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Age-related differences in striatal, medial temporal, and frontal involvement during value-based decision processing

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Appropriate neural representation of value and application of decision strategies are necessary to make optimal investment choices in real life. Normative human aging alters neural selectivity and control processing in brain regions implicated in value-based decision processing including striatal, medial temporal, and frontal areas. However, the specific neural mechanisms of how these age-related functional brain changes modulate value processing in older adults remain unclear. Here, young and older adults performed a lottery-choice functional magnetic resonance imaging experiment in which probabilities of winning different magnitudes of points constituted expected values of stakes. Increasing probability of winning modulated striatal responses in young adults, but modulated medial temporal and ventromedial prefrontal areas instead in older adults. Older adults additionally engaged higher responses in dorso-medio-lateral prefrontal cortices to more unfavorable stakes. Such extrastriatal involvement mediated age-related increase in risk-taking decisions. Furthermore, lower resting-state functional connectivity between lateral prefrontal and striatal areas also predicted lottery-choice task risk-taking that was mediated by higher functional connectivity between prefrontal and medial temporal areas during the task, with this mediation relationship being stronger in older than younger adults. Overall, we report evidence of a systemic neural mechanistic change in processing of probability in mixed-lottery values with age that increases risk-taking of unfavorable stakes in older adults. Moreover, individual differences in age-related effects on baseline frontostriatal communication may be a central determinant of such subsequent age differences in value-based decision neural processing and resulting behaviors.

1. Introduction

Real life investments typically entail an expected gain proportional to the invested resource but also a possible loss, depending on outcomes. For instance, one spends money to buy an apple expecting to eat a juicy fruit but there is always a probability that there is a worm in the apple and the money spent is wasted. To maximize investments and minimize losses during such mixed lottery situations, neural networks in the human brain must be able to represent information about stimuli value, such as the expected value (EV) of investments, as accurately as possible with respect to physical outcomes. Neural processing of mixed lotteries might also engage relevant strategies or beliefs where necessary or effective (Kahneman and Tversky, 1979), such as noting past negative experiences at a particular grocery store, or prioritizing physical or mental health over money, or using only partial information to simplify decisions. Aging changes human brain functions such that neural representations of different stimuli are less distinctive (Goh et al., 2010; Park et al., 2004; Yassa et al., 2011) and the flexible engagement of goal-directed control and strategic processing is diminished (Ardiale and Lemaire, 2012; Hakun et al., 2015; Harris and Wolbers, 2014; Konishi et al., 2013). Older adults also display distinct decision behaviors compared with young adults that, across different experimental contexts, reflect more variable decision

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criteria, such as not always choosing options with higher EVs, and more reactive decision strategies, such as being more sensitive to recent outcomes (Pachur et al., 2017; Rutledge et al., 2016; Tymula et al., 2013; Worthy et al., 2016). These brain and behavioral differences between young and older adults motivate the need to determine the mechanistic links between changes in human neural processing of value and decision-making behavior as a person ages, particularly in light of the aging world demographic (Vaupel, 2010). Here, we reconcile how age effects on neural operations that selectively process information and apply goal-directed strategies impact assessment of EV in a risky lottery choice task (LCT).

In the LCT (Goh et al., 2016), which tests mixed lottery decisions, different probabilities (P) of winning (and simultaneously, losing; 1−P) are combined with different magnitudes (M) of points such that EV = P×M + (1−P)×(−M) for any given trial (Fig. 1A). Stakes and outcomes are independent across trials so that the optimal approach is to decide to accept or reject the given stakes based solely on the objective information about EV provided in each trial. Moreover, because for any given magnitude of points, the probability of winning also determines the probability of losing the points, risk-neutral agents should have an acceptance decision threshold (DT) or certainty equivalence set at EV = 0 (or $p = 50\%$) (Dohmen et al., 2011). DTs greater or less than EV = 0 indicate risk-averse or risk-taking preferences, respectively.

Performance in this task might, in principle, rely on neural representations of EV (or even more simply, P) in ventral striatum (VS) that shows sensitivity to different levels of expected rewards or losses (Berns et al., 2001; Knutson et al., 2001; Preuschoff et al., 2006; Schultz, 2000; Tom et al., 2007). Differential sensitivity to value underlies the role of VS in gating and selecting adaptive motor responses to obtain rewards or avoid losses (Nicola, 2007). However, the main neurotransmitter that operates in this region, dopamine, has reduced efficacy with age (Dreher et al., 2008; Erixon-Lindroth et al., 2005; Kaasinen et al., 2000; Wong et al., 1997). Neurocomputational theory projects that reduced dopaminergic efficacy results in lower signal-to-noise ratio during information processing that underlies less distinctive neuronal responses (or lower neural sensitivity) to different stimuli in target brain areas (Bäckman et al., 2010; Li and Sikström, 2002). In older adults then, we expect less neural sensitivity to valuative information in VS. This increases the likelihood that decisions will be less influenced by objective EV information and more influenced by more subjective processes in other brain regions that bias decision criteria.

Experiments have shown dissociable age-related biases in loss processing compared with gains (Mather et al., 2012; Pachur et al., 2017; Samanez-Larkin et al., 2007, 2010). This is consistent with socioemotional selectivity theory (Carstensen, 2006; Carstensen et al., 1999; Mather and Carstensen, 2005) that posits a shift in life goals toward senescence such that maintenance of well-being or positive affect has greater influence on older than younger adult decision-making. Two extensions are made in relation to EV processing. First, there should be enhanced affective reactions to prospects in general in older compared with younger adults, who should be more apathetic. Specifically, neural responses that track the desirability of EVs should be more evident in older than young adults in brain areas involved in affective processing. In our whole-brain

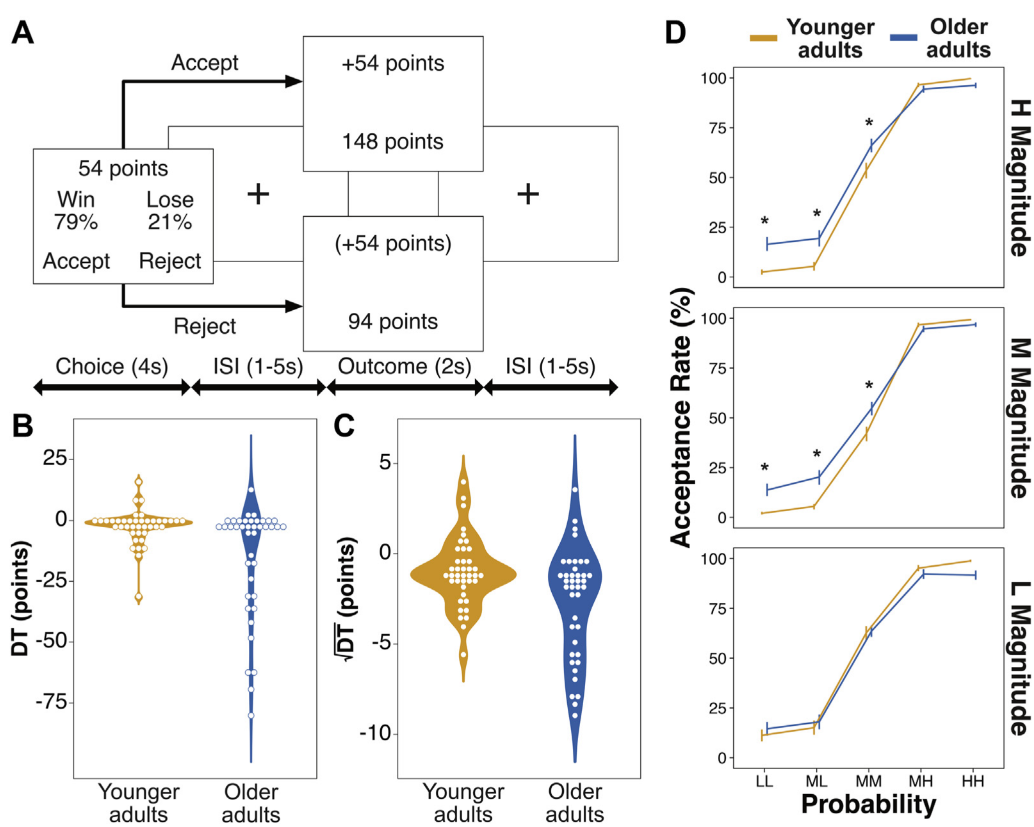

Fig. 1. (A) Sample trial from the LCT showing the percentage probability of winning (or losing) a given magnitude of points during the choice phase. If participants decide to accept the given stake, the outcome points are given (outcome top number; example depicts a winning trial outcome) with the accumulated points (outcome bottom number) updated accordingly. If the participants decide to reject the stake, the missed outcome is given in parentheses with no change in accumulated points. (B, C) Violin plots depicting probability density distributions of young and older adult DT EVs and adjusted DTs ($\sqrt{DT}$). White circles are individual data points. (D) Acceptance rates across the different levels of probability to win (or lose) and points magnitudes (see Supplementary Table S2) for young and older adults. * denote $p < 0.05$ with Bonferroni correction for multiple comparisons. Error bar indicates SEM. Abbreviations: DT, decision threshold; EV, expected value; ISI, interstimulus interval; LCT, lottery choice task.