behav. Processes* 87, 253–259.
- Kable, J. W., and Glimcher, P. W. (2007). The neural correlates of subjective value during intertemporal choice. *Nat. Neurosci.* 10, 1625–1633.
- Knutson, B., and Greer, S. M. (2008). Anticipatory affect: neural correlates and consequences for choice. *Philos. Trans. R Soc. Lond. B Biol. Sci.* 363, 3771–3786.
- Lachman, M. E., Röcke, C., Rosnick, C., and Ryff, C. D. (2008). Realism and illusion in Americans' temporal views of their life satisfaction: age differences in reconstructing the past and anticipating the future. *Psychol. Sci.* 19, 889–897.
- Laibson, D. I. (1997). Golden eggs and hyperbolic discounting. Q. J. Econ. 112, 443–477.
- Löckenhoff, C. E. (2011). Age, time, and decision making: from processing speed to global time horizons. Ann. N. Y. Acad. Sci. 1235, 44–56.
- Löckenhoff, C. E., O'Donoghue, T., and Dunning, D. (2011). Age differences in temporal discounting: the role of dispositional affect and anticipated emotions. *Psychol. Aging* 26, 274–284.
- Loewenstein, G., and Prelec, D. (1992). Anomalies in intertemporal choice: evidence and an interpretation. Q. J. Econ. 107, 573–597.
- Logue, A. W., Rodriguez, M. L., Peña-Correal, T. E., and Mauro, B. C.

(1984). Choice in a self-control paradigm: quantification of experiencebased differences. *J. Exp. Anal. Behav.* 41, 53–67.

- Luo, S., Ainslie, G., Giragosian, L., and Monterosso, J. R. (2009). Behavioral and neural evidence of incentive bias for immediate rewards relative to preferencematched delayed rewards. *J. Neurosci.* 29, 14820–14827.
- Mata, R., Helversen von, B., and Rieskamp, J. (2010). Learning to choose: cognitive aging and strategy selection learning in decision making. *Psychol. Aging* 25, 299–309.
- Mata, R., Josef, A. K., Samanez-Larkin, G. R., and Hertwig, R. (2011). Age differences in risky choice: a metaanalysis. *Ann. N. Y. Acad. Sci.* 1235, 18–29.
- McClure, S. M., Ericson, K. M., Laibson, D. I., Loewenstein, G., and Cohen, J. D. (2007). Time discounting for primary rewards. *J. Neurosci.* 27, 5796–5804.
- McClure, S. M., Laibson, D. I., Loewenstein, G., and Cohen, J. D. (2004). Separate neural systems value immediate and delayed monetary rewards. *Science* 306, 503–507.
- Mell, T., Wartenburger, I., Marschner, A., Villringer, A., Reischies, F. M., and Heekeren, H. R. (2009). Altered function of ventral striatum during reward-based decision making in old age. *Front. Hum. Neurosci.* 3:34. doi:10.3389/neuro.09.034.2009
- Mikels, J. A., Löckenhoff, C. E., Maglio, S. J., Goldstein, M. K., Garber, A., and Carstensen, L. L. (2010). Following your heart or your head: focusing on emotions versus information differentially influences the decisions of younger and older adults. J. Exp. Psychol. Appl. 16, 87–95.
- Mohr, P. N. C., Li, S.-C., and Heekeren, H. R. (2009). Neuroeconomics and aging: neuromodulation of economic decision making in old age. *Neurosci. Biobehav. Rev.* 34, 678–688.
- Montague, P. R., Dayan, P., and Sejnowski, T. J. (1996). A framework for mesencephalic dopamine systems based on predictive Hebbian learning. *J. Neurosci.* 16, 1936–1947.
- Nielsen, L., Knutson, B., and Carstensen, L. L. (2008). Affect dynamics, affective forecasting, and aging. *Emotion* 8, 318–330.
- Peters, J., and Büchel, C. (2009). Overlapping and distinct neural systems code for subjective value during intertemporal and risky decision making. *J. Neurosci.* 29, 15727–15734.
- Peters, J., and Büchel, C. (2010). Episodic future thinking reduces reward delay discounting through

an enhancement of prefrontalmediotemporal interactions. *Neuron* 66, 138–148.

- Peters, J., and Büchel, C. (2011). The neural mechanisms of intertemporal decision-making: understanding variability. *Trends Cogn. Sci. (Regul. Ed.)* 15, 227–239.
- Read, D., and Read, N. L. (2004). Time discounting over the lifespan. Organ. Behav. Hum. Decis. Process. 47, 22–32.
- Reimers, S., Maylor, E. A., Stewart, N., and Chater, N. (2009). Associations between a one-shot delay discounting measure and age, income, education and real-world impulsive behavior. *Pers. Individ. Dif.* 47, 973–978.
- Rogers, A. R. (1994). Evolution of time preference by natural selection. Am. Econ. Rev. 84, 460–481.
- Samanez-Larkin, G. R., and D'Esposito, M. (2008). Group comparisons: imaging the aging brain. Soc. Cogn. Affect. Neurosci. 3, 290–297.
- Samanez-Larkin, G. R., Gibbs, S. E. B., Khanna, K., Nielsen, L., Carstensen, L. L., and Knutson, B. (2007). Anticipation of monetary gain but not loss in healthy older adults. *Nat. Neurosci.* 10, 787–791.
- Samanez-Larkin, G. R., Kuhnen, C. M., Yoo, D. J., and Knutson, B. (2010). Variability in nucleus accumbens activity mediates age-related suboptimal financial risk taking. *J. Neurosci.* 30, 1426–1434.
- Samanez-Larkin, G. R., Wagner, A. D., and Knutson, B. (2011). Expected value information improves financial risk taking across the adult life span. Soc. Cogn. Affect. Neurosci. 6, 207–217.
- Scheibe, S., Mata, R., and Carstensen, L. L. (2011). Age differences in affective forecasting and experienced emotion surrounding the 2008 US presidential election. *Cogn. Emot.* 25, 1029–1044.
- Schott, B. H., Niehaus, L., Wittmann, B. C., Schütze, H., Seidenbecher, C. I., Heinze, H.-J., and Düzel, E. (2007). Ageing and early-stage Parkinson's disease affect separable neural mechanisms of mesolimbic reward processing. *Brain* 130, 2412–2424.
- Schultz, W., Dayan, P., and Montague, P. R. (1997). A neural substrate of prediction and reward. *Science* 275, 1593–1599.
- Shamosh, N. A., DeYoung, C. G., Green, A. E., Reis, D. L., Johnson, M. R., Conway, A. R. A., Engle, R. W., Braver, T. S., and Gray, J. R. (2008). Individual differences in delay discounting: relation to intelligence, working memory, and

anterior prefrontal cortex. *Psychol. Sci.* 19, 904–911.

- Simon, N. W., Lasarge, C. L., Montgomery, K. S., Williams, M. T., Mendez, I. A., Setlow, B., and Bizon, J. L. (2010). Good things come to those who wait: attenuated discounting of delayed rewards in aged Fischer 344 rats. *Neurobiol. Aging* 31, 853–862.
- Sutton, R. S., and Barto, A. G. (1998). *Reinforcement Learning*. Cambridge, MA: The MIT Press.
- Trostel, P. A., and Taylor, G. A. (2001). A theory of time

preference. *Econ. Inq.* 39, 379–395.

- Voon, V., Reynolds, B., Brezing, C., Gallea, C., Skaljic, M., Ekanayake, V., Fernandez, H., Potenza, M. N., Dolan, R. J., and Hallett, M. (2010). Impulsive choice and response in dopamine agonist-related impulse control behaviors. *Psychopharmacology (Berl.)* 207, 645–659.
- Whelan, R., and McHugh, L. A. (2009). Temporal discounting of hypothetical monetary rewards by adolescents, adults, and older adults. *Psychol. Rec.* 59, 247–258.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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APPENDIX

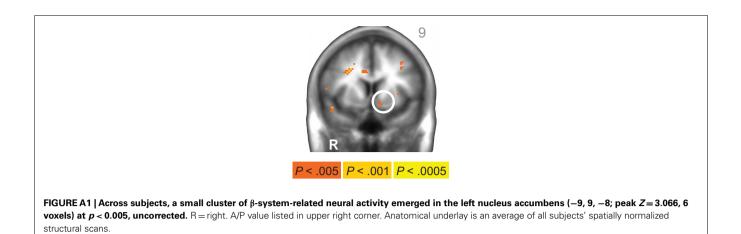
Table A1 | Brain regions representing subjective value using a hyperbolic model of discounting (with discounting parameter, *k*) across all subjects.

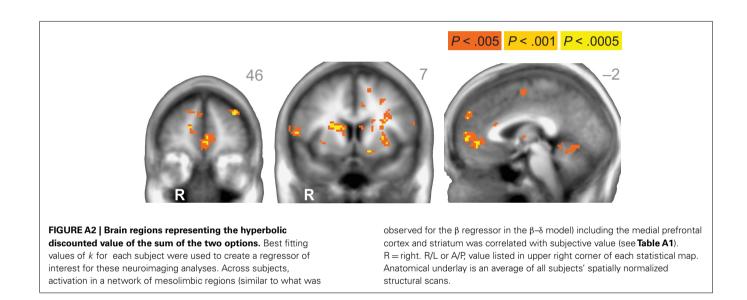
Region	R	Α	S	Ζ	Voxels
SUBJECTIVE VALUE (k)					
R superior frontal gyrus	7	49	30	4.045	109
L superior frontal gyrus	-33	47	32	4.129	67
L middle frontal gyrus	-25	11	36	3.897	57
R caudate/putamen	23	9	18	5.184	1142
L claustrum/putamen/nucleus accumbens	-29	3	24	4.762	2624
R inferior frontal gyrus	57	1	16	4.019	134
L insula	-43	-1	14	3.900	99
R thalamus	11	-1	6	3.904	71
R caudate body	15	-5	20	3.861	103
L thalamus	-7	-7	4	4.074	64
L inferior parietal lobule	-35	-27	26	3.987	104
R caudate tail	35	-29	0	3.672	89
R posterior cingulate	17	-43	28	3.874	74
R culmen	13	-57	-10	4.020	297
L precuneus	-17	-59	36	4.766	122
L posterior cingulate	-21	-59	16	3.905	78
R precuneus	21	-71	20	3.844	64
R middle occipital gyrus	33	-71	4	3.828	59
R middle temporal gyrus	39	-79	18	4.147	70

Table A2 | No age differences emerged in regions representing subjective value using a hyperbolic model of discounting (older > younger).

Region	R	Α	S	Z	Voxels
SUBJECTIVE VALUE	(<i>k</i>)				
None					

Again, the results are similar to the null age differences observed with the β component in the β - δ model.





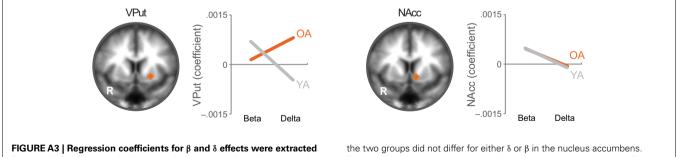
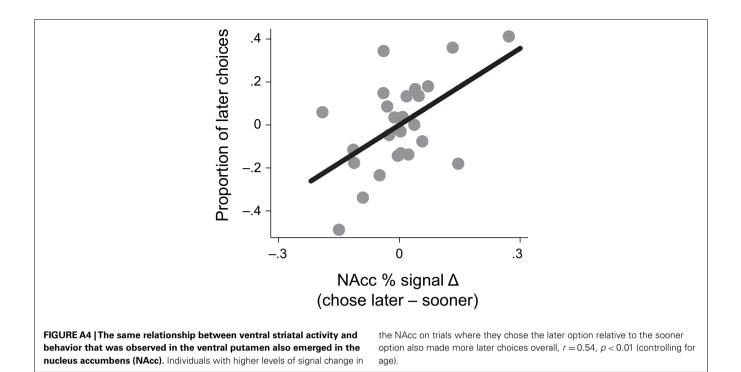


FIGURE A3 | Regression coefficients for β and δ effects were extracted from regions of interest in the ventral putamen and nucleus accumbens. As reported in the main text, older adults (OA) and younger adults (YA) showed significantly different δ but not β effects in the ventral putamen, but the two groups did not differ for either δ or β in the nucleus accumbens. Regions of interest were adjusted within subjects to only extract coefficients from gray matter. Anatomical underlay is an average of all subjects' spatially normalized structural scans.





Risk, reward, and decision-making in a rodent model of cognitive aging

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Jennifer L. Bizon, Department of Neuroscience, University of Florida College of Medicine, McKnight Brain Institute, P.O. Box 100244, Gainesville, FL 32610-0244, USA. e-mail: bizonj@ufl.edu Impaired decision-making in aging can directly impact factors (financial security, health care) that are critical to maintaining quality of life and independence at advanced ages. Naturalistic rodent models mimic human aging in other cognitive domains, and afford the opportunity to parse the effects of age on discrete aspects of decision-making in a manner relatively uncontaminated by experiential factors. Young adult (5-7 months) and aged (23-25 months) male F344 rats were trained on a probability discounting task in which they made discrete-trial choices between a small certain reward (one food pellet) and a large but uncertain reward (two food pellets with varying probabilities of delivery ranging from 100 to 0%). Young rats chose the large reward when it was associated with a high probability of delivery and shifted to the small but certain reward as probability of the large reward decreased. As a group, aged rats performed comparably to young, but there was significantly greater variance among aged rats. One subgroup of aged rats showed strong preference for the small certain reward. This preference was maintained under conditions in which large reward delivery was also certain, suggesting decreased sensitivity to reward magnitude. In contrast, another subgroup of aged rats showed strong preference for the large reward at low probabilities of delivery. Interestingly, this subgroup also showed elevated preference for probabilistic rewards when reward magnitudes were equalized. Previous findings using this same aged study population described strongly attenuated discounting of delayed rewards with age, together suggesting that a subgroup of aged rats may have deficits associated with accounting for reward costs (i.e., delay or probability). These deficits in cost-accounting were dissociable from the age-related differences in sensitivity to reward magnitude, suggesting that aging influences multiple, distinct mechanisms that can impact cost-benefit decision-making.

Keywords: aged, choice, rats, probability, discounting, reward sensitivity, memory

INTRODUCTION

Life requires continuous weighing of costs and benefits to make decisions among outcomes which differ with respect to magnitude, probability, and delay to their arrival. Such choices may prove particularly critical at advanced ages when poor decision-making (e.g., with respect to finances or healthcare) could have deleterious consequences for maintenance of independence and overall quality of life. Many of the neural, cognitive, emotional, and social factors that influence decision-making processes are known to change across the lifespan, but how such alterations integrate to impact decision-making remains poorly understood (Mohr et al., 2010; Eppinger et al., 2011). Such questions are becoming increasingly important, however, given that average life expectancy and the cognitive disabilities associated with advanced age continue to rise (AgingStats.gov, 2005).

Risk-taking has been most often evaluated in aged individuals within the context of economic decisions. Conventional wisdom suggests that risk-taking decreases in normal aging (Kumar, 2007),

consistent with evidence that aged individuals report less impulsivity and sensation-seeking than their younger cohorts (Roalf et al., 2011). Indeed, such risk-aversion may be an adaptive strategy under some circumstances (e.g., to preserve accumulated wealth toward the end of life), although excessive risk-aversion could be maladaptive in circumstances in which some degree of risktaking provides a greater net gain. Notably, however, other studies show that aged adults can actually be less likely than young to choose low-risk options in some circumstances (Denburg et al., 2005; Henninger et al., 2010). Broadly speaking, whether decisionmaking improves, declines, or remains stable across the lifespan seems to depend on the type of decision-making and the context in which decisions are framed (Mather, 2006; Mata et al., 2011; Mienaltowski, 2011; Strough et al., 2011). Indeed, relationships between some aspects of decision-making and aging may be non-linear, with decision quality increasing up to approximately age 50 and then declining thereafter (Agarwal et al., 2007).

Within this context, substantial variability in risk-based decision-making has been reported among aged individuals, implicating multiple cognitive and neural mechanisms (Denburg et al., 2005; Brown and Ridderinkhof, 2009). The degree to which an individual is able to accurately anticipate both future rewards and costs will influence choice behavior (Eppinger et al., 2011); however, studies directly investigating rewards and costs in aging have yielded somewhat disparate results. Gilbert and colleagues reported robust deficits in anticipation of a sucrose reward in aged rats (Maasberg et al., 2011), and Frank and Kong (2008) found enhanced learning about negative compared to positive outcomes in an older compared to a younger subgroup of aged adults. In contrast, Samanez-Larkin et al. (2007) reported that aged subjects showed no difference in their behavioral or neural responses to anticipated rewards but significantly attenuated responses to anticipated costs (although in the same study they found no age difference in subjects' ability to learn about positive vs. negative outcomes). Together, these studies indicate that the effects of age on processing of rewards and costs may be largely dissociable, and support a multiple factor causal framework for age-related changes in decision-making (Brown and Ridderinkhof, 2009). Indeed, deficits in mnemonic abilities are also prevalent among aged individuals, and at least one study found that individual differences in memory and information processing speed could account for some aspects of risk-based decision-making in aged individuals (Henninger et al., 2010).

Naturalistic rodent models mimic human aging in a number of cognitive domains, such as memory and aspects of executive function (e.g., cognitive flexibility). As in humans, there are robust individual differences in cognitive performance among aged rats (Gallagher et al., 1993; Barense et al., 2002; Schoenbaum et al., 2006; LaSarge et al., 2007; Bizon et al., 2009). Because the laboratory rearing environment is largely homogeneous, these individual differences in cognitive aging can be largely dissociated from experiential factors in a way that is difficult to achieve in human populations. In previous work, our laboratory used young and aged Fischer 344 (F344) rats to determine how normal aging affects inter-temporal decision-making, and found that aged rats showed strongly attenuated discounting of delayed rewards relative to young (Simon et al., 2010). To our knowledge, however, there are no studies in which animal models have been used to evaluate the effects of age on risk-based decision-making. In the current study, young and aged F344 rats were assessed on a probability discounting task which involved making discrete-trial choices between small certain rewards and large probabilistically delivered rewards (Cardinal and Howes, 2005; Floresco et al., 2008). The same rats were also assessed in the Morris water maze to determine how age-related alterations in decision-making are related to spatial learning and memory.

MATERIALS AND METHODS

SUBJECTS

Young (5–6 months) and aged (22–24 months) male F344 rats were obtained from the National Institute on Aging colony (Taconic Farms, Hudson, NY, USA) and housed in the AAALACaccredited vivarium facility in the Psychology Building at Texas A&M University in accordance with the rules and regulations of the Texas A&M University Laboratory Animal Care Committee. The facility was maintained at a consistent 25°C with a 12-h light/dark cycle (lights on at 0800 hours) with free access to food and water except as noted below. Rats were tested in five cohorts (each including at least n = 3 of each age). These cohorts were tested in the probability discounting and associated control conditions, and a subset was also tested in the Morris water maze, either immediately before or immediately after the decision-making tasks. There was some attrition across experiments, particularly in the aged group, such that only a portion of the rats tested in the probability discounting task completed all of the other tasks.

Experiment 1: assessing the effects of age on probability discounting

Apparatus. Testing in the probability discounting task and control conditions was conducted in eight identical standard rat behavioral test chambers $(30.5 \text{ cm} \times 25.4 \text{ cm} \times 30.5 \text{ cm}, \text{ Coul-}$ bourn Instruments, Whitehall, PA, USA) with metal front and back walls, transparent Plexiglas side walls, and a floor composed of steel rods (0.4 cm in diameter) spaced 1.1 cm apart. Each test chamber was housed in a sound attenuating cubicle, and equipped with a recessed food pellet delivery trough fitted with a photobeam to detect head entries and a 1.12-W lamp to illuminate the trough. This trough, into which the 45-mg grain-based food pellet rewards (PJAI, Test Diet, Richmond, IN, USA) were delivered, was located 2 cm above the floor in the center of the front wall. Two retractable levers were located to the left and right of the food trough, 11 cm above the floor. Experiments were controlled and data were collected by a computer interfaced with the behavioral test chambers and equipped with Graphic State 3.01 software (Coulbourn Instruments).

Experimental procedures. Prior to the start of behavioral testing, rats (n = 20 young and 20 aged) were reduced to 85% of their free feeding weight over the course of 1 week, and maintained at this weight for the duration of the experiments (except during water maze training). On the day prior to shaping, each rat was given five 45 mg food pellets in its home cage to reduce neophobia to the food reward used in the task. Shaping procedures for the probability discounting task followed those used previously (Cardinal et al., 2000; LaSarge et al., 2007; Simon et al., 2010). Shaping began with a 64-min session of magazine training consisting of 38 deliveries of a single food pellet with an inter-trial interval (ITI) of 100 ± 40 s. Following magazine training, rats were trained to press a single lever (either the left or right, counterbalanced across groups; the other lever was retracted during this phase of training) to receive a single food pellet. After reaching a criterion of 50 lever presses in 30 min, rats were then trained on the opposite lever under the same criterion. This protocol was followed by further shaping sessions in which both levers were retracted and rats were trained to nose poke into the food trough during simultaneous illumination of the trough and house lights. When a nose poke occurred, a single lever was extended (left or right, pseudorandomly determined, such that each lever was presented once in every two-trial block), and a lever press resulted in immediate delivery of a single food pellet. Immediately following the lever press, the trough light was extinguished and the lever was retracted. Rats were trained to a criterion of 30 presses on each lever within 60 min, with an ITI of 40 ± 10 s.

Test sessions in the probability discounting task were 60 min long and contained five blocks of 18 trials each. Each 40 s trial began with a 10-s illumination of the food trough and house lights. A nose poke into the food trough during this time extinguished the food trough light and triggered extension of either a single lever (forced choice trials) or of both levers simultaneously (free choice trials). If rats failed to nose poke within the 10-s time window, the lights were extinguished and the trial was scored as an omission. A press on one lever (either left or right, counterbalanced across age groups) resulted in immediate delivery of one food pellet (the small reward). A press on the other lever resulted in immediate delivery of two food pellets (the large reward) on a probabilistic basis. The probability of large reward delivery in the first block of trials was set at 100%. In subsequent blocks of trials, the probability of large reward delivery decreased to 75, 50, 25, and 0%. Each block began with eight forced choice trials in which only a single lever was extended and which were used to establish the probabilities in effect for that block (four for each lever), followed by 10 free choice trials (Cardinal and Howes, 2005; Simon et al., 2009). Once either lever was pressed, the levers were immediately retracted. Food delivery was accompanied by re-illumination of both the food trough and house lights, which were extinguished upon entry to the food trough to collect the food or after 10s, whichever occurred sooner. Failure to press either lever within 10 s of their extension resulted in the levers being retracted and lights extinguished, and the trial was scored as an omission. Rats were tested in the probability discounting task until stable performance was observed across a five session block (at least 25 sessions - see Data Analysis for description of stable performance).

Experiment 2: assessing the effects of age on sensitivity to reward probability (equal rewards condition)

To assess the rats' ability to detect and respond to the different probabilities of reward delivery employed in the probability discounting task, the amount of food associated with each of the levers was equalized (i.e., one food pellet for either choice) while the probabilities of delivery remained the same as in Experiment 1. Rats were tested under these conditions until stable performance was achieved (at least 10 sessions).

Experiment 3: assessing the effects of age on sensitivity to reward magnitude (equal probabilities condition)

To assess the rats' ability to detect and respond to differences in reward magnitude, the amounts of food associated with each lever were restored to their initial conditions (one food pellet vs. two food pellets) and the probability of large reward delivery was set to 100% for all five blocks. Rats were tested under these conditions until stable performance was achieved (at least 10 sessions).

Data analysis. For Experiments 1–3, raw data files were exported from Graphic State software and compiled using a custom macro written for Microsoft Excel (Dr. Jonathan Lifshitz, University of Kentucky). Statistical analysis was conducted in SPSS 19.0. Analyses of stable performance in the decision-making tasks were conducted using a two-factor repeated measures ANOVA (trial block X

test session) conducted on the last five consecutive sessions of testing in each experiment. Stable performance was defined as a main effect of trial block in the absence of main effects or interactions involving test session (Mar and Robbins, 2007; Simon et al., 2010). Comparisons between groups in the decision-making tasks were conducted on averaged data collapsed across these last five (stable) sessions, using two-factor repeated measures ANOVA (group X trial block), with Tukey's *post hoc* tests when warranted. For all analyses, *p* values less than 0.05 were considered significant.

Experiment 4: are age-related alterations in decision-making related to spatial memory impairment?

Apparatus. The water maze consisted of a circular tank (diameter 183 cm, wall height 58 cm) painted white and filled with water (27°C) made opaque with the addition of non-toxic white tempera paint. The maze was surrounded by black curtains to which were affixed large white geometric designs, which provided extramaze visual cues. For the spatial reference memory (hidden platform) task, a retractable escape platform (12 cm diameter, HVS Image, UK) was submerged 2 cm below the surface of the water in the center of the southwest quadrant of the maze. For the cued (visible platform) task, the platform protruded 2 cm above the surface of the water, and was located in a different quadrant of the maze on each trial. A video camera mounted above the center of the maze was connected to a DVD recorder and computer, which were used for data storage and analysis using a video tracking system (Water 2020, HVS Image, UK).

Procedures.

Spatial reference memory (hidden platform) task. Spatial reference memory was assessed as described previously (LaSarge et al., 2007; Bizon et al., 2009). Briefly, rats received three daily training trials with a 30-s ITI over eight consecutive days. On each trial, rats were placed into the water facing the wall of the maze at one of four equally spaced start positions (north, south, east, or west). The start positions were varied in a pseudo-random fashion, such that all rats started from each of the locations approximately the same number of times. Once in the water, rats were allowed to swim until they found the hidden platform or until 90 s elapsed, at which time they were guided to the escape platform by the experimenter. Rats remained on the platform for 30s and then were placed in a holding chamber for 30s before the next trial. Every sixth trial was a probe trial in which the platform was lowered to the bottom of the maze for the first 30 s of the trial, after which it was raised to allow the rats to escape.

Cued (visible platform) task. On the day after the last session of spatial reference memory training, rats were given a single session with six trials of cue training. For cue training, rats were trained to escape to a visible platform (painted black and protruding 2 cm above the water's surface). Both the start position and platform location were varied on each trial, making the extramaze cues explicitly irrelevant to the platform location. On each trial, rats were allowed to search for the platform for a maximum of 90 s and then were allowed to remain there for 30 s before a 30-s ITI.

Behavioral and statistical analyses. For each task, data files were created by the Water 2020 software and were exported to Microsoft

Excel and SPSS (v. 19.0) for analysis. Training trial data in the spatial reference memory task were averaged into four blocks consisting of the five trials preceding each probe trial, and performance was analyzed using a pathlength measure (pathlength is the total distance traveled from the start position to the platform and is reported in centimeters). To provide an overall measure of spatial learning ability for each rat, a "spatial learning index" was calculated using mean search error from interpolated probe trials, as described in Bizon et al. (2009), Gallagher et al. (1993). To calculate search error, the rat's distance from the platform was sampled 10 times/s and these distances were averaged into 1 s bins. Mean search error is the sum of these 1 s bins minus the optimal path from the start location to the platform, divided by the 30-s duration of the probe trials. Mean search error on probe trials is weighted and summed to provide the spatial learning index (Gallagher et al., 1993; Bizon et al., 2009). Comparisons between groups on training trials (in both the hidden and visible platform tasks) were conducted using two-factor ANOVA (group X training trial), with Tukey post hoc tests when warranted. In all cases, p values less than 0.05 were considered significant.

RESULTS

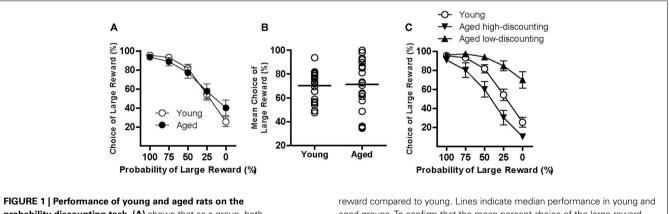
EXPERIMENT 1: ASSESSING THE EFFECTS OF AGE ON PROBABILITY DISCOUNTING

Rats (n = 20 young and 20 aged) were first tested in the probability discounting task, which involved discrete-trial choices between a small certain reward and a large reward for which the probability of delivery decreased in blocks of trials across the course of each test session. As shown in **Figure 1A**, all rats decreased their choice of the large reward as the probability of reward delivery decreased across trial blocks, but there were no differences between young and aged rats. This was confirmed by a two-factor repeated measures ANOVA (age X probability), which revealed a main effect of

probability $[F_{(4, 152)} = 88.06, p < 0.05]$, but neither a main effect of age $[F_{(1,38)} = 0.06, \text{ n.s.}]$ nor an interaction between age and probability $[F_{(4, 152)} = 2.14, \text{ n.s.}]$. Notably, there was significantly greater variance in performance among aged rats relative to young (Levene's test for equality of variances conducted on the mean percent choice of the large reward averaged across all five trial blocks, F = 5.30, p < 0.05; Figure 1B). This greater variance in the aged rats fell on both ends of the distribution relative to young rats, suggesting that differences in individual performance may be mediated by multiple underlying factors. To investigate this further, a median split was performed on data from aged rats, creating "highdiscounting" and "low-discounting" subgroups (n = 10/group,Figure 1C). A two-factor repeated measures ANOVA comparing young, aged high-discounting, and aged low-discounting rats revealed a main effect of probability $[F_{(4, 148)} = 91.29, p < 0.05],$ a main effect of group $[F_{(2, 37)} = 19.03, p < 0.05]$, and an interaction between probability and group $[F_{(8, 148)} = 7.01, p < 0.05]$. Post hoc tests revealed that each of the three groups was significantly different from the others (ps < 0.05). This subgrouping was used to further investigate behavioral mechanisms underlying the different patterns of discounting observed in aged rats (see below).

EXPERIMENT 2: ASSESSING THE EFFECTS OF AGE ON SENSITIVITY TO PROBABILITY (EQUAL REWARDS CONDITION)

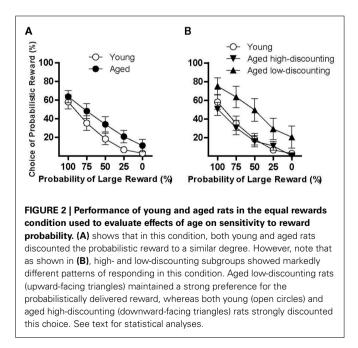
Differences in discounting of probabilistic rewards could be due to a number of variables, including sensitivity to probability and reward magnitude. To determine whether age-related alterations in preference for probabilistic reward could mediate the increased variance observed in aged rats, the task contingencies were altered such that responses on both levers earned a single food pellet, but the probabilities of reward delivery were the same as in the probability discounting task (100, 75, 50, 25, 0%). This task condition tested preference for certain vs. probabilistic



probability discounting task. (A) shows that as a group, both young (open circles) and aged (closed circles) rats discounted the value of the large reward to a comparable degree as indicated by decreased choice of the large reward as the probability of large reward delivery decreased. Notably, however, significantly greater variance in discounting performance was observed among aged rats. (B) shows the mean percent choice of the large reward for individual young and aged rats. By this measure, while some aged rats performed comparably to young, a large subset of aged rats showed a strong preference for the large reward. In contrast, another subset of aged rats showed less preference for the large reward compared to young. Lines indicate median performance in young and aged groups. To confirm that the mean percent choice of the large reward measure reflected true differences in discounting performance, aged rats were subgrouped via a median split into aged high- (downward-facing triangles) and aged low-discounting (upward-facing triangles) subgroups, **(C)**. Note that patterns of responding were significantly different between these two aged subgroups, falling on either side of young performance. This distinction between high- and low-discounting subgroups was used in subsequent conditions to further investigate factors that might contribute to these robustly different patterns of responding. See text for statistical analyses.

rewards, uncontaminated by differences in reward magnitude. Young (n = 17) and aged (n = 15) rats were tested in this condition until reaching stable performance. Both young and aged rats decreased their choice of the probabilistic reward as the probability of delivery decreased $[F_{(4, 120)} = 53.90, p < 0.05]$, but there was no main effect or interaction involving age (Fs < 2.30, n.s.; Figure 2A). There were, however, dramatic differences between the aged high- (n = 7) and low- (n = 8) discounting rats relative to young rats. Young rats and aged high-discounting rats performed similarly, while aged low-discounting rats showed greater preference for the probabilistic reward than either of the other two groups (Figure 2B). A two-factor ANOVA (group X probability) revealed main effects of both probability $[F_{(4,116)} = 44.60,$ p < 0.05] and group $[F_{(2, 28)} = 4.72, p < 0.05]$, but no interaction $[F_{(8, 116)} = 0.58, \text{ n.s.}]$. Post hoc tests confirmed that the aged lowdiscounting rats had a significantly greater preference for the probabilistic reward compared to the young and aged high-discounting rats (ps < 0.05), but that the young and aged high-discounting rats did not differ from each other.

To confirm that the observed differences between aged highand low-discounting rats in the equal rewards condition were not an artifact of the median split of the aged group, the same median split procedure was performed on the young group based on performance in the probability discounting task. As expected, young high- and low-discounting rats differed significantly from each other on the probability discounting task in Experiment 1 [main effect of probability, $F_{(4,72)} = 82.99$, p < 0.05; main effect of group, $F_{(1,18)} = 33.26$, p < 0.05; interaction between probability and group, $F_{(4,72)} = 4.76$, p < 0.05]. Importantly, however, these groups did not differ in the equal rewards condition [main effect of probability, $F_{(4,60)} = 27.81$, p < 0.05; main effect of group, $F_{(1,15)} = 0.05$, n.s.; interaction between probability and group, $F_{(4,60)} = 0.88$, n.s.], suggesting that the difference between the aged high- and



low-discounting rats on the equal rewards condition was representative of true phenotypic differences between the aged subgroups.

EXPERIMENT 3: ASSESSING THE EFFECTS OF AGE ON SENSITIVITY TO REWARD MAGNITUDE (EQUAL PROBABILITIES CONDITION)

Data from the equal rewards condition suggested that differential preference for probabilistic rewards could account for some of the variance in probability discounting in the aged rats. To determine whether differential sensitivity to reward magnitude might also contribute to probability discounting performance in aged rats, the task contingencies were altered such that the reward magnitudes were returned to their original condition (one vs. two food pellets), but the probability of the large reward remained at 100% across all trial blocks. This task condition tested preference for the large vs. small reward, uncontaminated by differences in reward probability. Young (n = 17) and aged (n = 11)rats were tested in this condition until stable performance was achieved. The pattern of performance differed between young and aged rats, with aged rats showing decreased preference for the large reward across trial blocks relative to young rats {twofactor ANOVA (age X trial block): main effect of trial block $[F_{(4, 104)} = 16.11, p < 0.05]$, main effect of age $[F_{(1, 26)} = 19.96,$ p < 0.05], interaction $[F_{(8, 104)} = 3.80, p < 0.05;$ Figure 3A]}. A similar analysis was also conducted using the aged high- and low-discounting subgroups as in Experiment 2 (Figure 3B). A two-factor ANOVA (group X trial block) revealed a main effect of trial block $[F_{(4,100)} = 18.99, p < 0.05]$, as well as a main effect of group $[F_{(2,25)} = 25.02, p < 0.05]$ and an interaction between group and trial block $[F_{(8, 100)} = 3.38, p < 0.05]$. In contrast to the pattern of results in Experiment 2, post hoc tests revealed that aged high-discounting rats (n = 5) had significantly reduced preference for the large reward compared to both young rats and aged low-discounting rats (ps < 0.05), but that young rats and aged low-discounting (n=6) rats did not differ from each other (n.s.). Importantly, although there was some mortality among aged rats prior to completing Experiments 2 and 3, this mortality likely did not account for differences between aged highand low-discounting subgroups in these experiments, as mortality was equivalent in the two subgroups. Finally, as in the equal rewards condition, there were no differences between the young subgroups in the equal probabilities condition following a median split [main effect of trial block, $F_{(4, 60)} = 6.81, p < 0.05$; main effect of group, $F_{(1, 15)} = 0.24$, n.s.; interaction between trial block and group, $F_{(4, 60)} = 1.33$, n.s.].

Relationships between performance on decision-making tasks

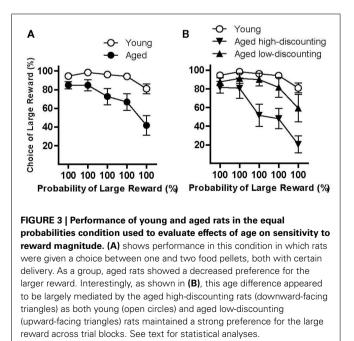
The distinct patterns of differences between the aged high- and low-discounting rats and young rats in the equal rewards and equal probabilities conditions suggest that probability discounting in aged rats was mediated by aged-related alterations in two independent factors. Consistent with this interpretation, among aged rats, both the equal rewards and equal probabilities conditions were correlated with probability discounting task performance (bivariate correlation, rs = 0.61 and 0.66 respectively, ps = 0.02 and 0.03), but not with each other (r = 0.40, p = 0.22).

EXPERIMENT 4: ARE AGE-RELATED DIFFERENCES IN DECISION-MAKING RELATED TO MEMORY IMPAIRMENT?

A subset of the rats tested in the choice tasks was also tested in the Morris water maze (n = 20 young, n = 17 aged). Figure 4A shows performance (pathlength to reach the hidden platform) on blocks of five training trials in the spatial reference memory task in young and aged rats. A repeated measures ANOVA (age X training trial block) revealed that rats improved over the course of training [main effect of training trial block, $F_{(3, 105)} = 27.73$, p < 0.05] and that aged rats had significantly longer pathlengths than young cohorts, demonstrating impaired performance [main effect of age, $F_{(1, 35)} = 14.15$, p < 0.05; interaction between age and training trial block, $F_{(3, 105)} = 7.34$, p < 0.05].

Performance on the four interpolated probe trials was used to calculate a spatial learning index (Gallagher et al., 1993; Bizon et al., 2009). Learning index scores have been shown to be associated with age-related changes in neurobiological substrates of spatial memory, as well as other aspects of cognition (Nicolle et al., 1999; Smith et al., 2000; Bizon et al., 2001; LaSarge et al., 2007). As expected, an unpaired *t*-test performed on the spatial learning index data indicated that aged rats were significantly impaired (higher learning index scores) relative to young [means \pm SE: young = 211.0 \pm 7.2, aged = 267.6 \pm 9.1; $t_{(35)} = 4.91$, p < 0.05].

To determine whether impaired water maze performance in the aged rats was specific to spatial learning, rats were trained in a cued (visible platform) version of the water maze task in a single session on the day following the last day of spatial reference memory training. Similar to previous findings in this study population (LaSarge et al., 2007; Bizon et al., 2009; Murchison et al., 2009), there were no differences between young and aged rats in their ability to locate the visible platform [mean \pm SE pathlength collapsed across the six visible platform training trials: young = 332.3 ± 23.7 . Aged = 306.5 ± 37.3 ; $t_{(35)} = 0.60$, n.s.],



demonstrating that water maze deficits in aged rats were not due to impairments in sensorimotor function, motivation, or ability to learn the procedural aspects of the task.

Relationships between probability discounting and water maze performance

The results of the analyses described above identified age-related alterations in performance on both the choice tasks and the spatial reference memory version of the Morris water maze. To determine whether performance in these tasks was related (i.e., whether differences in water maze performance could account for individual differences in probability discounting), spatial reference memory performance was compared between aged high- and low-discounting subgroups. A repeated measures ANOVA (subgroup X training trial block) conducted on training trials revealed main effects of training trial block $[F_{(3, 102)} = 16.81, p < 0.05]$ and subgroup $[F_{(2,34)} = 6.91, p < 0.05]$, as well as a significant interaction $[F_{(6, 102)} = 3.93, p < 0.05]$. However, post hoc comparisons revealed that these effects were driven by differences between young rats and each of the two aged subgroups (ps < 0.05), and that there were no differences between the aged high- and lowdiscounting subgroups with respect to spatial learning ability (Figure 4B). Moreover, a bivariate correlation confirmed that there was no significant relationship among aged rats between mean percent choice of the large reward in the probability discounting task and the spatial learning index in the water maze (r = 0.35, n.s.).

DISCUSSION

With the aging of populations in developed countries and the importance of sound decision-making for quality of life, there is increasing interest in understanding and optimizing decision-making at advanced ages. Rodent models offer several advantages for addressing such issues, including a relatively short lifespan, the ability to largely control life experience, and the ability to manipulate a range of neurobiological variables. In addition, a large literature indicates that analogous behavioral and neural mechanisms govern animal and human decision-making in young subjects (Floresco et al., 2008; Winstanley, 2011). The experiments

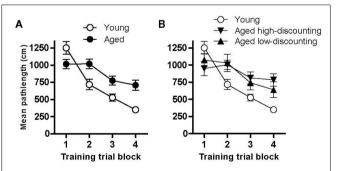


FIGURE 4 | Performance of young and aged rats on the spatial water maze and probability discounting tasks. (A) shows that aged rats were impaired relative to young in their ability to learn and remember the platform location. Notably, as shown in (B), aged high- and low-discounting rats did not differ in their spatial learning performance, indicating that mnemonic deficits are not associated with the different patterns of responding observed in the probability discounting task. See text for statistical analyses.

presented here examined the effects of age on a probability discounting task requiring choices between small certain rewards and large rewards for which there were varying risks of reward omission. Although, as a group, aged rats performed comparably to young, there was considerable individual variability in aged rats' performance. Discounting performance in aged (but not young) rats was related to two distinct factors: preference for risky vs. certain rewards (as evident in the equal rewards condition), and preference for large vs. small rewards (as evident in the equal probabilities condition). Importantly, the fact that age-related alterations in these two factors drove performance on the probability discounting task in opposite directions appears to account for the absence of group age differences, and highlights the importance of considering individual differences in studies of cognition in aging (Bizon et al., 2009; Gallagher et al., 2011). Together, these findings suggest that age-related changes in two independent factors (sensitivity to costs and rewards) influence the degree to which probabilistic rewards are discounted (Brown and Ridderinkhof, 2009; Eppinger et al., 2011).

The finding that some aged rats (the low-discounting subgroup) demonstrated elevated preference for probabilistic rewards is consistent with studies in which (some) aged individuals make riskier choices than young, leading to suboptimal outcomes (Denburg et al., 2005; Henninger et al., 2010). This pattern of behavior could reflect impaired perception/discrimination of probabilities in the aged low-discounting subgroup. Another interpretation, however, is that performance in this subgroup reflects a broader deficit in sensitivity to the costs associated with the risky choice, possibly resulting from attenuated negative affect in anticipation of losses (Samanez-Larkin et al., 2007). This latter explanation fits the pattern of results observed previously in our laboratory in which the same study population of F344 rats was assessed on a delay discounting task (Simon et al., 2010). In that study, aged rats discounted delayed rewards to a significantly lesser degree than young rats. Although this pattern of behavior (strong preference for large rewards in spite of the delay to their delivery) was advantageous in the context of the delay discounting task, it could also reflect a failure to account for the costs (having to wait longer for food delivery) incurred by choosing a delayed reward. Indeed, as shown in Figure 5A, a median split performed on the aged rat data from this previous delay discounting study reveals a pattern of results that is similar to that from the present probability discounting experiment (i.e., some aged rats failed to adjust their choice behavior in response to the delay - Figure 5B shows data from Figure 1C replotted for comparison). This similarity is consistent with a subset of aged rats across both experiments failing to account for the costs (delay or probability) associated with the large reward. Future studies in which performance on the delay and probability discounting tasks is compared directly are needed to determine whether deficits in cost-accounting are present in the same subset of aged rats across different types of reward costs.

In addition to possible deficits in cost-accounting, other aged rats (the aged high-discounting subgroup) showed patterns of choice behavior that were consistent with reduced sensitivity to the reward itself. Findings from the human literature regarding reward sensitivity in aging are somewhat contradictory. For example, Samanez-Larkin et al. (2007) reported maintained affective

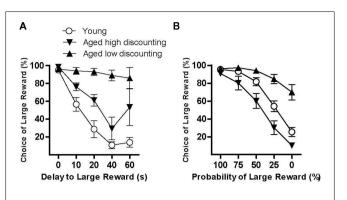


FIGURE 5 | Subsets of aged rats may have deficits in "cost-accounting." (A,B) show data from two cohorts of young and aged rats that were assessed on either the delay discounting [(A), adapted from Simon et al., 2010] or probability discounting task [(B), present study, replotted from Figure 1C for comparison]. Together these findings suggest that attenuated discounting in a subset of aged rats may be associated with failure to properly integrate costs (probability, delay) rather than factors associated solely with the ability to detect and respond to probabilities. See text for further discussion.

responses in anticipation of gains in aged subjects performing a monetary incentive delay task. In contrast, other studies have reported reduced neural activity and learning in aged subjects' response to rewards, indicating potential reductions in reward sensitivity (Frank and Kong, 2008; Hammerer et al., 2011). Consistent with these latter findings as well as the findings in the present study, a recent paper by Maasberg et al. (2011) found a reduction in reward anticipation in aged rats performing a sucrose preference task. In contrast, in our previous study of delay discounting in aged F344 rats (Simon et al., 2010), we did not find evidence for age-related differences in sensitivity to reward magnitude (aged rats preferred large over small rewards to the same degree as young cohorts). Differences with respect to reward sensitivity in the Simon et al. (2010) study and our current results are likely due to the fact that the magnitude of the difference between the small and large rewards differed across the two studies. In our previous study, the difference between the large (four food pellets) and small (one food pellet) rewards may have been salient enough to overcome any age-related decrements in sensitivity to reward magnitude. In the current study, the smaller difference between the large (two food pellets) and small (one food pellet) rewards may have rendered such sensitivity decrements more readily obvious. Related to this issue, a recent study by Singh et al. (2011) showed no effect of age on a Pavlovian reward devaluation procedure. Devaluation of a food reward via conditioned taste aversion reduced Pavlovian conditioned responding to a cue predictive of that reward to a similar degree in young and aged rats. These findings could be viewed as contrary to age-related changes in representation of reward value; however, in the devaluation paradigm the change in reward value is arguably quite large. Considered together, these data highlight the fact that age-related deficits in reward sensitivity or anticipation are likely to affect behavior to a greater extent when the differences between rewards are small. This hypothesis may help to account for discrepant findings related to age influences on reward sensitivity.

Probability discounting was correlated with performance in both the equal rewards and equal probabilities conditions, but performance in these two conditions was not related. These findings suggest that sensitivity to costs and sensitivity to reward magnitude are distinct factors that can influence probabilistic decision-making, and that an individual's choice performance may be driven by the relative balance of these two factors (Brown and Ridderinkhof, 2009; Eppinger et al., 2011). Deficits in other cognitive functions in aging also have the potential to influence risk-based decision-making. For example, it has been suggested that due to suboptimal mnemonic abilities, aged subjects tend to rely less on new information and more on previous experience to make decisions (Sanfey and Hastie, 2000; Gilsky, 2007). Indeed, Henninger et al. (2010) showed a relationship between memory and information processing abilities in aged subjects and performance on a risk-based decision task. The current findings did not support such a relationship inasmuch as probability discounting was not correlated with spatial learning in the Morris water maze. Notably, the multiple-day water maze protocol used here is dependent upon hippocampus and related circuitry but is not sensitive to working memory abilities that may be more relevant for probability discounting performance (Sloan et al., 2006). Working memory deficits have been reported in this study population of aged rats, but are not related to individual differences in spatial reference memory (Frick et al., 1995; Bizon et al., 2009). Nevertheless, the fact that performance in the probability discounting and water maze tasks was not correlated indicates that age-related alterations in choice behavior are not secondary to more global cognitive impairments.

In addition to working memory, other cognitive operations mediated by prefrontal cortex, such as cognitive flexibility, decline with age and may impact probability discounting performance (Robbins et al., 1998; Barense et al., 2002; Schoenbaum et al., 2002). Age-related impairments in cognitive flexibility are of particular note because aged rats' performance in the present study could be viewed as "inflexible," in that the degree of preference for the large reward in both aged subgroups tended to remain similar across the three choice conditions. While possible, several lines of evidence argue against this interpretation. First, when the contingencies changed across the three conditions, all young and aged rats shifted their performance to a significant degree (compare Figures 1C, 2B, and 3B). Second, despite the fact that performance in both the equal rewards and equal probabilities conditions was correlated with probability discounting, they were not correlated with each other. This lack of relationship was observed despite the fact that these two conditions occurred in close temporal proximity. Third, in our previous study of delay discounting in young and aged rats, we found no evidence for perseverative behavior across many additional task conditions (Simon et al., 2010). Together, these findings argue against explicitly perseverative behavior as the sole mediator of the current results. It remains possible, however, that elevated preference for the large reward in the aged low-discounting subgroup in the probability discounting task was due in part to some form of impaired cognitive flexibility (specifically a reduced ability to alter choice behavior in response to the within-session changes in reward contingencies). Previous findings reporting that a subset of aged

rats show impaired cognitive flexibility in other tasks are consistent with this possibility (Barense et al., 2002; Schoenbaum et al., 2006).

The dopaminergic system has been strongly linked to riskbased decision-making (Brown and Ridderinkhof, 2009; Mohr et al., 2010). Stimulation of both D1 and D2 dopamine receptors increases preference for the large risky reward in the probability discounting task in rats, while stimulation of D3 receptors has the opposite effect (St Onge and Floresco, 2009). In addition, the activity of midbrain dopamine neurons encodes information regarding both reward probability and delay (Fiorillo et al., 2003; Kobayashi and Schultz, 2008), suggesting that this neurochemical system processes information regarding outcome costs. Consistent with this hypothesis, a recent study found that suboptimal increases in preference for the large risky reward in the probability discounting task in a chronic ethanol exposure model were associated with a failure of mesolimbic dopamine activity to encode information about risk of reward omission (Nasrallah et al., 2011). Given that dopaminergic neurotransmission is attenuated with age (Burwell et al., 1995; Kaasinen and Rinne, 2002), it is possible that reductions in dopaminergic encoding of reward costs could account for the increased preference for the risky reward in some rats in the present study. Serotonergic systems have also been linked to decision-making processes. Although serotonin depletion appears to have minimal effects on probability discounting (Mobini et al., 2000; Anderson et al., 2003), it can affect reward sensitivity by reducing discrimination between different reward magnitudes and/or by enhancing the effects of punishment relative to reward (Rogers et al., 2003; Cools et al., 2008). Given that serotonergic signaling appears to decline with age (Arranz et al., 1993; Wang et al., 1995), such deficits could account for the decreased preference for the large reward observed in a subgroup of aged rats in the present study. Importantly, this distinction between the possible functions of the dopaminergic and serotonergic systems is not absolute (e.g., dopaminergic signaling also encodes reward magnitude, and serotonin can modulate dopaminergic activity); nevertheless, it provides a framework for future investigation of the neural mechanisms of age-related alterations in decision-making (Eppinger et al., 2011).

The study presented here is, to our knowledge, the first to investigate the effects of aging on risk-based decision-making in an animal model. The results indicate substantial variability in preference for large risky vs. small guaranteed rewards in aged rats, which appears to be mediated by two distinct factors (sensitivity to costs, and sensitivity to reward). While deficits in both of these factors were observed among the aged cohort, they appeared largely dissociable, and neither was evident in all subjects. These findings suggest that variations in (at least) these two factors may account for altered decision-making at advanced ages, consistent with evidence from studies in humans (Brown and Ridderinkhof, 2009). In addition, the findings of robust individual differences in probability discounting in aged rats are consistent with evidence for individual differences in aged rat performance in other cognitive domains (Gallagher et al., 1993, 2011; Barense et al., 2002; Schoenbaum et al., 2006; Bizon et al., 2009), as well as with evidence for both impaired and preserved decision-making abilities in subsets of aged humans (Denburg et al., 2005, 2007). Such findings highlight the importance of taking into account individual differences when investigating cognitive aging.

REFERENCES

- Agarwal, S., Driscoll, J. C., Gabaix, X., and Laibson, D. (2007). The Age of Reason: Financial Decision Over the Life Cycle. Cambridge: Department of Ecomonics, Massachusetts Institute of Technology.
- AgingStats.gov. (2005). Older Americans 2004: Key Indicators of Well-Being. Available at: http://www.agi ngstats.gov/agingstatsdotnet/Main_ Site/Data/Data_2004.aspx
- Anderson, I. M., Richell, R. A., and Bradshaw, C. M. (2003). The effect of acute tryptophan depletion on probabilistic choice. J. Psychopharmacol. (Oxford) 17, 3–7.
- Arranz, B., Eriksson, A., Mellerup, E., Plenge, P., and Marcusson, J. (1993). Effect of aging in human cortical preand postsynaptic serotonin binding sites. *Brain Res*. 620, 163–166.
- Barense, M. D., Fox, M. T., and Baxter, M. G. (2002). Aged rats are impaired on an attentional set-shifting task sensitive to medial frontal cortex damage in young rats. *Learn. Mem.* 9, 191–201.
- Bizon, J. L., Helm, K. A., Han, J. S., Chun, H. J., Pucilowska, J., Lund, P. K., and Gallagher, M. (2001). Hypothalamic-pituitaryadrenal axis function and corticosterone receptor expression in behaviourally characterized young and aged Long-Evans rats. *Eur. J. Neurosci.* 14, 1739–1751.
- Bizon, J. L., LaSarge, C. L., Montgomery, K. S., McDermott, A. N., Setlow, B., and Griffith, W. H. (2009). Spatial reference and working memory across the lifespan of male Fischer 344 rats. *Neurobiol. Aging* 30, 646–655.
- Brown, S. B., and Ridderinkhof, K. R. (2009). Aging and the neuroeconomics of decision making: a review. *Cogn. Affect. Behav. Neurosci.* 9, 365–379.
- Burwell, R. D., Lawler, C. P., and Gallagher, M. (1995). Mesostriatal dopamine markers in aged Long-Evans rats with sensorimotor impairment. *Neurobiol. Aging* 16, 175–186.
- Cardinal, R. N., and Howes, N. J. (2005). Effects of lesions of the nucleus accumbens core on choice between small certain rewards and large uncertain rewards in rats. *BMC Neurosci.* 6, 37. doi:10.1186/1471-2202-6-37

- Cardinal, R. N., Robbins, T. W., and Everitt, B. J. (2000). The effects of d-amphetamine, chlordiazepoxide, alpha-flupenthixol and behavioural manipulations on choice of signalled and unsignalled delayed reinforcement in rats. *Psychopharmacology (Berl.)* 152, 362–375.
- Cools, R., Roberts, A. C., and Robbins, T. W. (2008). Serotoninergic regulation of emotional and behavioural control processes. *Trends Cogn. Sci.* (*Regul. Ed.*) 12, 31–40.
- Denburg, N. L., Cole, C. A., Hernandez, M., Yamada, T. H., Tranel, D., Bechara, A., and Wallace, R. B. (2007). The orbitofrontal cortex, real-world decision-making, and normal aging. Ann. N. Y. Acad. Sci. 1121, 480–498.
- Denburg, N. L., Tranel, D., and Bechara, A. (2005). The ability to decide advantageously declines prematurely in some normal older persons. *Neuropsychologia* 43, 1099–1106.
- Eppinger, B., Hammerer, D., and Li, S. C. (2011). Neuromodulation of reward-based learning and decision making in human aging. *Ann. N. Y. Acad. Sci.* 1235, 1–17.
- Fiorillo, C. D., Tobler, P. N., and Schultz, W. (2003). Discrete coding of reward probability and uncertainty by dopamine neurons. *Science* 299, 1898–1902.
- Floresco, S. B., St Onge, J. R., Ghods-Sharifi, S., and Winstanley, C. A. (2008). Cortico-limbic-striatal circuits subserving different forms of cost-benefit decision making. *Cogn. Affect. Behav. Neurosci.* 8, 375–389.
- Frank, M. J., and Kong, L. (2008). Learning to avoid in older age. *Psychol. Aging* 23, 392–398.
- Frick, K. M., Baxter, M. G., Markowska, A. L., Olton, D. S., and Price, D. L. (1995). Age-related spatial reference and working memory deficits assessed in the water maze. *Neurobiol. Aging* 16, 149–160.
- Gallagher, M., Burwell, R., and Burchinal, M. (1993). Severity of spatial learning impairment in aging: development of a learning index for performance in the Morris water maze. *Behav. Neurosci.* 107, 618–626.
- Gallagher, M., Stocker, A. M., and Koh, M. T. (2011). Mindspan: lessons from rat models of neurocognitive aging. *ILAR J.* 52, 32–40.

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- Gilsky, E. L. (2007). "Changes in cognitive function in human aging," in *Brain Aging: Models, Methods, and Mechanisms*, p. Chapter 1, ed. D. R. Riddle (Boca Raton: CRC Press), 3–20.
- Hammerer, D., Li, S. C., Muller, V., and Lindenberger, U. (2011). Life span differences in electrophysiological correlates of monitoring gains and losses during probabilistic reinforcement learning. *J. Cogn. Neurosci.* 23, 579–592.
- Henninger, D. E., Madden, D. J., and Huettel, S. A. (2010). Processing speed and memory mediate agerelated differences in decision making. *Psychol. Aging* 25, 262–270.
- Kaasinen, V., and Rinne, J. O. (2002). Functional imaging studies of dopamine system and cognition in normal aging and Parkinson's disease. *Neurosci. Biobehav. Rev.* 26, 785–793.
- Kobayashi, S., and Schultz, W. (2008). Influence of reward delays on responses of dopamine neurons. J. Neurosci. 28, 7837–7846.
- Kumar, A. (2007). Who gambles in the stock market? Austin: McCombs School of Business, University of Texas at Austin.
- LaSarge, C. L., Montgomery, K. S., Tucker, C., Slaton, G. S., Griffith, W. H., Setlow, B., and Bizon, J. L. (2007). Deficits across multiple cognitive domains in a subset of aged Fischer 344 rats. *Neurobiol. Aging* 28, 928–936.
- Maasberg, D. W., Shelley, L. E., Gracian, E. I., and Gilbert, P. E. (2011). Agerelated differences in the anticipation of future rewards. *Behav. Brain Res.* 223, 371–375.
- Mar, A. C., and Robbins, T. W. (2007). Delay discounting and impulsive choice in the rat. *Curr. Protoc. Neurosci.* Chapter 8, Unit 8.22.
- Mata, R., Josef, A. K., Samanez-Larkin, G. R., and Hertwig, R. (2011). Age differences in risky choice: a metaanalysis. *Ann. N. Y. Acad. Sci.* 1235, 18–29.
- Mather, M. (2006). "A review of decision-making processes: weighing the risks and benefits of aging," in When I'm 64, eds L. L. Carstensen and C. R. Hartel (Washington, DC: The National Academies Press), 145–173.
- Mienaltowski, A. (2011). Everyday problem solving across the adult life

span: solution diversity and efficacy. *Ann. N. Y. Acad. Sci.* 1235, 75–85.

- Mobini, S., Chiang, T. J., Ho, M. Y., Bradshaw, C. M., and Szabadi, E. (2000). Effects of central 5hydroxytryptamine depletion on sensitivity to delayed and probabilistic reinforcement. *Psychopharmacol*ogy (Berl.) 152, 390–397.
- Mohr, P. N., Li, S. C., and Heekeren, H. R. (2010). Neuroeconomics and aging: neuromodulation of economic decision making in old age. *Neurosci. Biobehav. Rev.* 34, 678–688.
- Murchison, D., McDermott, A. N., Lasarge, C. L., Peebles, K. A., Bizon, J. L., and Griffith, W. H. (2009). Enhanced calcium buffering in F344 rat cholinergic basal forebrain neurons is associated with age-related cognitive impairment. J. Neurophysiol. 102, 2194–2207.
- Nasrallah, N. A., Clark, J. J., Collins, A. L., Akers, C. A., Phillips, P. E., and Bernstein, I. L. (2011). Risk preference following adolescent alcohol use is associated with corrupted encoding of costs but not rewards by mesolimbic dopamine. *Proc. Natl. Acad. Sci. U.S.A.* 108, 5466–5471.
- Nicolle, M. M., Colombo, P. J., Gallagher, M., and McKinney, M. (1999). Metabotropic glutamate receptor-mediated hippocampal phosphoinositide turnover is blunted in spatial learning-impaired aged rats. J. Neurosci. 19, 9604–9610.
- Roalf, D. R., Mitchell, S. H., Harbaugh, W. T., and Janowsky, J. S. (2011). Risk, reward, and economic decision making in aging. J. Gerontol. B. Psychol. Sci. Soc. Sci. doi: 10.1093/geronb/gbr099. [Epub ahead of print].
- Robbins, T. W., James, M., Owen, A. M., Sahakian, B. J., Lawrence, A. D., McInnes, L., and Rabbitt, P. M. (1998). A study of performance on tests from the CANTAB battery sensitive to frontal lobe dysfunction in a large sample of normal volunteers: implications for theories of executive functioning and cognitive aging. Cambridge Neuropsychological Test Automated Battery. J. Int. Neuropsychol. Soc. 4, 474–490.
- Rogers, R. D., Tunbridge, E. M., Bhagwagar, Z., Drevets, W. C., Sahakian, B. J., and Carter, C. S. (2003). Tryptophan depletion alters the decision-making of healthy volunteers through altered processing of

reward cues. *Neuropsychopharmacology* 28, 153–162.

- Samanez-Larkin, G. R., Gibbs, S. E., Khanna, K., Nielsen, L., Carstensen, L. L., and Knutson, B. (2007). Anticipation of monetary gain but not loss in healthy older adults. *Nat. Neurosci.* 10, 787–791.
- Sanfey, A. G., and Hastie, R. (2000). "Judgment and decision making across the adult life span: a tutorial review of psychological research," in *Cognitive Aging: A Primer*, eds D. Park and N. Schwarz (Philadelphia: Psychology Press), 253.
- Schoenbaum, G., Nugent, S., Saddoris, M. P., and Gallagher, M. (2002). Teaching old rats new tricks: agerelated impairments in olfactory reversal learning. *Neurobiol. Aging* 23, 555–564.
- Schoenbaum, G., Setlow, B., Saddoris, M. P., and Gallagher, M. (2006). Encoding changes in orbitofrontal cortex in reversal-impaired aged rats. *J. Neurophysiol.* 95, 1509–1517.
- Simon, N. W., Gilbert, R. J., Mayse, J. D., Bizon, J. L., and Setlow, B.

(2009). Balancing risk and reward: a rat model of risky decision making. *Neuropsychopharmacology* 34, 2208–2217.

- Simon, N. W., LaSarge, C. L., Montgomery, K. S., Williams, M. T., Mendez, I. A., Setlow, B., and Bizon, J. L. (2010). Good things come to those who wait: attenuated discounting of delayed rewards in aged Fischer 344 rats. *Neurobiol. Aging* 31, 853–862.
- Singh, T., Jones, J. L., McDannald, M. A., Haney, R. Z., Cerri, D. H., and Schoenbaum, G. (2011). Normal aging does not impair orbitofrontaldependent reinforcer devaluation effects. *Front. Aging Neurosci.* 3:4. doi:10.3389/fnagi.2011.00004
- Sloan, H. L., Good, M., and Dunnett, S. B. (2006). Double dissociation between hippocampal and prefrontal lesions on an operant delayed matching task and a water maze reference memory task. *Behav. Brain Res.* 171, 116–126.
- Smith, T. D., Adams, M. M., Gallagher, M., Morrison, J. H., and Rapp, P. R. (2000). Circuit-

specific alterations in hippocampal synaptophysin immunoreactivity predict spatial learning impairment in aged rats. *J. Neurosci.* 20, 6587–6593.

- St Onge, J. R., and Floresco, S. B. (2009). Dopaminergic modulation of risk-based decision making. *Neuropsychopharmacology* 34, 681–697.
- Strough, J., Karns, T. E., and Schlosnagle, L. (2011). Decision-making heuristics and biases across the life span. Ann. N. Y. Acad. Sci. 1235, 57–74.
- Wang, G. J., Volkow, N. D., Logan, J., Fowler, J. S., Schlyer, D., Mac-Gregor, R. R., Hitzemann, R. J., Gur, R. C., and Wolf, A. P. (1995). Evaluation of age-related changes in serotonin 5-HT2 and dopamine D2 receptor availability in healthy human subjects. *Life Sci.* 56:PL249-53.
- Winstanley, C. A. (2011). The utility of rat models of impulsivity in developing pharmacotherapies for impulse control disorders. *Br. J. Pharmacol.* 164, 1301–1321.

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A neuropsychological test of belief and doubt: damage to ventromedial prefrontal cortex increases credulity for misleading advertising

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We have proposed the False Tagging Theory (FTT) as a neurobiological model of belief and doubt processes. The theory posits that the prefrontal cortex is critical for normative doubt toward properly comprehended ideas or cognitions. Such doubt is important for advantageous decisions, for example in the financial and consumer purchasing realms. Here, using a neuropsychological approach, we put the FTT to an empirical test, hypothesizing that focal damage to the ventromedial prefrontal cortex (vmPFC) would cause a "doubt deficit" that would result in higher credulity and purchase intention for consumer products featured in misleading advertisements. We presented 8 consumer ads to 18 patients with focal brain damage to the vmPFC, 21 patients with focal brain damage outside the prefrontal cortex, and 10 demographically similar healthy comparison participants. Patients with vmPFC damage were (1) more credulous to misleading ads; and (2) showed the highest intention to purchase the products in the misleading advertisements, relative to patients with brain damage outside the prefrontal cortex and healthy comparison participants. The pattern of findings was obtained even for ads in which the misleading bent was "corrected" by a disclaimer. The evidence is consistent with our proposal that damage to the vmPFC disrupts a "false tagging mechanism" which normally produces doubt and skepticism for cognitive representations. We suggest that the disruption increases credulity for misleading information, even when the misleading information is corrected for by a disclaimer. This mechanism could help explain poor financial decision-making when persons with ventromedial prefrontal dysfunction (e.g., caused by neurological injury or aging) are exposed to persuasive information.

Keywords: prefrontal cortex, deception, advertising, lesion, credulity, false tagging theory, belief, doubt

INTRODUCTION

It may seem like a stroke of good luck to be contacted by a Nigerian prince who is in trouble. The individual often claims to have some connection to a large fortune but needs a foreign investor's help to access it. Victims of this fraud scheme may send thousands of dollars to this individual with the promise of a 10fold payoff in return. Unfortunately for victims, the reward never arrives.

Fraud, an intentional deception made for personal gain, is a crime and has reached epidemic levels in older adults. An estimated 7.3 million adults 65 years of age or older (20% of older Americans) have been the victims of financial fraud according to a 2010 survey (Infogroup/ORC, 2010). Research has suggested older adults are disproportionally vulnerable to fraud and deception in general (Gaeth and Heath, 1987; Chen and Blanchard-Fields, 2000; Chen, 2002, 2007). However, we remain without an adequate understanding of the elderly individual's propensity toward credulity when exposed to persuasive messages. Moreover, we still do not understand the neuroanatomical mechanisms

which (1) are critical in belief and doubt processes, and (2) might show disproportional dysfunction in connection with age-related increases in credulity. A central goal of our research is to investigate the underlying neuroanatomical mechanisms which are engaged when one becomes dubious or skeptical. The studies highlighted above have indicated that older adults may have impairments in these mechanisms but do not address from a neuroanatomical perspective why older adults are more vulnerable to deception and misleading information, which often results in poor financial decision-making.

Denburg et al. (2007) have indicated that the vulnerability to misleading information in older adults may be linked to an impairment in prefrontal cortex functioning. The structural integrity of the prefrontal cortex is preferentially diminished relative to other brain regions in some older adults (Dempster, 1992; Raz et al., 1997; Pfefferbaum et al., 2005); and there is a decline in frontal lobe functioning beyond the sixth decade of life (West, 1996; Phillips et al., 2002). However, this leaves us with the question of how pre-frontal cortex dysfunction results in vulnerability to misleading

information. As another way of putting the question, what does the prefrontal cortex do to prevent credulity and gullibility?

To address this question, Asp and Tranel (2012) recently developed the False Tagging Theory (FTT), a neuroanatomically based theoretical model of belief and doubt processes. In brief, the FTT asserts that (1) the process of belief occurs in two stages, mental representation and assessment (Gilbert, 1991); (2) all ideas that are represented are initially believed, but a secondary psychological analysis (assessment) can produce disbelief (or doubt) (Gilbert, 1991; Gilbert et al., 1993); (3) the mental representation of the idea, which is initially believed or regarded as true, must be "tagged" to indicate false value, producing doubt (Gilbert, 1991); (4) the prefrontal cortex is necessary for the "false tag" in the assessment component of belief; and (5) "false tags" are affective in nature, akin to the central tenets of Damasio's (1994) "somatic marker hypothesis." Our model suggests that the key function of the prefrontal cortex is "false tagging" which, in the cognitive domain, acts to doubt cognitive representations (which are initially believed). The FTT views the prefrontal cortex as providing a singular function that multiple modalities can access and use (Asp and Tranel, 2012); however, certain prefrontal regions are more inclined to "false tag" for particular modalities, and we suggest that the ventromedial prefrontal cortex (vmPFC) is particularly critical for false tagging cognitive representations. Therefore, the ventromedial portion of the prefrontal cortex is of central interest to the study of cognitive belief and doubt. Other prefrontal regions may also play critical roles in doubting, e.g., acting as a false tagging resource "reserve" (Asp and Tranel, 2012). However, this study will focus exclusively on the vmPFC's role in the belief and doubt process. The FTT predicts that dysfunction of the vmPFC should result in a "doubt deficit," consequences of which should be credulity and a tendency to believe inaccurate information. Several preliminary studies have bolstered the theory, including the findings that patients with focal damage to the vmPFC (1) often have a general personality trait that is overconfident, boastful, grandiose, obstinate, and egocentric (Stuss and Benson, 1984; Damasio et al., 2011), indicating a lack of normative doubt; (2) are more gullible to disreputable characters (Damasio, 1994; Croft et al., 2010); and (3) are more likely to believe fundamentalist religious dogma (Asp et al., 2012). Thus, vmPFC patients and older adults may have a vulnerability to believe deceptive or misleading information because vmPFC dysfunction impairs normative doubt.

Under our FTT, beliefs are broad and cover all mental representation, including all cognitive representations such as knowledge, ideas, opinions, attitudes, and rules (Asp and Tranel, 2012). Traditional perspectives of cognitive representation have suggested that these cognitions are like tools in a warehouse; they are actual objects in the brain that can be retrieved and used (Gilbert, 1993). The underlying assumption is that cognitions in these models are static; they are the bits, the 1's and 0's, of the mind's computer. There are several shortcomings to this computational view, most notably, that (1) the mind's "CPU" (the person getting the tools from the warehouse) must perform homuncular-type operations (e.g., Baddeley, 2002) and (2) cognitions are impotent (Gilbert, 1993). Computational models require a faculty or mechanism (a "CPU") to do action with static cognitions (the 1's and 0's), which cannot produce effects on their own. However, the FTT asserts that all cognitions are beliefs; they are "empowered" intrinsically with simple comprehension (Gilbert, 1993). Thus, when an individual understands a novel proposition, the individual is automatically put in a "state" of belief. Here, the mental representation is not impotent but will induce action, given appropriate circumstances. To avoid every passing idea to be acted on, the vmPFC can doubt or disbelieve cognitions by applying false tags to mental representations. Understanding a cognition is, then, more like the "state" of a shot of an ice hockey player directed at a goalie. If the goalie does not stop the shot (false tag the cognition), the shot will go in the net (a cognition-consistent action will be performed). The belief will be acted upon if not blocked by the vmPFC. In this model, post-rolandic cortices are constantly firing shots and the vmPFC is reliably blocking some percentage of them.

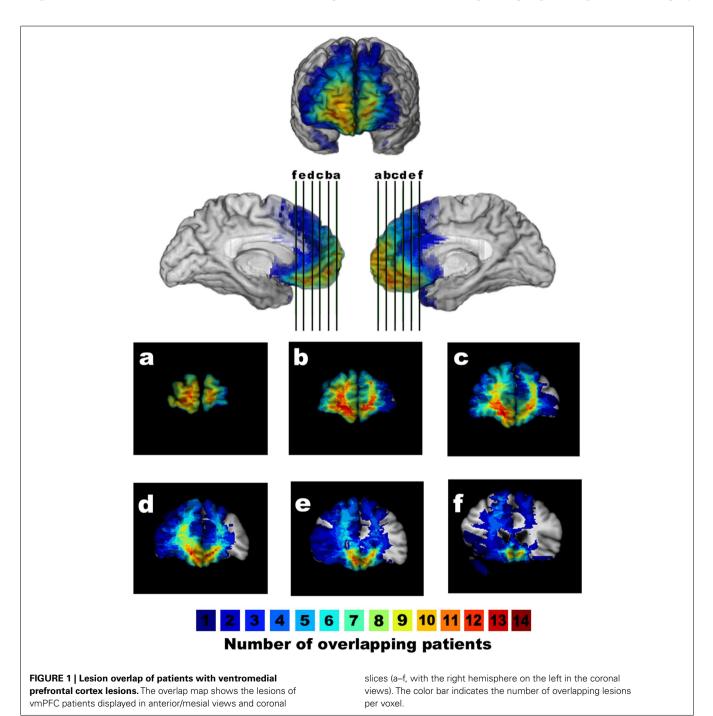
If this logic is applied to a decision-making scenario, each choice that is identified (i.e., understood) is a belief ("if this, then that" cognitions) and "false tags" block disadvantageous or inappropriate choices for the context. False tags (or doubt) via the vmPFC act to select appropriate responses during decision-making by negatively biasing the inappropriate (i.e., "untrue") representations. Therefore, we propose that dysfunction or damage to the vmPFC has a two-pronged, but intimately related, effect: (1) a tendency toward credulity for deceptive or misleading information; and (2) disadvantageous behavioral decision-making.

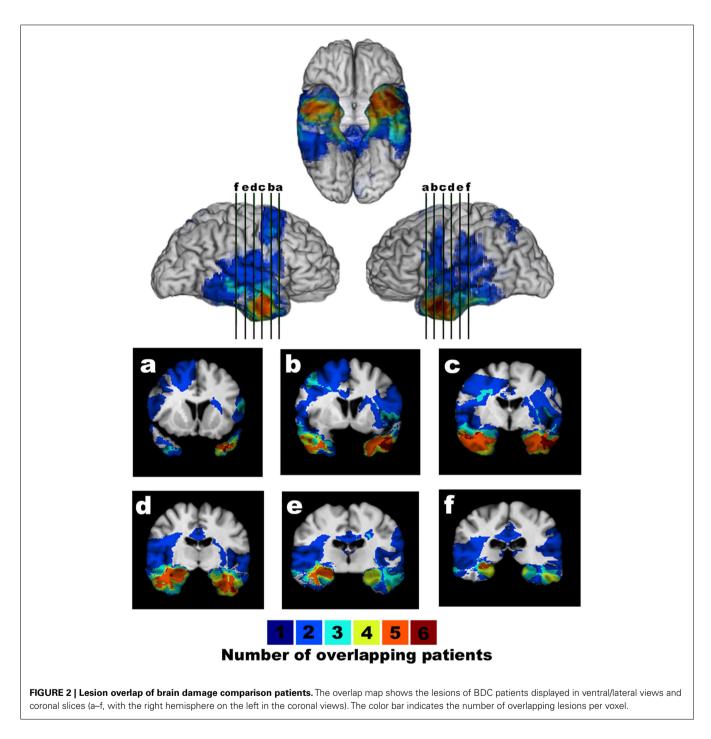
The purpose of the present study was to investigate credulity and financial decision-making for misleading information presented in a real-world, ecologically valid paradigm (deceptive advertising) in patients with focal brain damage, with the goal of identifying a systems-level neuroanatomical correlate for these cognitive functions. We chose consumer advertisements which had been deemed deceptive and deliberately misleading by the Federal Trade Commission (FTC), and examined participants' credulity toward the advertisements. Our theory suggests that when normal individuals are exposed to misleading information they will initially believe the information but then will tend to self-generate doubt from their store of knowledge and experience. To examine the interaction between "self-generated" doubt and doubt from explicit information, we created two types of misleading ads: (1) "deceptive-uncorrected" ads, which are misleading and do not have any explicit information that may induce doubting, and (2) "deceptive-corrected" ads, which are misleading but do have an end disclaimer which should induce doubting. The FTT asserts that doubt is mediated by the vmPFC. Thus, we hypothesized that patients with damage to the vmPFC, compared to patients with brain damage outside the prefrontal cortex and healthy individuals, (1) would be more likely to believe the misleading aspects in both the "deceptive-uncorrected" and the "deceptive-corrected" ads, and (2) would indicate higher intention to purchase the products featured in both types of ads.

MATERIALS AND METHODS

PARTICIPANTS

We studied 39 individuals with adult-onset brain lesions from the Patient Registry of the Division of Behavioral Neurology and Cognitive Neuroscience at the University of Iowa. The etiologies of the lesions included cerebrovascular disease (n = 21), surgical resection for treatment of a meningioma or seizure control (n = 15), and focal contusions from trauma (n = 3). In connection with their enrollment in the Patient Registry, the brain damaged patients have been extensively characterized neuropsychologically and neuroanatomically, using standard protocols of the Benton Neuropsychology Laboratory and the Laboratory of Brain Imaging and Cognitive Neuroscience (Tranel, 2007). Eighteen patients had damage to the vmPFC and were classified into our vmPFC group (**Figure 1**); while 21 patients had lesions outside the prefrontal cortex and were classified into our brain damaged comparison group (BDC; **Figure 2**). Patients with prefrontal cortex damage to areas primarily outside the ventromedial regions were excluded from analysis. While other prefrontal areas are predicted to have a role in "false tagging" it is beyond the scope of this study to address more specific relationships within the prefrontal cortices. All neuropsychological and neuroanatomical data were collected in the chronic phase of recovery, at least 3 months post-lesion onset. We also included a normal comparison group (n = 10) which was comprised by individuals of similar age and education to our patient groups. BDC patients were slightly





younger and had more females relative to males than our vmPFC group and normal group (**Table 1**), so we corrected for these differences in the main analyses. VMPFC patients had significantly larger lesions relative to BDC patients (**Table 1**); thus, a secondary analysis directly comparing credulity in the BDC and vmPFC groups was conducted to account for lesion size. Participants with significant language, memory, or visuoperceptual deficits which might impair their ability to adequately complete the task were excluded. We excluded patients with significant aphasia (defined as two standard deviations below the mean on the Boston Naming Test or the Token Test), reading deficits (defined as two standard deviations below the mean on the Iowa Chapman Reading Test), memory deficits (defined as two standard deviations below the mean on the Auditory Verbal Learning Test delayed recall or the Complex Figure Test delayed recall), or visuoperceptual impairments (defined as two standard deviations below the mean on the Facial Recognition Test). There were no significant differences between vmPFC and BDC patients on the various neuropsychological measures (**Table 2**). All participants were free from mental retardation, learning disabilities, psychiatric disease,

Table 1 | Demographic and neuroanatomical data.

	vmPFC	BDC	Normal
Number	18	21	10
Age (SD)*	60.4 (10.6)	50.2 (11.0)	60.7 (8.9)
Education (SD)	13.8 (2.7)	14.3 (2.3)	15.8 (3.0)
Sex**	12 M; 6 F	6 M; 15 F	7 M; 3 F
Lesion size (SD) †	51.7(40.3)	21.9 (15.3)	NA

Age and education are presented in years; lesion size is presented in cubic centimeters.

*BDC patients were significantly younger than vmPFC patients and normal participants.

**The BDC group had a significantly lower proportion of males relative to females than the vmPFC and normal groups.

[†]VMPFC lesions were significantly larger than BDC lesions.

Table 2 | Neuropsychological data for the lesion groups.

	vmPFC	BDC
WAIS III – FSIQ (SD)	108.5 (16.8)	104.7 (11.5)
WRAT – Read (SD)	99.4 (9.8)	96.6 (8.2)
AVLT – 30 min recall (SD)	8.5 (3.6)	9.2 (2.9)
CFT – 30 min recall (SD)	20.0 (7.5)	17.2 (5.4)
TMT – Part B (SD)	76.7 (34.9)	77.8 (43.2)
WCST – Pers. Errors (SD)	22.1 (24.7)	12.6 (8.1)

WAIS-III, Wechsler Adult Intelligence Scale-III scores (FSIQ, full-scale IQ). WRAT, Wide Range Achievement Test scores (Read, Reading Standard Score). AVLT, Auditory Verbal Learning Test scores (an index of memory function at 30 min). CFT, Complex Figure Test recall scores (an index of memory function at 30 min). TMT, Trail Making Test Part B scores, an index of divided attention and multi-tasking. WCST, Wisconsin Card Sorting Test Perseverative Errors, an index of reasoning and concept formation (executive functioning). There were no significant differences between the groups for any of the neuropsychological tests.

substance abuse, and dementia. Participants gave informed consent approved by the Institutional Review Board of the University of Iowa.

STIMULI AND PROCEDURE

Participants were given a booklet that consisted of eight advertisements that one might encounter in a magazine or newspaper. Each ad was based on real-world misleading advertisements as deemed by the rulings of the FTC, as shown in *FTC Decisions* (Federal Trade Commission, 1991) and *Complying with the Made in USA Standard* (Federal Trade Commission Bureau of Consumer Protection, 1998). These advertisements were misleading for a number of reasons, ranging from the withholding of crucial information about the product to the use of biased graphs. For example, in an advertisement for "Legacy Luggage," the original misleading version had the headline "Legacy brings you the finest American Quality luggage." The FTC stated that any advertisement that has "American Quality" on it conveys that the item in question was made in the U.S.A. In fact, the luggage was actually not made in the U.S.A., but instead was manufactured in

Mexico, and then inspected in Tennessee, and thus was misleading. Three ads were classified as "deception-uncorrected" and were left unchanged from the FTC-ruled "misleading advertisement" classification. However, "deception-uncorrected" ads assume that all individuals have a similar knowledge base regarding potential objections to the misleading portions of the ads. This assumption leaves open the possibility that some individuals may not have, or cannot access, cognitions that should induce doubting. To address this issue, we developed "deception-corrected" ads which provide explicit information that should induce doubting, by modifying three misleading ads with a disclaimer at the end of the ad. The disclaimers in the "deception-corrected" ads specifically rebutted the misleading aspect of the ad. For example, in an advertisement for "NatureCure," the misleading ad describes a natural pain reliever that provides relief from headaches "without the side effects of over-the-counter pain relievers." The end disclaimer refutes this claim by noting, "This product can cause nausea in some consumers when taken regularly." Thus, for the "deception-corrected" ads, all participants were given the same specific knowledge to doubt the misleadingly advertised claim. Finally, there were two "filler" advertisements, one placed at the beginning and the other at the end of the booklet. These were used to help buffer against primacy and recency effects, and were not scored. This left six critical advertisements: three "deception-uncorrected" and three "deception-corrected." Each ad highlighted a distinct product: the "deception-uncorrected" stimuli advertised a doll, luggage, and a vitamin supplement drink; the "deception-corrected" stimuli advertised a car, a pain reliever, and mutual funds. Participants read over the advertisements at their own pace and when finished, they were given a paper questionnaire which assessed participant reactions to each advertisement and product. Participants could not refer back to the advertisements during the questionnaire; instead, they needed to recall their impressions of each product from memory. Readers who are interested in knowing more about the advertising stimuli and their development may contact the senior author via email.

Two critical dimensions were assessed for each advertisement: (1) credulity toward the misleading aspect of the advertisement, and (2) purchase intention, i.e., how likely was the participant to buy each item should it become available in their area. The credulity measure asked "What do you believe to be true about this product?" and was assessed on a Likert scale, anchored at each end by a belief about the product being advertised. The Likert scales on the questionnaire contained no numerals but had 7 empty spaces (of equal size) between the two anchors. Participants marked the empty space they considered appropriate. Numbers for the Likert scale were added post hoc, and ranged from 1 to 7, with lower values reflecting increased belief in the misleading aspects of the ads and higher values reflecting increased skepticism for the misleading aspects of the ads. For example, the previously mentioned Legacy Luggage advertisement dealt with whether or not the luggage was made in the U.S.A. The credulity question concerning that advertisement was anchored at space 1 by "The Legacy Luggage Set is made in the United States" and at space 7 by "The Legacy Luggage Set is NOT made in the United States." The purchase intention measure was assessed by asking, "What is the probability that you would buy the product when it becomes available in the area?"

Participants' responses were measured on a Likert scale, anchored by "Likely" and "Unlikely." This scale ranged from 1 to 5, with 1 reflecting a higher intention to purchase the item and 5 reflecting a lower intention to purchase the item.

NEUROANATOMICAL ANALYSIS

The neuroanatomical analysis of the vmPFC and BDC patients (**Figures 1** and **2**) was based on magnetic resonance data for 30 patients and on computerized tomography data for 9 patients. Using Brainvox (Frank et al., 1997), each patient's lesion was reconstructed in three dimensions for the different groups. The lesion contour for each patient was manually warped into a normal template brain using the MAP-3 method. The overlap of lesions in these volumes, calculated by the sum of n lesions overlapping at any single voxel, is color-coded in **Figures 1** and **2**. As **Figure 1** shows, the greatest overlap of vmPFC patient lesions is in the mesial orbital region, especially the anterior half of the gyrus rectus. The greatest overlap of lesions in **Figure 2** is in the inferior temporal lobes. No BDC lesions encompassed the prefrontal cortex.

RESULTS

All statistical *t*-tests are one-tailed in accordance with our directional predictions.

CREDULITY DIMENSION

The first question we addressed was whether patients with vmPFC damage were more likely to be credulous to the misleading advertising overall (including both "deception-uncorrected" and "deception-corrected"). VMPFC patients were more credulous to the misleading advertising (M = 3.89, SD = 1.11) than BDC patients (M = 5.25, SD = 0.81) and normal participants (M = 5.10, SD = 0.88; Figure 3). Because BDC patients were slightly younger and had more females relative to males (Table 1), we ran an ANCOVA with age and sex as covariates. The covariate, age, was not significantly related to credulity, F(1,44) = 0.01, p = 0.93; and the covariate, sex, was also not significantly related to credulity, F(1,44) = 0.01, p = 0.92. There remained a significant difference in group credulity after controlling for the covariates, F(2,44) = 9.26, p < 0.001. Planned contrasts revealed that vmPFC patients were more credulous than BDC patients, t(44) = 3.17, p = 0.002, and normal participants, t(44) = 3.88, p < 0.001.

Ventromedial prefrontal cortex patients had significantly larger lesions that BDC patients (**Table 1**) and there was a modest correlation between lesion size and credulity to the ads, r = -0.31, p = 0.06. Thus, a secondary analysis was conducted to directly examine the influence of lesion size on the credulity measure in the two patient groups. The covariate, lesion size, was not significantly related to credulity, F(1,36) = 0.12, p = 0.74. There remained a significant difference in group credulity after controlling for the covariate, F(1,36) = 13.70, p = 0.001.

Splitting the overall credulity results into the three "deceptionuncorrected" ads and the three "deception-corrected" ads helps clarify our initial analysis. VMPFC patients were more credulous to the "deception-uncorrected" ads (M = 3.24, SD = 1.38) than BDC patients (M = 4.86, SD = 1.03) and normal participants (M = 4.83, SD = 1.47; Figure 3). There was a significant

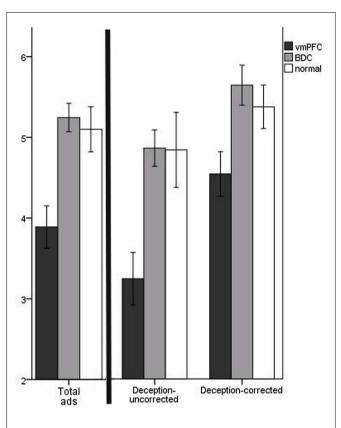


FIGURE 3 | Mean belief scores for misleading ads. The scale is from 1 to 7 (*y*-axis), with lower values corresponding to increased belief in misleading aspects of the ads and higher values corresponding to increased skepticism for misleading aspects of the ads. Error bars indicate SEM. The graph on the left of the black bar represents results for all six misleading ads; the graph on the right of the black bar breaks the results down according to "deception-uncorrected" and "deception-corrected" ads. For all the ads, vmPFC patients had more credulity than BDC patients and normal comparison participants.

difference for group credulity on the "deception-uncorrected" ads, F(2,46) = 9.25, p < 0.001. Planned contrasts revealed that vmPFC patients were more credulous than BDC patients, t(46) = 4.18, p < 0.001, and normal participants, t(46) = 3.20, p = 0.002. vmPFC patients were also more credulous to the "deception-corrected" ads (M = 4.54, SD = 1.17) than BDC patients (M = 5.64, SD = 1.13) and normal participants (M = 5.37, SD = 0.85; **Figure 2**). There was a significant difference for group credulity on the "deception-corrected" ads, F(2,46) = 5.06, p = 0.01. Planned contrasts revealed that vmPFC patients were more credulous than BDC patients, t(46) = 2.90, p = 0.003, and normal participants, t(46) = 1.92, p = 0.03. These data suggest that higher credulity toward misleading ads in vmPFC patients was obtained even when explicit disclaimers should induce doubt for the misleading information.

A secondary repeated measures ANOVA analysis was conducted to see if the "correction" in the ads had a significant main effect. While the participants were generally more skeptical for the "deception-corrected" ads, there was not a significant main effect of "correction," F(1,44) = 0.15, p = 0.70. In addition, the groups were not significantly different in the way they were affected by the presence of corrective information, F(2,44) = 1.02, p = 0.37. Thus, the corrective information did help the vmPFC patients increase their skepticism similarly to the comparison groups.

PURCHASE INTENTION DIMENSION

For the purchase intention dimension, we addressed first whether vmPFC patients overall were more likely to have intent to purchase the advertised products. VMPFC patients had higher purchase intention for the misleadingly advertised products (M = 4.17, SD = 0.64) than BDC patients (M = 4.40, SD = 0.43) and normal participants (M = 4.70, SD = 0.27; **Figure 4**). Again, we used age and sex as covariates in an ANCOVA analysis. The covariate, age, was not significantly related to purchase intention, F(1,44) = 0.93, p = 0.34; and the covariate, sex, was also not significantly related to purchase intention after controlling for the covariates, F(2,44) = 3.75, p = 0.03. Planned contrasts revealed that vmPFC patients had significantly higher purchase intention than normal participants, t(44) = 2.74, p = 0.005; vmPFC patients

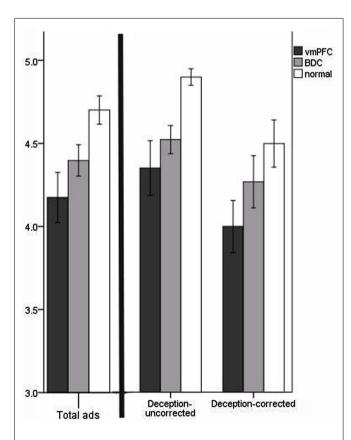


FIGURE 4 | Mean purchase intention scores for misleading ads. The scale is from 1 to 5 (*y*-axis). Lower values reflect increased purchase intention for the products misleadingly advertised, and higher values reflect decreased purchase intention. Error bars indicate SEM. The graph on the left of the black bar represents results for all six misleading ads; the graph on the right of the black bar breaks the results down according to "deception-uncorrected" and "deception-corrected" ads. For all the ads, vmPFC patients had higher purchase intention than BDC patients and normal comparison participants for the products in the misleading ads.

did not have significantly higher purchase intention than the BDC patients, t(44) = 1.13, p = 0.13. Lesion size was uncorrelated with purchase intention, r = 0.04, p = 0.81.

When the purchase intention data were divided into "deception-uncorrected" and "deception-corrected," the results indicated that vmPFC patients had higher purchase intent for the "deception-uncorrected" ads (M = 4.35, SD = 0.70) than BDC patients (M = 4.52, SD = 0.39) and normal participants (M = 4.90, SD = 0.16; Figure 4). There was a significant difference for group purchase intention on the "deception-uncorrected" ads, F(2,46) = 3.86, p = 0.03. Planned contrasts showed that vmPFC patients had higher purchase intention than normal participants, t(20) = -3.18, p = 0.003; but did not significantly differ from BDC patients, t(26) = -0.93, p = 0.18. VMPFC patients also had higher purchase intent to the "deception-corrected" ads (M = 4.00,SD = 0.67) than BDC patients (M = 4.27, SD = 0.72) and normal participants (M = 4.50, SD = 0.45; Figure 3). However, group differences on "deception-corrected" ads for purchase intention did not reach significance, F(2,46) = 1.99, p = 0.14. Planned contrasts revealed that vmPFC patients had significantly higher purchase intention than normal participants, t(46) = -1.94, p = 0.03; but did not significantly differ from BDC patients, t(46) = -1.28, p = 0.11.

DISCUSSION

Our findings support the hypothesis that credulity toward misleading information can result from damage to the vmPFC. Patients with vmPFC damage tended to (1) believe misleading advertisements, and (2) show higher intent to purchase the products featured in the misleading advertisements, relative to patients with brain damage outside of the prefrontal cortex and normal comparison participants. Remarkably, the pattern of credulity results was evident even when vmPFC patients were given specific information that rebuts the misleading claim. This suggests that the deficiency in vmPFC patients is specific to the doubt process, not a lack of knowledge regarding misleading information. Thus, the results indicate that given a deceptive ad (with or without a disclaimer) vmPFC patients are more credulous. The disclaimer did increase skepticism in vmPFC patients (similarly to the comparison groups) but overall the disclaimer did not produce normative skeptical levels in vmPFC patients. Thus, there is a deficiency in skepticism generally, even when specific rebutting knowledge cues a doubting process.

The conclusion that damage to the vmPFC causes an increase in credulity to misleading information is bolstered by the facts that (1) brain damage, *per se*, when outside of the prefrontal cortex, does not account for the results (as evident from the BDC data); (2) demographic variables such as age, education, or sex, *per se*, do not account for the results; and (3) general cognitive functioning, such as intelligence, memory, reading performance, or executive functioning, *per se*, does not account for the results. Instead, the vmPFC patients' deficit in skepticism to the misleading information is specific to their lesion location and is not accounted for by generally poor cognitive functioning.

The vmPFC patients did have larger lesions relative to the BDC patients (**Table 1**). However, it is unlikely that lesion size, *per se*, influenced the credulity or purchase intention results. A detailed

analysis revealed: (1) lesion size as a covariate was not significantly related to credulity, and (2) when the patients were ranked on the credulity measure (the total ads together), the top 5 most credulous vmPFC patients (M = 28.8, SD = 15.5) actually had a slightly smaller mean lesion size than the bottom 5 least credulous BDC patients (M = 29.6, SD = 23.7). Moreover, an appropriate lesion size measure interpretation must be understood in the context of the region which is damaged. Small lesions to critical structures such as the amygdala, hippocampus, or thalamic nuclei may critically impair a variety of functions, while a similar size lesion to the relatively large and uniform vmPFC may not have similar functional disruptions. Thus, lesion size, per se, while different between the two groups, was unlikely to contribute to the increased credulity and purchase intent in the vmPFC group relative to the BDC group, i.e., the deficit is specific not to lesion size but to lesion location.

Our findings support the FTT, which posits that the prefrontal cortex is critical in mediating doubt (Asp and Tranel, 2012), and thus damage to the critical ventromedial region of the prefrontal cortex should result in a "doubt deficit." While it has been noted that ventromedial prefrontal patients are often vulnerable to shady business ventures and snake-oil salesmen (Damasio, 1994), the current study provides the first direct evidence beyond anecdotal reports that damage to vmPFC increases credulity. Indeed, this specific deficit may explain why highly intelligent vmPFC patients can fall victim to seemingly obvious fraud schemes. Warnings from friends and family often go unheeded and vmPFC patients' susceptibility can result in bankruptcy if they continue to make their own financial decisions. Moreover, in the acute phase of recovery following vmPFC damage, patients often confabulate and are markedly suggestible (Berlyne, 1972) to other individuals and, on rare occasions, even to the environment around them (Lhermitte, 1986). Taken together, this evidence indicates that the vmPFC is a critical neural structure preventing unwarranted belief toward unscrupulous companies or individuals who try to bilk one's money.

In our study, we gave novel external persuasive information to vmPFC patients and found that they tend to be credulous to that information. However, as suggested in the Introduction, vmPFC patients can also be obstinate and bull-headed toward novel information. Intuitively, it may appear contradictory that an individual can both be credulous and rigidly obstinate to information. Yet, this is the strange state often exhibited by patients with vmPFC damage. We hypothesize that the critical factor determining the easy acceptance or rigid rejection of information in vmPFC patients is whether the cognitive representation is initially generated by external or internal information. If the cognitive representation is initially generated by external information (as in the present study), it is believed, but then it fails to be falsified by comparisons with extant mental information. Thus, the new information is not doubted, and credulity ensues. If the cognitive representation is initially generated by internal information, it is believed, but then it fails to be falsified by comparisons with new external information. Thus, the old information is not doubted, and a pertinacious belief is evinced. This suggests the initial cognition is always first believed and it is the comparison and falsification to other beliefs that is disrupted. vmPFC patients,

then, should have "compartmentalized minds," where discordant ideas are rarely compared and falsified with one another. Indeed, vmPFC patients tend to be high in authoritarianism (Asp et al., 2012), a trait highlighted by a capacity to hold mutual agreement of contradictory ideas (Altemeyer, 1996). vmPFC patients are also prone to pathological confabulation, where they truly believe their (sometimes florid) assertions, even though contradictory evidence to these assertions is salient and obvious (Gilboa and Moscovitch, 2002).

Our results also indicated that vmPFC patients had higher intention to purchase the misleadingly advertised products than BDC or normal comparisons. Undoubtedly, other, independent factors outside the study's design likely have stronger influences during an actual purchase decision process (e.g., the usefulness of the product and available financial means for an individual), than a single misleadingly advertised product aspect. These independent factors may have differentially affected the purchase intention data; e.g., the participants gave higher purchase intention ratings to the "deception-corrected" ads compared to the "deceptionuncorrected" ads. Thus, because the experimental design used different (and unmatched) products across the types of ads, other issues such as usefulness and monetary concerns probably factored greater in the participants' purchase intention.

However, it is notable that vmPFC patients had the highest purchase intent of any group. VMPFC patients are notorious for their poor decision-making in financial and social situations. They often claim that an inappropriate decision "feels right"; and there is substantial evidence suggesting that vmPFC patients lack affective signals which normally steer individuals toward advantageous decisions (Damasio, 1994; Bechara et al., 1996, 2000). The FTT asserts that the cognitive process which selects the item eventually chosen from a decision-making process is governed by doubt (or false tags) which are affective in nature (Asp and Tranel, 2012). As an individual mentally represents each potential choice, the vmPFC acts to "doubt" or to negatively bias the inappropriate or undesirable representations away from a behavioral action. Appropriate or desirable response selection, then, is the result of the "fittest" choice representation; i.e., the representation with the least negative biases (or false tags) attached to it. Here, we suggest the cognition to purchase a specific item is a belief and individuals must "false tag" this belief with other extant cognitive information. For instance, in regard to the "Legacy Luggage" we propose that normal individuals believe the initial cognition "I will purchase the Legacy Luggage" but then "falsify" that cognition with discordant extant cognitions, e.g., "I just bought new luggage" or "I don't have time to go on any trips." Other product aspects (including the misleading aspects) may play a role in the purchase decision, e.g., "It is made in the US" (strengthening the belief) or "The color of the luggage is unappealing" (increasing false tags) as well. Although we cannot specify what potential cognitions individuals may offer for falsification, in this decision-making scenario, vmPFC patients should be more likely to intend to purchase advertised products. Our results provide some initial evidence for this view.

We believe our results have implications that extend beyond unethical marketing campaigns, although they do directly impact marketing ethics in brain damaged individuals. This study adds to the growing evidence that belief and disbelief are not governed by balanced cognitive processes (Gilbert, 1991). Belief is first, easy, inexorable with comprehension of any cognition, and substantiated by representations in the post-rolandic cortex. Disbelief is retroactive, difficult, vulnerable to disruption, and mediated by the vmPFC. This asymmetry in the process of belief and doubt suggests that false doctrines in the "marketplace of ideas" (Mill, 1975) may not be as benign as is often assumed (Gilbert et al., 1993). Indeed, normal individuals are prone to misleading information, propaganda, fraud, and deception (Zuckerman et al., 1981; Gilbert, 1991), especially in situations where their cognitive resources are depleted. In our theory, the more effortful process of disbelief

REFERENCES

- Altemeyer, B. (1996). *The Authoritarian Specter.* Cambridge, MA: Harvard University Press.
- Asp, E. W., Ramchandran, K., and Tranel, D. (2012). Authoritarianism, religious fundamentalism, and the human prefrontal cortex. *Neuropsychology*.
- Asp, E. W., and Tranel, D. (2012). "False tagging theory: toward a unitary account of prefrontal cortex function," in *Principles of Frontal Lobe Function*, 2nd Edn., eds D. T. Stuss and R. T. Knight (New York: Oxford University Press).
- Baddeley, A. (2002). "Fractionating the central executive," in *Principles of Frontal Lobe Function*, eds D. T. Stuss and R. T. Knight (New York: Oxford University Press), 246–260.
- Bechara, A., Tranel, D., and Damasio, H. (2000). Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. *Brain* 123, 2189–2202.
- Bechara, A., Tranel, D., Damasio, H., and Damasio, A. R. (1996). Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. *Cereb. Cortex* 6, 215–225.
- Berlyne, N. (1972). Confabulation. Br. J. Psychiatry 120, 31–39.
- Chen, Y. W. (2002). Unwanted beliefs: age differences in beliefs of false information. Aging Neuropsychol. Cogn. 9, 217–230.
- Chen, Y. W. (2007). "Age differences in social judgments: why are old adults more susceptible to scams," in Advances in Psychology Research, ed. A. Columbus (Hauppauge, NY: Nova Science Publishers), 145–161.
- Chen, Y. W., and Blanchard-Fields, F. (2000). Unwanted thought: age differences in the correction of social judgments. *Psychol. Aging* 15, 475–482.
- Croft, K., Duff, M., Kovach, C., Anderson, S. W., Adolphs, R., and Tranel,

D. (2010). Detestable or marvelous? Neuroanatomical correlates of character judgments. *Neuropsychologia* 48, 1789–1801.

- Damasio, A. (1994). Decartes' Error: Emotion, Reason and the Human Brain. New York: Grosset/ Putnam.
- Damasio, A. R., Anderson, S. W., and Tranel, D. (2011). "The frontal lobes," in *Clinical Neuropsychology*, 5th Edn., eds K. M. Heilman and E. Valenstein (New York: Oxford University Press).
- Dempster, F. N. (1992). The rise and fall of the inhibitory mechanism: toward a unified theory of cognitive development and aging. *Dev. Rev.* 12, 45–75.
- Denburg, N. L., Cole, C. A., Hernandez, M., Yamada, T. H., Tranel, D., Bechara, A., and Wallace, R. B. (2007). The orbitofrontal cortex, real-world decision making, and normal aging. *Ann. N. Y. Acad. Sci.* 1121, 480–498.
- Federal Trade Commission. (1991). Lewis Galoob Toys Inc. Federal Trade Commission Decisions 114, 187–217.
- Federal Trade Commission Bureau of Consumer Protection. (1998). *Complying with the Made in USA Standard.* Federal Trade Commission Report.
- Frank, R. J., Damasio, H., and Grabowski, T. J. (1997). Brainvox: an interactive, multimodal visualization and analysis system for neuroanatomical imaging. *Neuroimage* 5, 13–30.
- Gaeth, G., and Heath, T. B. (1987). The cognitive processing of misleading advertising in young and old adults: assessment and training. *J. Consum. Res.* 14, 43–54.
- Gilbert, D. T. (1991). How mental systems believe. *Am. Psychol.* 46, 107–119.
- Gilbert, D. T. (1993). "The assent of man: mental representation and the

(to items initially believed) is mediated by the vmPFC; which, in old age, tends to disproportionally lose structural integrity and associated functionality. Thus, we suggest that vulnerability to misleading information, outright deception, and fraud in older persons is the specific result of a deficit in the doubt process which is mediated by the vmPFC.

To conclude, the present findings suggest that the vmPFC is a critical neural substrate for psychological doubt affecting post-rolandic representations. Damage to the vmPFC disrupts a "false tagging mechanism" which normally produces doubt and skepticism for cognitive representations.

control of belief," in *Handbook of Mental Control*, eds D. M. Wegner and J. W. Pennebaker (Englewood Cliffs, NJ: Prentice Hall), 57–87.

- Gilbert, D. T., Tafarodi, R. W., and Malone, P. S. (1993). You can't not believe everything you read. J. Pers. Soc. Psychol. 65, 221–233.
- Gilboa, A., and Moscovitch, M. (2002). "The cognitive neuroscience of confabulation: a review and a model," in *Handbook of Memory Disorders*, 2nd Edn., eds A. D. Baddeley, Kopelman, M. D., and B. A. Wilson (Chichester: John Wiley), 315–342.
- Infogroup/ORC. (2010). Elder Investment Fraud and Financial Exploitation. Washington, DC: Investor Protection Trust.
- Lhermitte, F. (1986). Human autonomy and the frontal lobes. Part II: patient behavior in complex and social situations: the "Environmental Dependency Syndrome". *Ann. Neurol.*19, 335–343.
- Mill, J. S. (1975). *On Liberty*. New York: Norton.
- Pfefferbaum, A., Adalsteinsson, E., and Sullivan, E. V. (2005). Frontal circuitry degradation marks healthy adult aging: evidence from diffusion tensor imaging. *Neuroimage* 26, 891–899.
- Phillips, L. H., Macpherson, S. E. S., and Dalla Sala, S. (2002). "Age, cognition and emotion: the role of anatomical segregation in the frontal lobes," in *Handbook of Neuropsychology*, ed. J. Grafman (Amsterdam: Elsevier), 73–97.
- Raz, N., Gunning, F. M., Head, D., Dupuis, J. H., Mcquain, J., Briggs, S. D., Loken, W. J., Thornton, A. E., and Acker, J. D. (1997). Selective aging of the human cerebral cortex observed in vivo: differential vulnerability of the prefrontal gray matter. *Cereb. Cortex* 7, 268–282.
- Stuss, D. T., and Benson, D. F. (1984). Neuropsychological studies of the

frontal lobes. *Psychol. Bull.* 95, 3–28.

- Tranel, D. (2007). "Theories of clinical neuropsychology and brainbehavior relationships: Luria and beyond," in *Textbook of Clinical Neuropsychology*, eds J. E. Morgan and J. H. Ricker (New York: Taylor & Francis), 27–39.
- West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychol. Bull.* 120, 272–292.
- Zuckerman, M., Depaulo, B. M., and Rosenthal, R. (1981). "Verbal and nonverbal communication of deception," in *Advances in Experimental Social Psychology*, ed. L. Berkowitz (San Diego, CA: Academic Press), 1–59.

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Ecological rationality: a framework for understanding and aiding the aging decision maker

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Rui Mata, Department of Psychology, University of Basel, Missionsstrasse 64A, 4055 Basel, Switzerland. e-mail: rui.mata@unibas.ch The notion of ecological rationality sees human rationality as the result of the adaptive fit between the human mind and the environment. Ecological rationality focuses the study of decision making on two key questions: First, what are the environmental regularities to which people's decision strategies are matched, and how frequently do these regularities occur in natural environments? Second, how well can people adapt their use of specific strategies to particular environmental regularities? Research on aging suggests a number of changes in cognitive function, for instance, deficits in learning and memory that may impact decision-making skills. However, it has been shown that simple strategies can work well in many natural environments, which suggests that age-related deficits in strategy use may not necessarily translate into reduced decision performance depend not only on how aging affects decision-relevant capacities but also on the decision environment in which decisions are made. In sum, we propose that the concept of the ecological rationality is crucial to understanding and aiding the aging decision maker.

Keywords: aging, decision making, ecological rationality, strategy selection, strategy execution

In Cicero's de Senectute (Cicero, 1909-1914), Cato, the elder, explains to two younger men how to flourish in old age: "Nor, again, do I now miss the bodily strength of a young man (...) any more than as a young man I missed the strength of a bull or an elephant. You should use what you have, and whatever you may chance to be doing, do it with all your might." Cato seems to suggest that the key to successful aging lies not in attempting to regain the strength of youth or to mourn its loss but in using the available resources wisely, so as to meet one's own aspirations and the challenges one faces (see Baltes, 1997, for a similar perspective). Elaborating on this suggestion, we first introduce the notion of *ecological rationality* and suggest that the wise selection of decision strategies that fit specific ecologies is crucial to achieving good decisions (Gigerenzer et al., 1999; Gigerenzer et al., 2011; Gigerenzer and Gaissmaier, 2011; Todd et al., in press). Second, we present specific examples of how the fit between simple decision strategies and ecologies can lead to successful decision making. In particular, we review empirical findings that suggest that while age-related cognitive decline may lead to changes in the selection and execution of decision strategies, the impact of such changes is a function of the structure of the environment. Consequently, we argue that age-related deficits in strategy selection and execution may not necessarily translate into diminished decision quality. We conclude by presenting an outlook for future work on the ecological rationality of aging.

ECOLOGICAL RATIONALITY: THE FIT BETWEEN MIND AND ENVIRONMENT

The concept of ecological rationality suggests three basic tenets regarding decision making. First, the mind's decision strategies are

adapted to particular environments. Therefore, decision strategies are not good or bad *per se* but can only be evaluated relative to the environments in which they are used. Here, we use the term environment to refer to the statistical properties of a set of objects, such as the correlations between attributes of these objects (i.e., cues) and a criterion. For example, it may be useful to describe the environment of health plans statistically as the correlation between the cost of monthly premium and the amount of coverage. Second, in certain environments, simple decision strategies are able to compete with complex strategies – less is (sometimes) more. Third, humans largely respond adaptively to task and environmental characteristics. In what follows, we provide support for these tenets and discuss their boundary conditions.

THE MIND-ENVIRONMENT FIT

According to the notion of ecological rationality, decision strategies are adapted to particular environments. **Table 1** gives an overview of various strategies that differ in complexity (e.g., in terms of the amount of information considered) and the environments under which they work well. Consider the following question: Which Swiss city has more inhabitants: Geneva or Thun? The recognition heuristic (Goldstein and Gigerenzer, 2002) is an inference strategy that predicts that a recognized object, most likely Geneva and not Thun, scores higher on some criterion (population) than an unrecognized one. The recognition heuristic is a prime example of how, by exploiting a match between mind and environment (i.e., all Swiss cities), a simple algorithm can lead to efficient decision making. It uses a single cue (i.e., whether or not the person recognizes the name of two cities) to predict the cities' relative population, the criterion of interest. The heuristic is thus ecologically rational in this environment because the likelihood of recognition is highly correlated with a city's population. In fact, recognition may be a useful cue in many domains; cities with more inhabitants, mountains with higher peaks, and rivers with longer courses tend to be more often recognized than objects with lower values on these dimensions (Goldstein and Gigerenzer, 2002). Recognition is not always a valid cue, however. For example, the population of Swiss cities, but not, say, their distance from the city Interlaken, is correlated with recognition. As a consequence, one is well advised to use recognition when judging which of two Swiss cities is larger, but not when asked to judge which is closer to Interlaken (Pohl, 2006). In sum, the recognition heuristic illustrates the notion of mind–environment fit by showing how a simple mental mechanism can exploit the structure of specific environments.

LESS CAN BE MORE

According to common wisdom, more knowledge, more information, and more computation should lead to better decisions, while cognitive limitations pose a liability (see Hertwig and Todd, 2003). Analyses of simple strategies have shown that this is not necessarily the case. For example, a person recognizing many Swiss cities can, if recognition is a good predictor, be less accurate in judging the sizes of Swiss cities than a person recognizing fewer cities - the less-is-more effect (Goldstein and Gigerenzer, 2002; for a review, see Pachur, 2010). The reason is that if many cities are recognized, the recognition heuristic cannot be applied (because recognition does not discriminate) and other, potentially less valid predictors need to be recruited - leading to lower inferential accuracy. Similarly, simple strategies may sometimes compete with or even outperform more complex strategies. Consider, for instance, the take-the-best (TTB) heuristic, a strategy that can be recruited when recognition does not discriminate to infer which of two objects has the higher criterion value, TTB simply selects the object that is supported by the most valid predictor or "cue" (see Table 1). TTB can be highly competitive in comparison with considerably more complex strategies (e.g., Gigerenzer and Brighton, 2009). How is that possible? First, TTB can do well because in natural environments cues are often highly correlated, and thus searching for more cues does not necessarily yield new information (Dieckmann and Rieskamp, 2007; Hogarth and Karelaia, 2007). Second, TTB is less susceptible to overfitting when making predictions - that is, it does not take into account (much) unsystematic variability in the data (i.e., noise). Therefore, TTB can be a robust strategy that leads to higher generalization performance relative to more complex inference strategies, like multiple regression, neural networks, and exemplar models (see Gigerenzer and Brighton, 2009, for a discussion of how TTB avoids overfitting).

ADAPTIVE DECISION MAKING

The existence of multiple decision environments and strategies poses a fundamental problem to decision makers – that of adaptively selecting a strategy that fits the particular environment. The available evidence suggests people are by and large adaptive decision makers. For example, participants show higher reliance on the recognition heuristic when recognition is a valid cue (Pachur et al., 2011). More generally, decision makers seem to be sensitive to a number of task characteristics and adjust their strategies accordingly, including monetary information costs (Bröder, 2000), time pressure (Rieskamp and Hoffrage, 2008), cue–criterion relations (Rieskamp and Otto, 2006), and memory demands (Bröder and Schiffer, 2003). There are, however, also boundary conditions for adaptive strategy selection. First, there are significant individual differences in adaptivity, that is, not all individuals adapt to task characteristics equally well (Bröder, 2003; Newell, 2005; Rieskamp and Otto, 2006; Rieskamp, 2008). Second, adaptivity in strategy selection is limited in dynamically changing environments (Bröder and Schiffer, 2006; Rieskamp, 2006).

ECOLOGICAL RATIONALITY AND THE AGING DECISION MAKER

How can ecological rationality inform research on the impact of aging on decision making? Research on aging suggests that there are basic structural and neuromodulatory brain changes with increased age that lead to cognitive decline and poor behavioral outcomes in several areas of functioning, such as workingmemory, episodic memory, and executive function (see Nyberg and Bäckman, 2010; Rodrigue and Kennedy, 2010, for reviews). The notion of ecological rationality, however, emphasizes the key role of the fit between (simple) strategies and environments for successful decision making and thus questions the inevitability of poor outcomes in the face of cognitive constraints. Indeed, the idea of ecological rationality suggests that superior cognitive abilities may not always be necessary or desired: Less is (sometimes) more, or at least enough (Hertwig and Todd, 2003). For example, results based on computer simulation suggest that the aging decision maker can afford to neglect information in consumer decisions because this leads to only small losses in decision quality (Mata and Nunes, 2010). Similarly, expertise research has provided demonstrations that experts often rely on less information than novices (Garcia-Retamero and Dhami, 2009), suggesting that expertise may enable superior decision performance through the use of simple strategies (see also Shanteau, 1992). In addition, there is some evidence that older adults relying on simple strategies can outperform younger adults in inference tasks for which these strategies are most appropriate (Merritt et al., 2010; Worthy and Maddox, 2012).

To the extent that people rely on simple and ecologically rational strategies, cognitive decline associated with aging need not always lead to decrements in decision-making quality. If the cognitive decline does not compromise the execution of the simple strategies, a high level of decision-making quality can be retained. Decrements, however, may occur whenever aging leads to a mismatch between the strategies used and the environments encountered. In what follows, we distinguish two ways in which aging may limit the strategy-environment fit and thus limit decision performance. First, aging may impact how well individuals can select the appropriate decision strategy for a particular task environment – the issue of strategy selection. Second, aging may impact how well individuals can execute a particular strategy in a given environment - the issue of strategy execution. Finally, we conclude by suggesting how the concept of ecological rationality can guide interventions to improve decision making in the elderly.

AGE DIFFERENCES IN STRATEGY SELECTION

Overall, research on aging and strategy selection suggests that older adults are adaptive decision makers. For instance, Pachur et al.

Strategy	Description	Appropriate environment	Study investigating neural substrates
Recognition (Goldstein	If one of two alternatives is recognized, infer that it	Recognition validity >0.5 (cf. Goldstein	Volz et al. (2006),
and Gigerenzer, 2002)	has the higher value on the criterion.	and Gigerenzer, 2002)	Rosburg et al. (2011)
Fluency (Schooler and	If both alternatives are recognized but one is	Fluency validity >0.5 (cf. Schooler and	Volz et al. (2010)
Hertwig, 2005)	recognized faster, infer that it has the higher value on the criterion.	Hertwig, 2005)	
Take-the-best	To infer which of two alternatives has the higher	High cue redundancy (cf. Hogarth and	Khader et al. (2011)
(Gigerenzer and	value (a) search through cues in order of validity, (b)	Karelaia, 2007)	
Goldstein, 1996)	stop search as soon as a cue discriminates, and (c)		
	choose the alternative this cue favors.		
Tallying (Dawes, 1979)	To infer which of two alternatives has the higher	Low cue redundancy, uncertainty	-
	value, count the number of positive cues of each	about cue weights (cf. Hogarth and	
	alterative and choose the one with the higher sum.	Karelaia, 2007)	
Weighted additive	To infer which of two alternatives has the higher	Low cue redundancy, good knowledge	-
(Payne et al., 1993)	value, multiply each cue value by the respective	about cue weights	
	cue weight, sum the results for each alternative,		
	and choose the one with the higher sum.		

Table 1 | Decision strategies, respective ecologies, and studies investigating their neural substrates.

(2009) showed that both younger (Mean age = 24, range = 19–33) and older adults (M = 70, range = 65–86) rely more on recognition in an environment in which recognition is highly predictive of the criterion (i.e., cities) than when it is not (i.e., diseases). This environment or task adaptivity has been demonstrated in other studies: Older adults adjust their search and decision strategies according to the amount of information available (Mata and Nunes, 2010), and cue-criterion relations (Mata et al., 2007, 2010). For example, Mata et al. (2007) asked younger (M = 24, age range = 18-37) and older adults (M = 71, 64-90) to make decisions in (a) a compensatory environment, in which all cues were equally predictive of a criterion or in (b) a non-compensatory environment, in which there was a clear ranking of cue importance. In the former, information-intensive strategies are appropriate, whereas the latter favors simple strategies (because some information may be ignored without leading to a performance decrement). Both younger and older adults tended to rely more on simpler strategies, such as TTB, in the appropriate non-compensatory environment, in which information could be ignored without sacrificing inferential accuracy. In sum, consistent with the concept of ecological rationality, most younger and older adults seem to be aware that simpler decision strategies can lead to satisfactory outcomes in some environments and adjust their strategy selection accordingly (Mata et al., 2007, 2010; Pachur et al., 2009).

Nevertheless, there is some indication that older adults have more difficulties in adapting their strategy selection as a function of environment characteristics relative to younger adults. In other words, aging may attenuate but not eliminate the ability to select strategies adaptively. Specifically, older adults in Mata et al. (2007) relied more on simpler strategies regardless of the environment. Importantly, this was related to individual differences in fluid abilities, suggesting that age-related cognitive decline may have limited access to more complex strategies. In addition, adaptive strategy selection in older adults also seems to be constrained by learning deficits. Mata et al. (2010) found that older adults (M = 69, 60-79) had more difficulties with strategy selection learning on the basis of performance feedback relative to younger adults (M = 24, 19-34). A meta-analysis by Mata et al. (2011b) on differences between younger and older adults' decision making under risk supported this finding. Specifically, the analysis revealed systematic age differences in risk taking in tasks where the probabilities of outcomes had to be learned from repeated exposure (decisions from experience). In contrast, although there were some significant differences between age groups, no systematic pattern arose in the tasks where probabilities and outcomes were conveniently summarized to decision makers (decisions from description). These results converge with behavioral, computational, and neuroimaging analyses showing age differences in reward learning, possibly linked to age-related decline in neuromodulatory efficiency such as dopaminergic function (e.g., Mutter et al., 2007; Mell et al., 2009; Samanez-Larkin et al., 2011).

Another aspect of successful strategy selection concerns item or trial-by-trial adaptivity (cf. Pachur, 2011). For example, despite its simplicity, the adaptive use of the recognition heuristic requires several abilities, including the ability to recognize objects but also the ability to assess whether recognition is a useful indicator in a particular environment or for a specific item. An investigation of the neural processes involved in applying the recognition heuristic supports the postulation of such distinct processes. Volz et al. (2006) examined the neurological underpinnings of the recognition heuristic using functional magnetic resonance imaging (fMRI). In this study participants repeatedly had to indicate which of two cities they thought was larger. When a decision could be made based on recognition, there was activation in the medial parietal cortex, which can be attributed to reliance on recognition memory. In addition, there was independent activation in the anterior frontomedial cortex (aFMC), a brain area involved in evaluating internal states, including self-referential processes and

social–cognitive judgments (e.g., relating an aspect of the external world to oneself). The processes underlying this aFMC activation are likely associated with evaluating whether recognition is a useful cue in the current judgment situation. Importantly, behavioral evidence suggests that this evaluation process requires considerable cognitive resources. Pachur and Hertwig (2006) asked participants to judge which of two infectious diseases is more prevalent, a decision environment in which recognition has low validity. It turned out that inferences were more likely to follow recognition under time pressure than without time pressure. This suggests that evaluating whether recognition should be applied on a specific item is an effortful process that requires some time.

Given the cognitive costs necessary to adaptively suspend the recognition heuristic on a trial-by-trial basis, older adults may fare worse than younger adults in doing so. Evidence for such age-related decrements in item adaptivity was found by Pachur et al. (2009). Investigating younger and older German adults' use of recognition in judging the relative frequency of diseases, it was shown that older adults were constrained in their ability to adaptively suspend the recognition heuristic on specific items for which recognition was not a good cue. For example, the disease Leprosy is recognized by most individuals but is also known to be practically extinct in the German population. As a result, one will do well to bet against recognition when faced with a pair involving Leprosy and some other unrecognized disease - but older adults were less able to do so, often picking the recognized disease. Importantly, these age differences were partly mediated by individual differences in fluid cognitive abilities, suggesting that age-related cognitive decline drives the age-related deficit in adaptive strategy selection (suspension) of the recognition heuristic on a trial-by-trial basis. Based on the results by Volz et al. (2006), one may hypothesize that age differences in the suspension of the recognition heuristic are mediated by frontal structures such as the aFMC. Future work in the decision neuroscience of aging could thus inform the debate concerning the impact of aging on adaptive strategy selection.

In sum, both young and older adults seem to adjust their strategy selection as a function of environment structure (*environment* or *task adaptivity*). Nevertheless, age-related decline in fluid abilities including learning deficits may somewhat constrain the strategies available to older participants and the ability to adjust strategy selection on a trial-by-trial basis (*item* or *trial-by-trial adaptivity*).

AGE DIFFERENCES IN STRATEGY EXECUTION

Selecting the right strategy for a given problem is a necessary but not sufficient condition for successful decision making. To make the right choice one must also be able to execute the strategy correctly. Some findings suggest that aging can lead to difficulties in strategy execution. Mata et al. (2010) used a computational model to decompose the strategy selection learning process of younger and older adults, which included a strategy execution component. The results suggest that there are considerable age differences in the execution errors of younger and older adults and that these differ by strategy: Older adults showed increased strategy execution errors relative to younger adults particularly in an environment favoring complex strategies that require extensive integration and weighing of information. Similar age differences in strategy execution have been reported in studies that explicitly instructed younger and older adults to apply decision strategies (e.g., Bruine de Bruin et al., 2007).

An additional factor mediating age differences in strategy execution may be the way in which decision-relevant information is represented - such as whether decisions are made from tabulated information or from memory. Retrieving information from memory can sometimes be an effortful process requiring considerable involvement of control structures. In a neuroimaging study, Khader et al. (2011) monitored the activation of specific representations of attribute knowledge in long-term-memory with fMRI while participants made memory-based decisions using TTB. The amount of information required for a decision was reflected in activation of the dorsolateral prefrontal cortex (dlPFC) and this activation seemed to modulate posterior areas responsible for memory storage. Because aging is associated with deficits in some frontal control structures as well as storage components of memory (Nyberg and Bäckman, 2010; Spreng et al., 2010) it is likely that older adults show difficulties in the selective retrieval of information in decisions from memory. Indeed, older adults seem to avoid strategies that rely heavily on memory retrieval in inference tasks (i.e., exemplar processing; Mata et al., 2011a). Neuroimaging studies focusing on the neural substrates of memory retrieval during decision making could help to better understand the contribution of frontal and posterior areas to age differences in decisions from memory.

Summing up, age-related cognitive decline may lead to deficits in strategy execution but these effects are likely to be moderated by strategy and task complexity, for example, the memory requirements of the task.

AIDING THE AGING DECISION MAKER

There is considerable interest in cognitive enhancement of the elderly (Hertzog et al., 2009), as well as in reducing the learning and memory requirements of decision tasks to reduce age differences in decision performance (Samanez-Larkin et al., 2011). However, as suggested above, the notion of ecological rationality suggests that enhancing cognitive abilities may not always be necessary or desired: Simple strategies can often do as well or even better than more complex ones (Gigerenzer and Brighton, 2009). Accordingly, rather than simply enhancing cognition, we must aim at identifying the specific situations that benefit from such enhancements to ensure successful decision making by the elderly. For example, we predict that enhancing older adults' fluid abilities could lead to improvements in decision quality in environments that require the integration of many pieces of information, and thus favor the use of complex decision strategies. In contrast, cognitive enhancement should not benefit and could even hinder performance in environments in which simple strategies work well, for example, in non-compensatory environments (Mata et al., 2007, 2011b; see also Hills and Hertwig, 2011).

The notion of ecological rationality also implies that enhancing the strategy–environment fit is key to improving decision making. One way to do this is to inform or train participants about the link between particular strategies and environments. Alternatively, one may want to change the task characteristics to fit the decision strategies of the elderly. For example, the provision of clear cue rankings may facilitate the subsequent use of non-compensatory strategies. No doubt more effort needs to be invested in understanding how task and environment characteristics can be used to improve decisions (Hibbard and Peters, 2003; Thaler and Sunstein, 2008).

OUTLOOK

Linking evidence from behavioral, computational, and neural analyses seems crucial to fully understand how aging impacts decision making. Unfortunately, to our knowledge there has been no work examining how aging impacts the neural substrates responsible for the selection or execution of decision strategies, and computational modeling in this domain is in its infancy. There is perhaps something to be gained by informing the study of the ecological rationality of aging through insights from more researched domains, such as arithmetic skill or memory (Lemaire, 2010; Nyberg and Bäckman, 2010).

Second, more work is needed to understand the factors that determine age differences in strategy selection. While most work emphasizes cognitive constraints, others suggest important

REFERENCES

- Baltes, P. B. (1997). On the incomplete architecture of human ontogeny: selection, optimization, and compensation as foundation of developmental theory. *Am. Psychol.* 52, 366–380.
- Bröder, A. (2000). Assessing the empirical validity of the "take-thebest" heuristic as a model of human probabilistic inference. J. Exp. Psychol. Learn. Mem. Cogn. 26, 1332–1346.
- Bröder, A. (2003). Decision making with the "adaptive toolbox": influence of environmental structure, intelligence, and working memory load. J. Exp. Psychol. Learn. Mem. Cogn. 29, 611–625.
- Bröder, A., and Schiffer, S. (2003). "Take the best" versus simultaneous feature matching: probabilistic inferences from memory and effects of representation format. J. Exp. Psychol. Gen. 132, 277–293.
- Bröder, A., and Schiffer, S. (2006). Adaptive flexibility and maladaptive routines in selecting fast and frugal decision strategies. J. Exp. Psychol. Learn. Mem. Cogn. 32, 904–918.
- Bruine de Bruin, W., Parker, A., and Fischhoff, B. (2007). Individual differences in adult decision-making competence (A-DMC). J. Pers. Soc. Psychol. 92, 938–956.
- Cicero. (1909–1914). *On Old Age*, Vol. 9, Part 2, trans. E. S. Shuckburgh. New York: P. F. Collier and Son.
- Dawes, R. M. (1979). The robust beauty of improper linear models in decision making. *Am. Psychol.* 34, 571–582.

- Dieckmann, A., and Rieskamp, J. (2007). The influence of information redundancy on probabilistic inferences. *Mem. Cognit.* 35, 1801–1813.
- Garcia-Retamero, R., and Dhami, M. K. (2009). Take-the-best in expertnovice decision strategies for residential burglary. *Psychon. Bull. Rev.* 16, 163–169.
- Gigerenzer, G., and Brighton, H. (2009). Homo heuristicus: why biased minds make better inferences. *Top. Cogn. Sci.* 1, 107–143.
- Gigerenzer, G., and Gaissmaier, W. (2011). Heuristic decision making. *Annu. Rev. Psychol.* 62, 451–482.
- Gigerenzer, G., and Goldstein, D. G. (1996). Reasoning the fast and frugal way: models of bounded rationality. *Psychol. Rev.* 103, 650–669.
- Gigerenzer, G., Hertwig, H., and Pachur, T. (2011). *Heuristics: The Foundations of Adaptive Behavior*. New York: Oxford University Press.
- Gigerenzer, G., Todd, P. M., and The ABC Research Group. (1999). Simple Heuristics that Make Us Smart. New York: Oxford University Press.
- Goldstein, D. G., and Gigerenzer, G. (2002). Models of ecological rationality: the recognition heuristic. *Psychol. Rev.* 109, 75–90.
- Hanoch, Y., Wood, S., and Rice, T. (2007). Bounded rationality, emotions and older adult decision making: not so fast and yet so frugal. *Hum. Dev.* 50, 333–358.
- Hertwig, R., and Todd, P. M. (2003). "More is not always better: the benefits of cognitive limits," in *Thinking: Psychological Perspectives*

goal-related and motivational aspects. For example, there may be systematic differences in how younger and older adults approach decision problems, with older adults tending to emphasize accuracy over speed (Ratcliff et al., 2007) or the valence of information (Hanoch et al., 2007).

Finally, the work reviewed above mostly concerns age differences observed in laboratory studies and artificial stimuli (see Pachur et al., 2009, for an exception). Consequently, we know relatively little about the natural decision environments of young and older adults, or differences in the representation of environments by different age groups. An ecological analysis of the decision environments that older adults face is necessary to assess the adaptivity of the specific decision strategies used. For example, do older adults or those looking out for them actively select or engineer environments so as to enable the use of simple strategies? Only by gaining a better understanding of both older adults' decision strategies and ecologies will we be able to provide decision aids and redesign environments that support good decisions. We can thus hope to fulfill Cicero's vision of successful aging by matching older adults' resources to the structure of their decision environments.

on Reasoning, Judgment and Decision Making, eds D. Hardman and L. Macchi (Chichester: Wiley), 213–231.

- Hertzog, C., Kramer, A. F., Wilson, R. S., and Lindenberger, U. (2009). Enrichment Effects on Adult Cognitive Development: Can the Functional Capacity of Older Adults be Preserved and Enhanced? Psychological Science in the Public Interest, Vol. 9, Whole No. 1. Washington, DC: Association for Psychological Science.
- Hibbard, J. H., and Peters, E. (2003). Supporting informed consumer health care choices: data presentation approaches that facilitate the use of information in choice. *Annu. Rev. Public Health* 24, 413–433.
- Hills, T., and Hertwig, R. (2011). Why aren't we smarter already? Evolutionary trade-offs and cognitive enhancements. *Curr. Dir. Psychol. Sci.* 20, 373–377.
- Hogarth, R. M., and Karelaia, N. (2007). Heuristic and linear models of judgment: matching rules and environments. *Psychol. Rev.* 114, 733–758.
- Khader, P., Pachur, T., Meier, S., Bien, S., Jost, K., and Rösler, F. (2011). Memory-based decision making with heuristics: evidence for a controlled activation of memory representations. J. Cogn. Neurosci. 23, 3540–3554.
- Lemaire, P. (2010). Cognitive strategy variations during aging. *Curr. Dir. Psychol. Sci.* 19, 363–369.
- Mata, R., Helversen, B., and Rieskamp, J. (2010). Learning to choose: cognitive aging and strategy selection learning in decision making. *Psychol. Aging* 25, 299–309.

- Mata, R., and Nunes, L. (2010). When less is enough: cognitive aging, information search, and decision quality in consumer choice. *Psychol. Aging* 25, 289–298.
- Mata, R., Schooler, L., and Rieskamp, J. (2007). The aging decision maker: cognitive aging and the adaptive selection of decision strategies. *Psychol. Aging* 22, 796–810.
- Mata, R., von Helversen, B., Karlsson, L., and Cüpper, L. (2011a). Adult age differences in categorization and multiple-cue judgment. *Dev. Psychol.* PMID: 22059450. [Epub ahead of print].
- Mata, R., Josef, A., Samanez-Larkin, G. R., and Hertwig, R. (2011b). Age differences in risky choice: a metaanalysis. Ann. N. Y. Acad. Sci. 1235, 18–29.
- Mell, T., Wartenburger, I., Marschner, A., Villringer, A., Reischies, F. M., and Heekeren, H. R. (2009). Altered function of ventral striatum during reward-based decision making in old age. *Front. Hum. Neurosci.* 3:34. doi: 10.3389/neuro.09.034. 2009
- Merritt, A., Karlsson, L., and Cokely, E. T. (2010). "Category learning and adaptive benefits of aging," in Proceedings of the 32nd Annual Conference of the Cognitive Science Society, Portland.
- Mutter, S. A., Strain, L. M., and Plumlee, L. F. (2007). The role of age and prior beliefs in contingency judgment. *Mem. Cognit.* 35, 875–884.
- Newell, B. R. (2005). Re-visions of rationality? *Trends Cogn. Sci. (Regul. Ed.)* 9, 11–15.

- Nyberg, L., and Bäckman, L. (2010). "Memory changes and the aging brain: a multimodal imaging approach," in *Handbook of the Psychology of Aging*, 7th Edn, eds K. W. Schaie and S. L. Willis (San Diego: Elsevier Press), 121–133.
- Pachur, T. (2010). Recognition-based inference: when is less more in the real world? *Psychon. Bull. Rev.* 17, 589–598.
- Pachur, T. (2011). The limited value of precise tests of the recognition heuristic. *Judgm. Decis. Mak.* 6, 413–422.
- Pachur, T., and Hertwig, R. (2006). On the psychology of the recognition heuristic: retrieval primacy as a key determinant of its use. J. Exp. Psychol. Learn. Mem. Cogn. 32, 983–1002.
- Pachur, T., Mata, R., and Schooler, L. (2009). Cognitive aging and the adaptive use of recognition in decision making. *Psychol. Aging* 24, 901–915.
- Pachur, T., Todd, P. M., Gigerenzer, G., Schooler, L. J., and Goldstein, D. G. (2011). The recognition heuristic: a review of theory and tests. *Front. Cogn. Sci.* 2:147. doi: 10.3389/fpsyg.2011. 00147
- Payne, J. W., Bettman, J. R., and Johnson, E. J. (1993). *The Adaptive Decision Maker*. Cambridge: Cambridge University Press.

- Pohl, R. (2006). Empirical tests or the recognition heuristic. J. Behav. Decis. Mak. 19, 251–271.
- Ratcliff, R., Thapar, A., and McKoon, G. (2007). Application of the diffusion model to two-choice tasks for adults 75-90 years old. *Psychol. Aging* 22, 56–66.
- Rieskamp, J. (2006). Perspectives of probabilistic inferences: reinforcement learning and an adaptive network compared. J. Exp. Psychol. Learn. Mem. Cogn. 32, 1355–1370.
- Rieskamp, J. (2008). The importance of learning when making inferences. *Judgm. Decis. Mak.* 3, 261–277.
- Rieskamp, J., and Hoffrage, U. (2008). Inferences under time pressure: how opportunity costs affect strategy selection. *Acta Psychol. (Amst.)* 127, 258–276.
- Rieskamp, J., and Otto, P. E. (2006). SSL: a theory of how people learn to select strategies. J. Exp. Psychol. Gen. 135, 207–236.
- Rodrigue, K. M., and Kennedy, K. M. (2010). "The cognitive consequences of structural changes to the aging Brain," in *Handbook of the Psychology* of Aging, 7th Edn, eds K. W. Schaie and S. L. Willis (San Diego: Elsevier Press), 121–133.
- Rosburg, T., Mecklinger, A., and Frings, C. (2011). When the brain decides: a familiarity-based approach to the recognition heuristic as evidenced by event-related brain potentials. *Psychol. Sci.* 22, 1527–1534.

- Samanez-Larkin, G. R., Wagner, A. D., and Knutson, B. (2011). Expected value information improves financial risk taking across the adult life span. Soc. Cogn. Affect. Neurosci. 6, 207–217.
- Schooler, L. J., and Hertwig, R. (2005). How forgetting aids heuristic inference. *Psychol. Rev.* 112, 610–628.
- Shanteau, J. (1992). How much information does an expert use? Is it relevant? Acta Psychol. (Amst.) 81, 75–86.
- Spreng, R. N., Wojtowicz, M., and Grady, C. (2010). Reliable differences in brain activity between young and old adults: a quantitative meta-analysis across multiple cognitive domains. *Neurosci. Biobehav. Rev.* 34, 1178–1194.
- Thaler, R. H., and Sunstein, C. R. (2008). Nugde: Improving Decisions about Health, Wealth, and Happiness. New Haven: Yale University Press.
- Todd, P., Gigerenzer, G., and the ABC Research Group (in press). *Ecological Rationality: Intelligence in the World*. New York: Oxford University Press.
- Volz, K. G., Schooler, L. J., Schubotz, R. I., Raab, M., Gigerenzer, G., and von Cramon, D. Y. (2006). Why you think Milan is larger than Modena: neural correlates of the recognition heuristic. *J. Cogn. Neurosci.* 18, 1924–1936.
- Volz, K. G., Schooler, L. J., and von Cramon, D. Y. (2010). It just felt

right: the neural correlates of the fluency heuristic. *Conscious. Cogn.* 19, 829–837.

Worthy, D. A., and Maddox, W. T. (2012). Age-based differences in strategy use in choice tasks. *Front. Neurosci.* 5:145. doi: 10.3389/fnins.2011.00145

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